On the importance and use of multiple social information sources for movement determinism

Mathieu Brevet

To cite this version:

Mathieu Brevet. On the importance and use of multiple social information sources for movement determinism. Animal biology. Université Paul Sabatier - Toulouse III, 2022. English. NNT : 2022TOU30150 . tel-03865164

HAL Id: tel-03865164
https://theses.hal.science/tel-03865164

Submitted on 22 Nov 2022

THÈSE

En vue de l'obtention du

DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par : *l'Université Toulouse 3 Paul Sabatier (UT3 Paul Sabatier)*

Présentée et soutenue le *23/06/2022* **par :**

Mathieu BREVET

Sur l'importance et l'utilisation de multiples sources d'informations sociales pour le déterminisme du mouvement.

JURY

Jean CLOBERT	Directeur de Recherche	Directeur
Staffan JACOB	Chargé de Recherche	Co-Directeur
Aurélie COULON	Maîtresse de Conférences	Rapporteure
Frédérique DUBOIS	Professeure d'université	Rapporteure
Jean-Michel GAILLARD	Directeur de Recherche	Rapporteur
Jennifer MORINAY	Post-doctorante	Examinatrice
Maud FERRARI	Professeure d'université	Examinatrice
Martin GIURFA	Professeur d'université	Examinateur

École doctorale et spécialité :

SEVAB : Écologie, biodiversité et évolution

Unité de Recherche :

Station d'Écologie Théorique et Expérimentale (UAR 2029)

Directeur(s) de Thèse :

Jean CLOBERT et *Staffan JACOB*

Rapporteurs :

Aurélie COULON, *Frédérique DUBOIS* et *Jean-Michel GAILLARD*

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Préambule

Cette thèse a été effectuée grâce à un financement par bourse ministérielle après obtention du concours de l'école doctorale SEVAB (Sciences Écologiques, Vétérinaires, Agronomiques et Bioingéniéries). Elle a été réalisée sous la tutelle de l'université Toulouse – Paul Sabatier, qui a également financé les charges d'enseignements doctorales que j'ai réalisé en 2019/2020 et 2020/2021 (de 68h chacune). La thèse s'est déroulée dans les locaux de la Station d'Écologie Théorique et Expérimentale (SETE, UAR 2029), qui m'a fourni les conditions matérielles au bon déroulement de ma thèse. J'ai travaillé au sein de l'équipe CHANGE (Réponses éco-évolutives aux environnements CHANGEants), dans laquelle je me suis plus particulièrement intégré aux projets CHOOSE (Choix d'habitat : évolution et conséquences écologiques) et AQUATHERM (Rôles de la régulation hydrique et thermique dans les réponses écologiques au changement climatique).
Un support financier et matériel à la réalisation de ma thèse ont été apporté par les organismes et projets suivants :

- Projet ANR AQUATHERM
- Projet ANR CHOOSE
- Laboratoire d'Excellence TULIP (LabEx "Vers une théorie unifiée des interactions biotiques : rôle des perturbations environnementales")
- Station d'Écologie Théorique et Expérimentale (SETE, UAR 2029)
- Université Toulouse III – Paul Sabatier
- École doctorale SEVAB

Productions scientifiques et enseignement

Articles

Brevet M, Jacob S, Rutschmann A, Richard M, Cote J, Clobert J. 2022. Social information use for spatial decisions in *Zootoca vivipara*. En cours de correction dans *Behavioral Ecology and Sociobiology*. **(Chapitre 2)**

Brevet M, Jacob S, Massot M, Richard M, Rutschmann A, Renoirt M, Rozen-Rechels D, Le Galliard JF, Clobert J. 2022. Multi-determinism and phenotype-dependence of dispersal in nature: insights from a 30-year long-term study. En préparation pour une soumission dans *Ecology*. **(Chapitre 1)**

Brevet M, Jacob S, Massot M, Richard M, Rutschmann A, Rozen-Rechels D, Le Galliard JF, Clobert J. 2022. The use of immigrant-based information for dispersal in natural conditions: importance, nature and interactions with the phenotype and local context. En préparation pour une soumission dans *Ecology Letters*. **(Chapitre 3)**

Brevet M, Lartillot N. 2021. Reconstructing the History of Variation in Effective Population Size along Phylogenies. *Genome Biology and Evolution*. 13(8):evab150. doi:10.1093/gbe/evab150. **(Extérieur aux travaux de thèse)**

Rutschmann A, Dupoué A, Miles DB, Megía-Palma R, Lauden C, Richard M, Badiane A, Rozen-Rechels D, Brevet M, Blaimont P, Meylan S, Clobert J, Le Galliard JF. 2021. Intense nocturnal warming alters growth strategies, colouration and parasite load in a diurnal lizard. *Journal of Animal Ecology*. 90(8):1864–1877. doi:10.1111/1365-2656.13502. **(Extérieur aux travaux de thèse)**

Conférences & Posters

Brevet M. 2019. Social information transfer during dispersal in *Zootoca vivipara*: mechanisms and implications for population dynamics. *European Society for Evolutionary Biology (ESEB) Congress*, Turku (Finland). Poster.

Brevet M. 2019. Transfert d'informations sociales pendant la dispersion chez *Zootoca vivipara*. *47ème congrès de la Société Herpétologique de France (SHF)*, Moulis (France). Poster.

Brevet M. 2021. Local and distant social information use for dispersal decisions in *Zootoca vivipara*. *Ecology across border, joint meeting of the British ecological society (BES) and the French society for ecology and evolution (SFE)*, Liverpool (United-Kingdom). Oral presentation.

Charges d’enseignement

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Année universitaire 2020/2021: Chargé de TD (travaux dirigés) en SIG (Système d’information géographique) appliqué à l’écologie – Niveau Licence 3 - Université Toulouse III Paul Sabatier, Département Biologie & Géosciences - 64h

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Droit d’auteur : Enseignement, Recherche - Université Fédérale de Toulouse Midi Pyrénées - Maison de la Recherche et de la Valorisation (MRV) – 6h

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Travaux de review pour la revue ’Movement ecology’ - Movement ecology editorial office – Online – 14h

Total participation : 106 heures / 7 modules

Remerciements

Je tiens tout d'abord à remercier mes encadrants de thèse, Jean Clobert et Staffan Jacob, pour leurs conseils tout au long de ma thèse, pour l'aide qu'ils m'ont apportés dans l'écriture de mes productions scientifiques, et pour avoir soutenu et amélioré mon projet de thèse.

Je salue également l'aide que m'ont apportée les différents membres de mon comité de thèse (Blandine Doligez, Julien Cote, Emmanuel Fronhofer, Nicolas Schtickzelle), au cours de discussions toujours intéressantes et pertinentes. Un remerciement particulier à Julien Cote qui m'a beaucoup aidé à monter mes designs expérimentaux sur le lézards vivipare au début de ma thèse.

Je remercie l'ensemble de mon jury de thèse (Aurélie Coulon, Fédérique Dubois, Jean-Michel Gaillard, Jennifer Morinay), d'avoir bien voulu accepter de lire et examiner mes travaux.

Un grand merci également à toutes les personnes m'ayant épaulé au cours de mon terrain, de mes analyses ou de l'écriture de mes papiers.
Un remerciement tout particulier à Alexis Rutschmann pour sa précieuse aide à la préparation et à la gestion du terrain et les expérimentations faites en parallèle, à ces commentaires sur mes différents manuscrits (et merci aussi pour le magnifique dessin qui m'a permis d'illustrer ce manuscrit de thèse !).
Un immense merci également à Murielle Robin pour son aide plus qu'indispensable dans la préparation et la gestion du terrain, ainsi que pour les nombreuses heures qu'elle a consacré à nettoyer et harmoniser le jeu de données du suivi naturel dans les Cévennes !
Je remercie aussi chaleureusement Michèle Huet pour sa gestion du laboratoire L2 et la formation qu'elle m'a apporté pour que je puisse mener à bien mes expériences.
Je n'oublie pas non plus tous les stagiaires ayant participé au terrain ou à l'exploitation des données qui en sont issue (en particulier ceux que j'ai pu croisé pendant ma thèse : Matthias Renoirt, Antoine Le Pajolec, Chloé Fosse, Solène Liégeois, Clémence Lauden, Samuel Delhaye) sans qui je n'aurais tout simplement pas de données exploitable, et un merci plus globalement à tous les participants de ce suivi à long terme dans les Cévennes (que je n'ai pas eu la chance de tous rencontrer, ni connaître) qui ont trimé dur chaque été et sans qui cette thèse n'aurait pas eu lieu !
Merci aussi à toutes les personnes de la SETE avec qui j'ai pu avoir des discussions scientifiques constructive (les membres de l'équipe Tetra, les nombreuses personnes travaillant sur le lézard vivipare que j'ai pu croiser, Jérôme Prunier pour des discussions statistiques qui m'ont souvent bien aidé, et bien évidemment toutes les personnes qui sont passé en salle thésard discuter au détour d'une pause !) et qui ont participé, chacun à leur manière, à la construction de cette thèse.

Un merci également aux personnes qui chaque jour facilitent le travail de milliers de scientifiques (Sci bub, libgen) et qui essayent de rendre la science plus accessible à tous et à toutes.

Un merci sans limite à Léa Lejeune, qui m'a épaulé tout au long de cette thèse, m'aura donné de précieux conseils qui m'ont évité de finir noyé sous mes pérégrinations, d'avoir relu mon manuscrit, et surtout pour m'avoir supporté dans mes longues discussions et errements scientifiques (the best rubber duck ever!). Merci d'être là, tout simplement.

Un clin d'œil aux meilleurs, le Comité à roulette (Coco, Franck, Max, Yo, Baba, Flo) ! Toujours chouette de boire un coup avec vous, de décompresser au crêt d'arjoux et un peu partout, bref toujours là pour l'apéro et ça, ça ne s'oublie pas ! Merci aussi aux autres lyonnais que j'ai pu recroiser au cours de ma thèse et avec qui j'ai pu passer des moments bien sympa, ça fait toujours plaisir ! Et merci au crew de toulousain avec qui j'ai partagé des soirées inoubliables (coucou Mathilde, Théo, Léo et Quentin !).

Merci à toute la team d'Ariègeois qui m'a accompagné tout au long de ma thèse, et dont les apéros, les soirées et les randos vont bien me manquer (avec une liste de zigotos bien fournie et non-exhaustive : Hugo, Jeremie, Léa, Laura, Pierre, Orlane, Laurane, Vinicius, Elodie, Nicolas, Diego, Malo, Marine, Vincent, Eloïse, Maya, Maxime, Léa, Léo, Kévin, Jérôme, Claire-Lise, Léo, Morgane...).
Un gros gros coucou à tous les résidents de la (regrettée) salle thésard (Jeremie, Léa, Marine, Maya), et à la génération de doctorants avec qui j'ai pu partager de belles galères et de beaux moments (Marine, Éloïse et Diego). Merci à Marine, Laura, Elodie et Jeremie pour leur lecture de dernière minute sur ma thèse !

Enfin, je remercie mes parents et mes frères (Guigui, Nathan et Nico), pour leur soutien, m'accueillant toujours avec plaisir les rares fois où j'ai pu remonter au bercail.

Abstract

In the literature, there are a lack of knowledge on how the movements of motile individuals are influenced by socially acquired information from multiple conspecifics. This thesis aims to better understand the relative importance of such information on the determinism of these movements, and its use, depending on the context, individual condition, or its nature.

I began by investigating how social information provided locally by many conspecifics influences dispersal, its relative importance, and its dependence on individual phenotype. Using a 30-year mark-recapture monitoring of the viviparous lizard (*Zootoca vivipara*), I was able to explore how natal dispersal depends on multiple components of the social context in the natal area, as well as other factors internal to the individual or abiotic. Results highlighted that dispersal is multi-determined, with several components of social context (sex ratio, age structure, body condition of conspecifics) having a concurrent impact. This study has highlighted, for this species, the particular relative importance of traits related to the sex of the individuals and the substrate's characteristics. Finally, the results obtained appear to reveal a match between the competitiveness of the individual and the use of social information related to intra-specific competition.

I also conducted experiments on the same species to test the ability to orientate when confronted with multiple sources of social information. For this, I considered the concurrent arrival of two conspecifics, from contrasting rearing conditions, in the habitat of a focal individual. Although no effect on orientation was observed, this experiment provided a better understanding of how information from competing sources was used on movement decisions, with the use of the mean information (resource accessibility and maternal phenotype), but not its contrast.

Then, by using the same tracking as in the first part, I explored how immigrants-based information influences natal dispersal. I investigated whether its use depended on the local context and/or phenotype of the individual, as well as distance, variability, and the number of information sources. I observed that this information was used depending on the needs of the individuals (defined by their phenotype and context), and that information was preferentially used when it was not too uncertain (too variable or transmitted by too few immigrants) or in a way that minimized costs (preference for habitats similar to the one of birth when the information is distant or uncertain). Interestingly, individuals seem to prefer the same habitats locally and at a distance.

Finally, experimental work was performed in microcosms to understand how conflicting social informa-

tion influences dispersal in a ciliate (*Tetrahymena thermophila*). Although the initial treatment resulted in minimal effects on dispersal rates or dispersal syndromes, significant variance and mean effects of informant cell traits were identified. This suggests the existence of important physiological signals provided by informants, of which determinism remains to be explored.
All these results underline the joint use of multiple social information, both local and distant, in individual movements such as dispersal. They highlight the importance of considering such information with the context in which it is studied, the individual who uses it, and its nature (What does it inform about? Is it reliable? Is it costly to exploit?).

Peu de choses sont connues sur la manière dont les mouvements d'individus motiles sont influencés par l'information socialement acquise auprès de multiples congénères. Cette thèse vise à mieux comprendre l'importance relative de telles informations sur le déterminisme de ces mouvements, et leur utilisation, en fonction du contexte, de la condition individuelle, ou de leur nature.
J'ai tout d'abord commencé par étudier comment l'information sociale apportée localement par de nombreux congénères influence la dispersion: quelle est son importance relative et comment dépend-elle du phénotype individuel ? En utilisant un suivi par maquage-capture-recapture de 30 ans sur le lézard vivipare (*Zootoca vivipara*), j'ai pu explorer comment la dispersion natale dépend de multiples composants du contexte social dans l'aire natale, ainsi que d'autres facteurs internes à l'individu ou abiotiques. Les résultats ont mis en valeur le fait que la dispersion soit multi-déterminée, avec en particulier plusieurs éléments du contexte social (sex-ratio, structure d'âge, condition corporelle des congénères) ayant un impact simultané. Cette étude a permis de souligner, chez cette espèce, l'importance relative toute particulière des traits en relation avec le sexe des individus et des caractéristiques du substrat. Enfin, les résultats obtenus semblent mettre à jour une correspondance entre la compétitivité de l'individu et son utilisation d'informations sociales liés à la compétition intra-spécifique J'ai ensuite réalisé des expérimentations sur la même espèce visant à tester la capacité à s'orienter lorsqu'on est confronté à de multiples sources d'informations sociales. Pour cela, j'ai considéré l'arrivée simultanée de deux congénères, provenant de conditions d'élevages contrastées, dans l'habitat d'un individu focal. Bien qu'aucun effet sur l'orientation n'ait été observé, cette expérience a permis de mieux comprendre comment étaient utilisées des informations provenant de sources concurrentes sur les décisions de déplacements, avec une utilisation de l'information moyenne (accessibilité en ressources et phénotypes maternels), mais non de son contraste.
Puis, en utilisant le même suivi que dans le premier volet, j'ai exploré comment des informations apportées par des immigrants influencent la dispersion natale. J'ai étudié si leur utilisation dépendait du contexte local et/ou du phénotype de l'individu, ainsi que de la distance, de la variabilité et du nombre de sources d'informations. J'ai observé que ces informations étaient utilisées en fonction des

besoins des individus (définis par leur phénotype et le contexte), et que les informations étaient préférentiellement utilisées lorsqu'elles n'étaient pas trop incertaines (trop variables ou transmises par trop peu d'immigrants) ou de manière à minimiser les coûts (préférence pour des habitats similaires à celui de naissance lorsque l'information est distante ou incertaine). De manière intéressante, les individus semblent préférer les mêmes habitats localement et à distance.

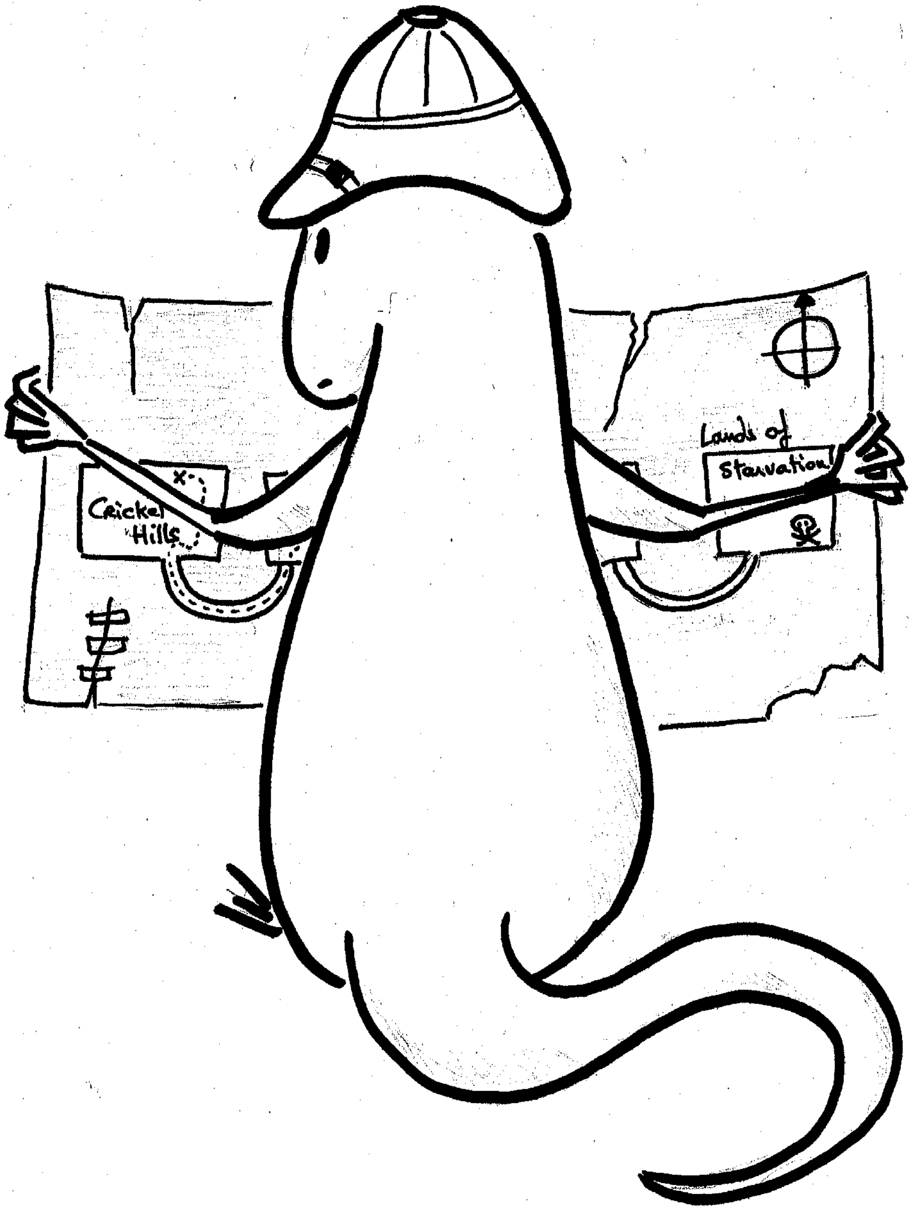
Enfin, des travaux expérimentaux ont été réalisés sur des microcosmes, afin de comprendre comment des informations sociales contradictoires influencent la dispersion chez un cilié (*Tetrahymena thermophila*). Bien que le traitement initial ne résulte qu'en des effets minimes sur les taux ou syndromes de dispersion, d'importants effets de la variance et de la moyenne des traits des cellules informantes ont été identifiés. Cela suggère l'existence de signaux physiologiques importants apportés par les informants, dont le déterminisme reste encore à explorer.

L'ensemble de ces résultats soulignent l'utilisation conjointe d'informations sociales multiples, aussi bien locales que distantes, dans les mouvements individuels telle que la dispersion. Ils mettent en exergue l'importance de les considérer vis-à-vis du contexte dans lequel on les étudie, de l'individu qui les utilise, et de leur nature (Sur quoi informent-elles ? Sont-elles fiables ? Coûteuses à exploiter ?).

Lay summary

This thesis aims to better understand the importance of socially acquired information from multiple conspecifics (through the perception of traits of other individuals) in determining individual movements, and especially dispersal movements (defining a long-term habitat change). To address this, I used a field monitoring on the viviparous lizard (*Zootoca vivipara*) and experiments on this species and a unicellular ciliate (*Tetrahymena thermophila*). These studies highlighted the multi-determinism of dispersal, with dispersal depending on many aspects of the local social context, but also distant social contexts informed by the arrival of immigrants from these habitats. Furthermore, my results emphasize that the use of this social information depends on the needs of the individual receiving the information, but also on the information itself, whose reliability or associated costs may vary.

Cette thèse a pour objectif de mieux comprendre l'importance des informations socialement acquises auprès de multiples congénères (par la perception des traits d'individus tiers) dans le déterminisme des mouvements individuels, et tout particulièrement des mouvements de dispersion (définissant un changement d'habitat pérenne). Pour répondre à cela j'ai utilisé un suivi naturel sur le lézard vivipare (*Zootoca vivipara*) et des expériences sur cette espèce et un cilié unicellulaire (*Tetrahymena thermophila*). Ces études ont mis en évidence le multi-déterminisme de la dispersion, cette dernière dépendant de nombreux aspects du contexte social local, mais aussi des contextes sociaux distants, informés par l'arrivée d'immigrants provenant de ces habitats. De plus, mes résultats soulignent que l'utilisation de ces informations sociales dépend des besoins de l'individu recevant l'information, mais aussi de l'information elle-même dont la fiabilité ou les coûts associés peuvent varier.



To go, or not to go...

On the importance and use of multiple social information sources for movement determinism

General introduction

Spatial decision-making

On the space use of motile individuals

Movement is central to the biology of many species. These motile organisms, being able to move actively by their own means, use this ability to respond to various environmental stimuli (Nathan et al. 2008; Figure 3). By moving, these individuals can position themselves in environments that are advantageous to them, allowing them to access vital resources (food, thermoregulation for ectotherms, reproduction, etc.). Moving in space is therefore a way to increase fitness by being located in an environment that is advantageous to the individual (Edelaar and Bolnick 2019). This is also of major importance for the distribution of individuals of a species as a whole, thus defining the spatial and temporal dynamics of the species' populations (Johst and Brandl 1997), but also at larger scales of metapopulations (Wang et al. 2015), communities (Ron et al. 2018) and ecosystems (Holland and Hastings 2008, Massol et al. 2017).

Motile organisms present a wide range of movement (Nathan et al. 2008), with high variability in distances, direction, or duration. These movements could have diverse ultimate causes (Rasmussen 2009, Teitelbaum and Muller 2019, Shaw et al. 2020, Abrahms et al. 2021, Doherty et al. 2021), as the research of food resources, suitable habitats mating, avoiding predators, parasites, or competitors, socializing, etc. Many motile organisms live in a delimited space, called their home range, and move inside their living area, mostly for the previously described reasons (*e.g.* Perry and Garland 2002, Börger et al. 2006). Yet, individuals could leave their initial living area to settle in a novel one, such dispersal movements are often associated with genes flow (Ronce et al. 2007). Dispersal is usually described in three phases: the departure, the transience, and the settlement. Again, dispersal could have different ultimate causes (Dobson and Jones 1985, Lidicker and Stenseth 1992, Clobert et al. 2004, Bowler and Benton 2005, Matthysen 2012) that could intervene during all three phases. External determinants could be further categorized (Bowler and Benton 2005, Clobert et al. 2009, 2012; Figure 1): between abiotic and biotic characteristics of the habitat, the latter being decomposed into inter- or intra-specific contexts, in which we can distinguish the interactions with kin and non-kin.

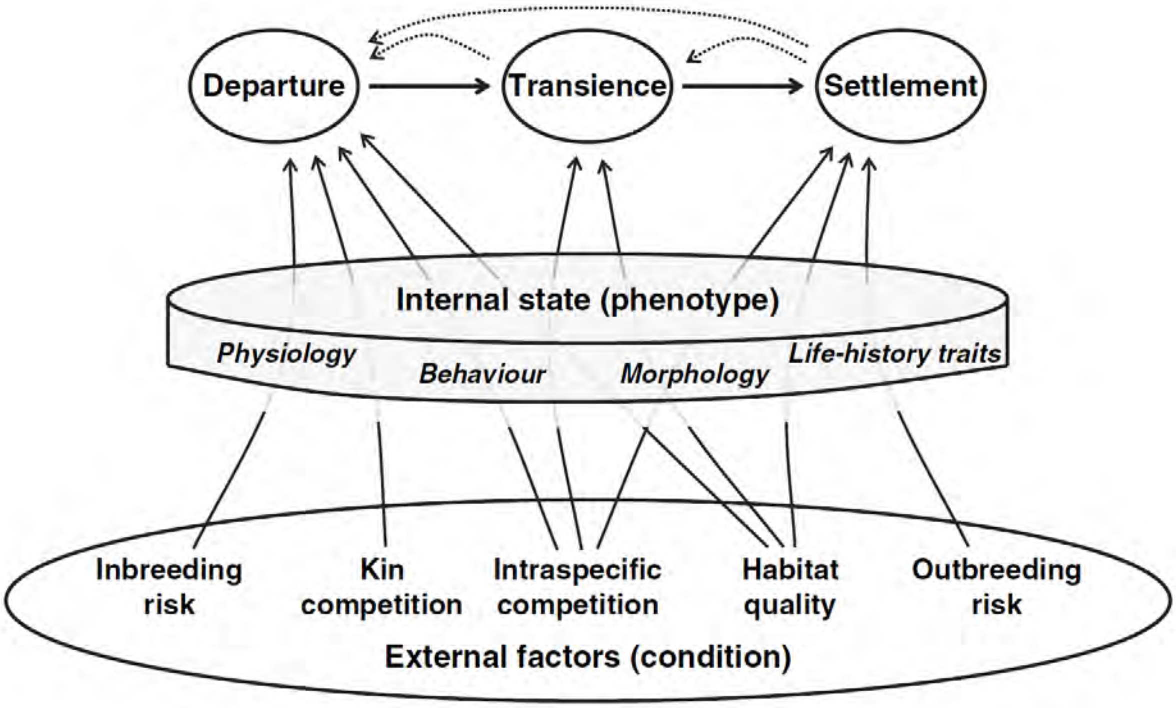


Figure 1: Main determinants of dispersal.
This figure is extracted from the article of Clobert et al. (2009) in *Ecology Letters*. All external drivers (*i.e.* the habitat context), representing the ultimate causes of dispersal, are displayed in the lowest circle. Here, habitat quality refers to habitat abiotic conditions and inter-specific drivers (predation, competition, prey availability, etc.). The influence of the internal state on the propensity to disperse and use information about the experienced context appears in the upper circle. The dotted arrows, at the top of the diagram, represent the potential feedback between dispersal phases (transient or settled individuals influencing conspecifics' departure, transience, or settlement).

Such context-dependence of dispersal movement has particularly well-described in the literature (Bowler and Benton 2005). First, kin competition and inbreeding avoidance were identified as important drivers of dispersal (Matthysen 2012, Lambin et al. 2001, theoretically predicted by Gandon 1999, *e.g.* Bollinger et al. 1993, Moore et al. 2005, Szulkin and Sheldon 2008), with multiple possible proximate factors as kin presence (*e.g.* Wolf 1994, Kasuya 2000), local relatedness (*e.g.* Bitume et al. 2013), interaction with kins (*e.g.* Aguillon and Duckworth 2015), the litter sex ratio (*e.g.* Le Galliard et al. 2012), or the maternal senescence (Ronce et al. 1998, 2000, Zedrosser et al. 2007). Dispersal could also be particularly impacted by cooperation among kin (Lambin et al. 2001, as theorized in Perrin and Lehmann 2001, Lehmann and Perrin 2002) with a decrease in dispersal when kin cooperation is observed (*e.g.* Schtickzelle et al. 2009, Armitage et al. 2011, Davis 2011), and with potential sibling coalitions or kin-oriented dispersal (Sharp et al. 2008, Chaine et al. 2010, Dawson Pell et al. 2021).

The intra-specific interactions more broadly shape the dispersal response, in particular with the avoidance of intra-specific competition (for mates or resources, *e.g.* Serrano et al. 2003, De Meester et al. 2014, Jacob et al. 2018, Grabowska et al. 2019), but also with social facilitation that may increase a habitat attractivity, as it is the case with Allee effects (Wang 2016, Crespo-Miguel et al. 2022, *e.g.* Serrano et al. 2005, Smith et al. 2014, Fronhofer et al. 2015a,b). It is also more broadly the case for species benefiting from crowding, with a so-called social attraction, as in colonial species (Danchin et al. 1998, Serrano and Tella 2003, Serrano et al. 2004), and for species cooperating for dispersal movements (*e.g.* Kümmerli et al. 2009, Ridley 2012) or breeding (Sinervo and Clobert 2003, Romano et al. 2019). Again multiple proximal factors associated with the intra-specific interactions influence the dispersal behavior, such as the conspecifics' density (Denno and Peterson 1995, Matthysen 2005, De Meester and Bonte 2010), sex ratio (Nelson and Greef 2011, *e.g.*Chaput-Bardy et al. 2010, Trochet et al. 2013), or social dominance (Wey et al. 2015, *e.g.* Serrano et al. 2003, McCauley 2010, Morales-Gonzalez 2021).

Inter-specific interactions also strongly influence dispersal, with avoidance of predators (*e.g.* Hakkarainen et al. 2001, Hauzy et al. 2007, Poethke et al. 2010, McCauley and Rowe 2010, Otsuki and Yano 2014), competitors (*e.g.* Danielson and Gaines 1987, Denno and Roderick 1992, Fronhofer et al. 2015a), parasites (*e.g.* Expósito-Granados et al. 2017, Baudoin et al. 2019, Baines et al. 2020, Brophy and Luong 2022), and dependence on a sufficient resources availability (Fronhofer et al. 2017b, *e.g.* Lurz et al. 1997, Hauzy et al. 2007, Bowler and Benton 2009, Aguillon and Duckworth 2015).

Finally, the abiotic context also drives dispersal by defining habitat suitability (physico-chemical conditions, such as temperature or humidity, *e.g.* Smith 1974, Jacob et al. 2018, Cullum et al. 2020, Crossley et al. 2022). Dispersal movements also depend on the connectivity between habitats, defined by the landscape matrix characteristics (Kuefler et al. 2010, Zajitschek et al. 2012, Nowicki et al. 2014, Evans et al. 2017), the fragmentation of the suitable habitat (Cote et al. 2017, *e.g.* Schtickzelle et al. 2006, Coulon et al. 2010), but also by the social context as described in the social fence and social resistance hypotheses (Hestbeck 1982 and Armansin et al. 2020, *e.g.* Smith and Batzli 2006).

All these causes are non-exclusive (Dobson and Jones 1985, Bowler and Benton 2005, Matthysen 2012, *e.g.* Clobert et al. 2012, Le Galliard et al. 2012, Cayuela et al. 2020), and dispersal is mostly multi-determined, all these factors concurrently impacting dispersal with different importance (Matthysen et al. 2012,*e.g.* Legrand et al. 2015), and sometimes interacting with one another (Morosinotto et al. 2014, Baines et al. 2014).

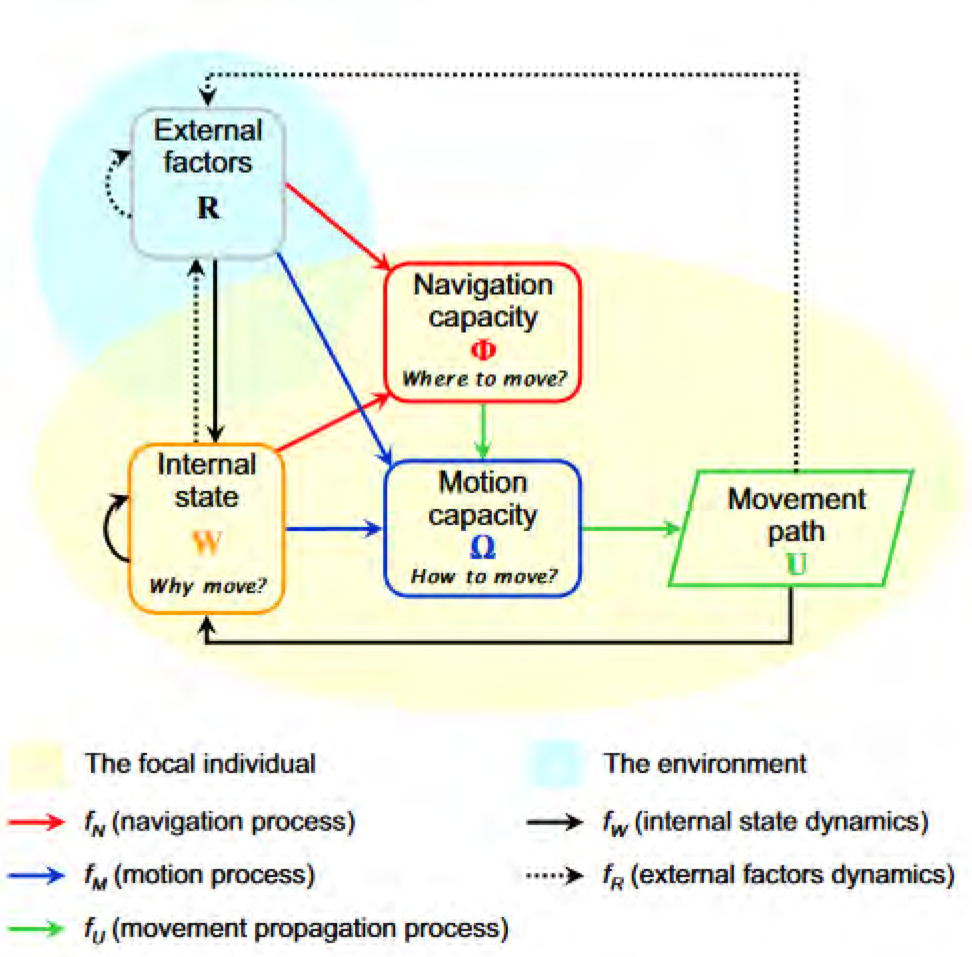


Figure 2: Costs associated with dispersal movements.
This figure is extracted from the article of Nathan et al. (2008) in *PNAS*. This framework describes the different movement causes and their interactions, to describe what drives a movement path. The different factors have been described in the previous section. The internal state refers to the focal individual's phenotype (personality, ability to compete, avoid predation, etc.) and reflects its motivation to move, in interaction with the external factors, referring to the environmental context.

In most cases, movements should depend on the individuals' abilities and need, *i.e.* on their surrounding context (as described previously) and their phenotype (Figure 2). The phenotype-dependence of dispersal movement should first be related with the propensity to move. This propensity should depend on the individual's motion capacity (Biewener and Piatek 2018, Wu and Seebacher 2022, *e.g.* Denton et al. 2017, Pennekamp et al. 2019, Claramunt 2021) and its ability to navigate in space (*i.e.* to orientate:

Jander 1975, Akesson et al. 2014, Kappeler 2022). Navigation in space can take place through memory (Fagan et al. 2013), and/or external cues (Bell 1990), implying important sensory processes (as for birds orientating through magnetic fields, Beason 2005), sometimes related to substantial cognitive abilities (*e.g.* Sutherland and Hamilton 2004), or more simply to metabolic responses to chemical stimuli (as for chemotaxis, Eisenbach et al. 2004, *e.g.* Hellung-Larsen et al. 1990). Such propensity to move also depends on personality, some individuals being more prone to explore, take risks, and/or avoid social interactions than others (Spiegel et al. 2016, Cote et al. 2010 for a review). The interaction between such ability to move and the landscape characteristics (biotic and abiotic) should define motile organisms' movements, as predicted by energy landscape and landscape of fear theories (Shepard et al. 2013, Gallagher et al. 2017).

Second, movement should vary with an individual's phenotypical state. An individual's traits could define the benefits to leave or settle in an environment, by reflecting its ability to avoid predation (*e.g.* Payo-Payo et al. 2018, Hermann et al. 2021), compete for resources (Gyllenberg et al. 2018, Kisdi et al. 2012), with traits such as body condition, metabolic rate, aggressiveness (*e.g.* Ellsworth and Belthoff 1999, Fjerginstad et al. 2007, McCauley 2010, Camacho et al. 2019, Sánchez-González and Nicieza 2021), and for mates (sex-biased dispersal, depending on mating systems and intra-sexual competition for mates and resources: Greenwood et al. 1980, Li and Kokko 2019, *e.g.* Doughty et al. 1994, Langen 1996). The environmental context could also imprint the individual's phenotype and mediate its propensity to disperse (Benard and Mc Cauley 2008) or to settle successfully in other habitats (silver-spoon effects: Stamps et al. 2006).

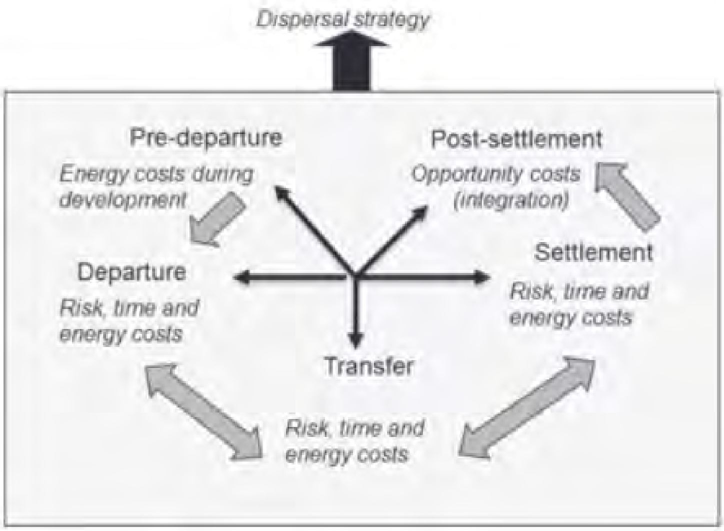
All the traits related to movement define specific movement syndromes (Abrahms et al. 2017, including dispersal syndromes: Ronce et al. 2012, Stevens et al. 2014), defining an individual propensity to move, potentially related to different life-history strategies (Raffard et al. 2022), as it could be the case for pace-of-life syndromes (Réale et al. 2010, *e.g.* Le Galliard et al. 2013). We can observe for example variation in foraging and mating strategies (*e.g.* MichelAngeli et al. 2021), reproductive strategies (*e.g.* Cotto et al. 2015), or sociability strategies (Cote et al. 2010). The co-existence of multiple syndromes could reflect specific trade-offs related to investment in contrasted strategies, for example, a competition-colonization trade-off could be observed when comparing philopatric individuals and dispersers (Burton et al. 2010, *e.g.* Hazell et al. 2005, Fjerginstad et al. 2007, Pennekamp et al. 2014a). Traits associated with dispersal could also result from plastic changes, with possible accommodation to variations in dispersal context as matrix harshness or resource availability (Jacob et al. 2019b, Junker et al. 2021). Dispersal syndromes could lead to directed gene flow (Edelaar and Bolnick 2012), with important repercussions on meta-population or meta-communities dynamics (colonizer-joiners dynamics: Clobert et al. 2009, Cote et al. 2010, effects on recolonization and rescue/reinforcement of meta-population patches) and a wide range of other evolutionary processes (Edelaar and Bolnick 2012, Raffard et al. 2022, *e.g.* Raffard et al. 2021). A part of the dispersal behavior could also be heritable, through genetic determinism (Saastamoinen et al. 2018, *e.g.* Greenwood et al. 1979) or maternal factors (Massot and Clobert 2000, Meylan et al. 2009).

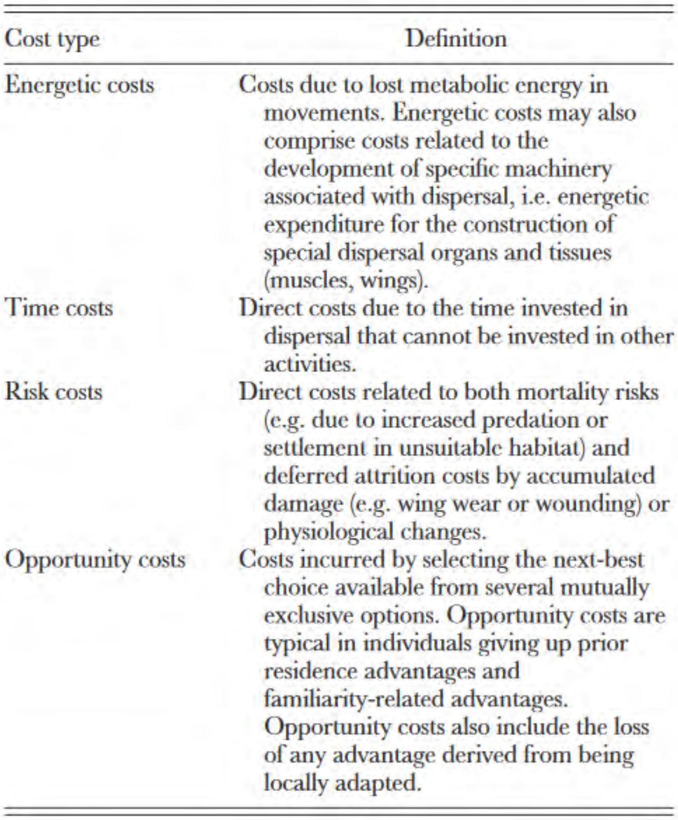
Optimizing fitness through movements

All displacement phases can be associated with costs (displacement costs, settlement costs, pre-departure or post-settlement costs, see Bonte et al. 2011 for a review, but also Shepard et al. 2013, Gallagher et al. 2017; Figure 3) and benefits (benefiting from a better environment than the initial one, avoiding inbreeding genetic burden). Therefore, an individual should optimize the way it uses its habitat, and we expect the movement in its living area to increase its fitness gain (habitat selection theory, *e.g.* Whitham 1980, see Levins 1962, 1968, Morris et al. 2004, for theoretical developments on fitness optimization). Thus, the optimal foraging theory predicts that an individual should optimize its net energy gain when foraging (Pyke et al. 1977): the cost of researching resources should never exceed the expected benefit of accessing them, with expectations of movement optimization in this perspective (Pyke 2019). More broadly, according to the ideal free distribution theory (Fretwell and Lucas 1970, Fretwell 1972), an individual is expected to maximize its fitness in space by balancing the benefit of a good habitat quality with the costs of competition due to conspecifics' density. This theory considers that individuals should distribute in all patches proportionally to the amount of resources defining each patch, so the density of conspecifics is balanced with the available amount of resources. This theory assumes that all individuals know all patches values (defined by the amount of resources associated with the patch and the density of conspecifics), are free to move in space, and are equally competitive. We could also expect that the individual's phenotype mediates the way it would distribute: the ideal despotic distribution (Fretwell and Lucas 1970, Parker and Sutherland 1986, *e.g.* Calsbeek and Sinervo 2002) consider that the previously presented trade-off varies in function of the individual's competitive abilities, with stronger competitors settling in the richest habitat.

The assumptions of these theoretical frameworks are yet important: the freedom of movement of individuals may be quite questionable (Stamps et al. 2005, *e.g.* social fence, social resistance, energy landscape hypotheses, see the previous section), as well as the quality depending only on resources amount (*e.g.*, ignoring the role of predation, Kennedy et al. 1994) and the complete knowledge of surrounding patches (cost of prospecting or perceptual constraints, Abrahams 1986, Parker and Sutherland 1986, Delgado et al. 2014, *e.g.* Shochat et al. 2002).

If the way individuals are distributed in space and their habitat use should optimize their fitness gain, we should expect an individual to optimize its dispersal in the same way, by balancing the benefits and costs of dispersal (reviewed in Bonte et al. 2011, Figure 3). Different hypotheses on dispersal strategies are based on the existence of such a cost-benefit balance. The matching habitat choice hypothesis (Edelaar et al. 2008) claims that an individual should settle in a habitat maximizing its fitness, *i.e.* there should be a match of the individual's phenotype with the habitat it selected (*e.g.* Camacho et al. 2015, 2020a,b, Jacob et al. 2017, 2018, Holtmann et al. 2017). Another hypothesis is the natal habitat pref-





Cost type	Definition
Energetic costs	Costs due to lost metabolic energy in movements. Energetic costs may also comprise costs related to the development of specific machinery associated with dispersal, i.e. energetic expenditure for the construction of special dispersal organs and tissues (muscles, wings).
Time costs	Direct costs due to the time invested in dispersal that cannot be invested in other activities.
Risk costs	Direct costs related to both mortality risks (e.g. due to increased predation or settlement in unsuitable habitat) and deferred attrition costs by accumulated damage (e.g. wing wear or wounding) or physiological changes.
Opportunity costs	Costs incurred by selecting the next-best choice available from several mutually exclusive options. Opportunity costs are typical in individuals giving up prior residence advantages and familiarity-related advantages. Opportunity costs also include the loss of any advantage derived from being locally adapted.

Figure 3: Costs associated with dispersal movements.
This figure is extracted from the article of Bonte et al. (2012) in *Biological reviews*. The upper graph represents all the different costs occurring at the different phases of dispersal, the table gives the definitions of all these costs. The different costs implied at a given phase can impact costs at other phases, through processes that impact later survival or fecundity (*e.g.* an important investment in locomotor traits before departure could reduce investment in the reproduction later in life, after settlement).

erence induction (Stamps 2001, Davis and Stamps 2004, Stamps and Davis 2006, Stamps et al. 2009b, Piper 2011), or natal habitat-biased dispersal (*e.g.* Selonen et al. 2007, Merrick and Koprowski 2016, Sanz-Perez et al. 2019, Milleret et al. 2019): an individual would prefer habitat with a context close to the individual's initial habitat, to benefit from habitat imprinting (with potentially better performance in such habitats), or recognition of natal habitat cues (reducing the cost of assessing or detecting such habitats). It could potentially lead to the selection of sub-optimal habitats contrary to what is expected under the ideal free distribution or the matching habitat choice hypotheses (Stamps 2001, *e.g.* Piper et al. 2013).

The non-randomness of movements that results from such dependencies is central for understanding genetic fluxes and impacts on demographic dynamics: contrary to what is expected under random dispersal (Kawecki and Ebert 2004, Bolnick and Nosil 2007), these directed gene flow could be adaptive (Stamps and Davis 2006, Edelaar et al. 2008, Nicolaus and Edelaar 2018), lead to genetic heterogeneity, and even speciation (Beltmann and Haccou 2005, Edelaar et al. 2008, Bernert Thibert-Plante 2015, Scheiner 2016, Nicolaus and Edelaar 2018). The natal habitat preference and phenotype-dependent dispersal could conflict and scramble these potential signals (*e.g.* Camacho et al. 2016). These non-random movements have also great influences on species range (Armsworth and Roughgarden 2005, Fronhofer et al. 2017a,b), metapopulations dynamic (Mortier et al. 2018, Jacob et al. 2015a), or species persistence (Pellerin et al. 2019). Although dispersal has long been thought to be random in most theoretical models and might be central to the understanding of some theoretical patterns (Skellam 1951, Slatkin 1981), considering random dispersal could be an oversimplification of what occurs in nature (Edelaar and Bolnick 2012).

These theories and hypotheses emphasize the importance of taking into account the environmental context and the individual condition to better understand the decision-making process as fitness gain should depend on these non-exclusive parameters.

Acquisition of information about the environmental context

As we saw earlier an individual is expected to make movement decisions according to the environmental surrounding context to optimize its fitness gain. To do so an individual should acquire information on such an environment (Fronhofer et al. 2013). Information acquisition (Danchin et al. 2004, Dall 2005, Dall et al. 2005, Schmidt et al. 2010; Figure 4) could either be directly obtained by interacting with its environment (personal information), or by perceiving the traits of conspecifics (socially acquired information, refer to as social information), but also of heterospecifics (Seppanen et al. 2007). Production of social information could be evolved, refer to as signals, or inadvertent. Social information could be continuous or not: Dall et al. (2005) refer to continuous social information as public information and discrete as social cues. Yet, public information could also be defined as information available to any individuals and social cues as “A detectable state or event that correlates to the present or future state of the environment and is non-intentionally produced by other individuals” (Schmidt et al. 2010). These

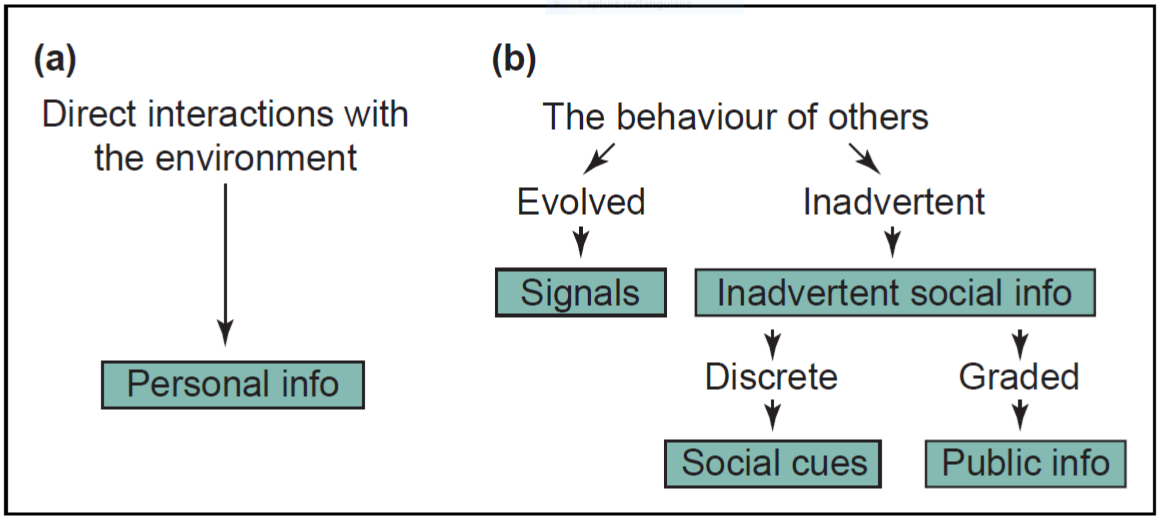


Figure 4: Classification of information accessible to an organism.
This figure is extracted from the article of Dall et al. (2005) in *TRENDS In Ecology and Evolution*. This figure was inspired by the one in Danchin et al. (2004). Personal information (a) can be distinguished from socially acquired information (b) (*i.e.* social information). The social information could then be inadvertently or "voluntarily" (evolved traits, referring to signaling communications) provided. The inadvertent social information can be either continuously graded (*e.g.* body condition) or discrete (*e.g.* presence/absence of conspecifics). In this thesis, we will use the generalist definitions provided in Schmidt et al. (2010): "*Public information*– Information that is in the public domain and potentially available to any organism.", "*Social (i.e, socially-acquired) Information*– Information extracted from other individuals (con- or heterospecific) be they signals or (inadvertent) cues (including actions and consequences). Note: all social information must be public.", "*Cues*– A detectable state or event that correlates to the present or future state of the environment and is non-intentionally produced. Includes state and events produced by physical agents or inadvertently produced by biological agents.", "*Signals*– A trait or behavior of a signaler evolved specifically to alter the behavior of the receiver in a way to benefit the signaler. The change in receiver behavior should also have evolved to enhanced receiver fitness.".

generalist definitions will be used in this manuscript.

Cues and signals could be highly diversified (Marler 1967, Maynard-Smith and Harper et al. 2003, Laidre and Johnstone 2013, Freeberg et al. 2017, *e.g.* Fleishman and Font 2019 for a review of signals in lizards, Grüter and Leadbeater 2014 in insects). These imply diverse sensory systems, like vision, olfaction (and more broadly perception of chemical compounds), or hearing. Visual cues or signals are particularly diversified (*e.g.* Hodl and Amézquita 2001, Hart et al. 2006, Rosenthal and Marshall 2011), with color signaling (Cuthill et al. 2017, *e.g.* Hill and McGraw 2006 for birds, Cooper and Greenberg 1992 for lizards), as with signaling through melanic coloration (Roulin 2015, Côte et al. 2018), carotenoids coloration (Moller et al. 2000, Blount and McGrow 2008, Svensson and Wong 2011), or coloration pattern (as it is the case for aposematic signals: Forsman and Merilaita 1999, Svensson and Wong 2011, Winters et al. 2017). Visual cueing or signaling can also emerge from specialized body structure (*e.g.* male quality assessed through tails feather in swallow: Moller et al.

1998, peacock train: Gadagkar 2003, or antler size in roe deer: Vanpé et al. 2007). The observation of behaviors is also often at stake (*e.g.* courtship postures for mates attraction: Rowland et al. 2002, Murai and Backwell 2006, Vanpé et al. 2007, display behaviors during agonistic interaction to assess social dominance: Terleph 2004, Scheel et al. 2016, or potential pursuit-deterrence signals for preventing predation: Caro 1995). Visual estimation of the presence of other individuals is also central (location cues, Stamps et al. 1991, D'adamo et al. 2003, Pérez-Cembranos and Pérez-Mellado 2015), potentially leading to conspecific attraction (Buxton et al. 2020), heterospecific attraction (Mönkkönen et al. 1999), or the avoidance of predators (Smolka et al. 2011, Flor et al. 2017). Such observations could also result in estimating density, which could inform on a habitat competition level or quality (*e.g.* Forsman et al. 2008, Bohenek and Resetarits 2018).

Use of chemical signals or cues is also extremely common (Halpern 1992 for a review on chemical signals in reptiles, D'Ettore and Moore 2008 in insects, Breithaupt and Thiel 2010 in crustaceans, Sorensen and Widensen 2015 in fishes) and is considered the most widespread form of communication among life forms (Steiger et al. 2011). Individuals can perceive secreted chemicals as pheromones (Wyatt 2014, 2017, *e.g.* Mason and Parker 2010 in reptiles) that could for example inform on the mating opportunity and location of potential partners (Johansson and Jones 2007, *e.g.* Marin and Lopez 2011, Caro et al. 2015). They can also perceive excreted cues that could inform on the presence of heterospecifics (*i.e.* kairomones, as in Williams et al. 2020, with an avoidance of scent cues of potential competitors, or Hugues et al. 2010, with detection of prey scents by predators), including predators (*e.g.* Hauzy et al. 2007, Hazlett 2011, Van Moorleghem et al. 2020), or conspecifics (Aragon et al. 2001, Gautier et al. 2006, Campos et al. 2017). These cues can even potentially inform the potential physiological state of the emitters (*e.g.* Schneider et al. 1999, Fisher and Rosenthal 2006, Lopez et al. 2006, Mas et al. 2009).

Sounds are also used as cues or signals (vibration communication, including vocalization: Owings and Morton 1998, Narins 2001, Kumar 2003, Dudzinski et al. 2009, Tavolga et al. 2012; sounds awareness for predation risk: Quinn et al. 2006, Pereira et al. 2012, MacLean and Bonter 2013), with a high variety of uses, from alarm signals (Macedonia and Evans 1993, Manser 2009, Gill and Bierema 2013) to territorial songs (*e.g.* Morse 1970, Marshall and Marshall 1976, Bhatt et al. 2000, Rivera-Gutierrez et al. 2011), or courtship songs (*e.g.* Ewing and Bennet-Clark 1964, Behr and von Helversen 2004, Nakano et al. 2008).

As we partly detailed, the information conveyed by cues or signals is highly diversified, with uses such as mate selection (Zuk 1991, Greenfield 1997, Searcy and Nowicki 2010, *e.g.* Roy 1997, Snowdown in Kappeler and Schaik 2004), habitat selection (Szymkowiak 2013, Buxton et al. 2020), and estimation of social dominance (*e.g.* Senar 2006, Jandt et al. 2014, Brena et al. 2018). Multiple cues could be perceived at the same time by an individual, and could provide an individual information about different parameters of the environment, confirm one another, back-up erroneous information, or qualify/precise co-existing information (Bro-Jørgensen et al. 2010, *e.g.* Ward and Mehner 2010, Bretman et al. 2011, Hotta et al. 2015, Damas-Moreira et al. 2018). The same cue could also have different use depending on the receiver condition (*e.g.* personality-dependence: Marchetti and Drent 2000, Kurvers et al. 2010, Trompf and Brown 2014, Smit and Van Oers 2019, Morinay et al. 2020b), its ability to perceive, process and use such information (Mesoudi et al. 2016, for example, variation with an individual's experience: Bougert et al. 2013, Sasaki and Pratt 2013, Leris and Reader 2016, Morinay et al. 2018), or the surrounding context (*e.g.* Pollock et al. 2006, Fletcher 2007, Sinervo et al. 2007, Rushing et al. 2015, Wurtz et al. 2021). The use of multiple cues could occur from the observation or detection of one or several individuals (*i.e.* multiply informed individuals, *e.g.* Damas-Moreira et al. 2018, Fletcher 2007), here we considered an individual that transmits the social information (*i.e.* the information vector) as the information source. These information sources could then reflect the different conditions of origin, according to the habitat from which they come. Using such information is associated with potential costs. It necessitates some abilities to perceive the cues or signals and exploit them (Bernays and Wcislo 1994, Figure 5), with developed sensory abilities and/or cognitive abilities (*e.g.* Page and Jones 2016) that could be costly to acquire and/or maintain (Carter et al. 2016, Schneeberger and Taborsky 2020). In the particular case of honest signals, the information could also be costly to maintain for the emitter

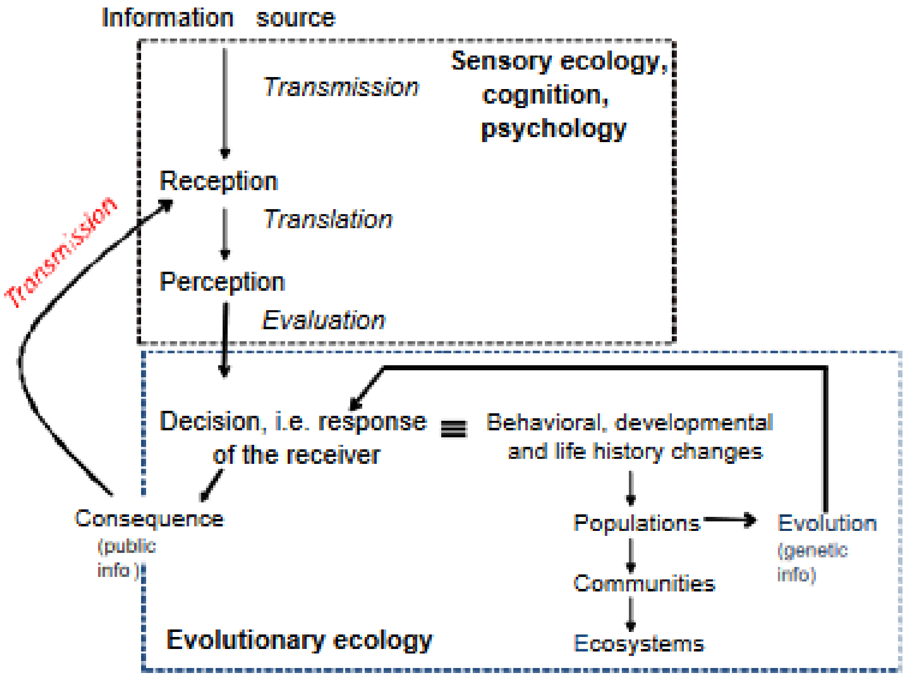


Figure 5: Integration of information in decision-making processes.
This figure is extracted from the article of Schmidt et al. (2010) in *Oikos*. The figure was partly adapted from Koops (1998). This graph details the different phases of the information integration (the perception of the cues or signals: "Transmission", the information processing: "Translation", and its use: "Evaluation") leading to a decision of the receiver, that may vary according to its genetic basis (or its experience, Mesoudi et al. 2016). The outcome of the decision could then, if perceptible, become a social cue or signal (red arrow, left of the graph).

(Higham 2014, *e.g.* Tibetts 2014). It could also be costly to acquire information when there is conflicting interest between the information receiver and emitter (Dubois et al. 2012, Schneeberger and Taborsky 2020), as during agnostic interactions (dishonest signals social costs: Webster et al. 2018, *e.g.* Tibetts and Izzo 2010, Kawamoto et al. 2021). Social information value may also quickly vary in spatially and temporally heterogeneous environments (risk of outdated or inaccurate information: Raffacz and Templeton 2003, Galef and Whiskin 2004, Fletcher and Sieving 2010, Heinen and Stephens 2016) or with the information transmitter (*e.g.*, its familiarity: Swaney et al. 2001, Kern and Radford 2017, social status: Canteloup et al. 2020, success: Goldman et al. 2021, physiological state: Pasqualone and Davis 2011, Szymkowiak et al. 2016, etc.). When potentially unreliable, social information use could also be associated with information cascade potentially leading to maladaptive decisions (Giraldeau et al. 2002, Rieucau and Giraldeau 2011), leading to an advantage of using it relatively to its personal experience (Giraldeau et al. 2002).

Yet, this social information acquisition should be particularly advantageous in decision-making as it reduces the randomness in decision processes, by informing on potential costs and benefits, often at less cost than with personal prospecting.

The importance of social information in decision making processes

Advantages of using social information

The use of social information could benefit an individual by giving it access to difficulty available information, such as information on distant habitats conveyed by immigrants (Cote and Clobert 2007a, Jacob et al. 2015b), information on recently explored habitats (*e.g.* habitat selection through fecal chemicals: Moreira et al. 2008, patch assessment in foraging contexts: Valone and Templeton 2002, or assessment for breeding habitat selection through reproductive success: Danchin et al. 1998, Doligez et al. 1999, 2002, 2004). It may also constitute information that is accessible only through social interactions (public information as conspecific's presence, *e.g.* Szymkowiak 2013, aggressiveness or social dominance, *e.g.* Schneider et al. 1999, Labra 2006, Martin et al. 2007a,b, Brena et al. 2018). This social information should be advantageous to use (Figure 6, Doligez et al. 2003, Riotte-Lambert and Matthiopoulos 2019) if associated with a sufficiently low temporal and spatial variability (*e.g.* Raffacz and Templeton 2003, Galef and Whiskin 2004, Heinen and Stephens 2016), but should also be associated with sufficiently high variability to be valuable, to give information an individual could not infer from the prior condition it was experiencing (Aguiñaga et al. 2021, *e.g.* Bauer et al. 2020, Deygout et al. 2010, Boyd et al. 2016).

Second, this information is often less costly to obtain compared to personal prospecting: it allows an individual to avoid the research cost (Delgado et al. 2014), by requiring only a perception of another individual's cue or signal. It can be specifically advantageous for information implying potentially high

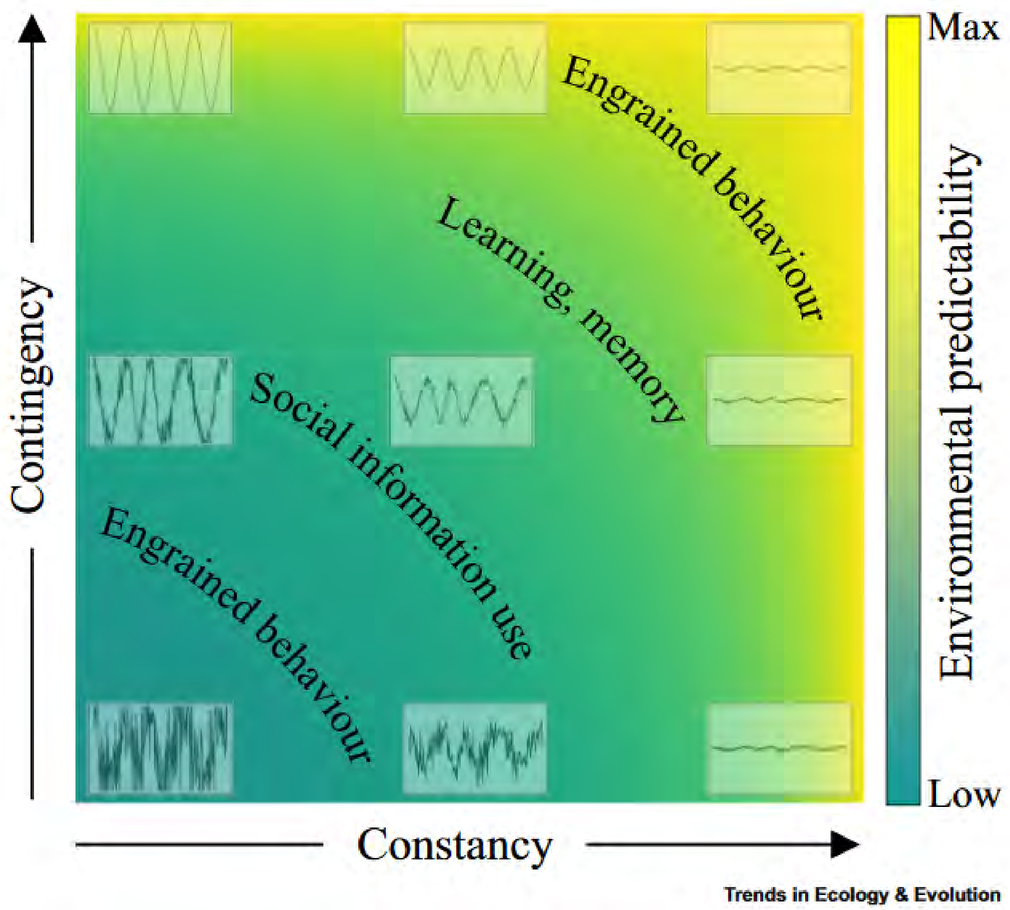


Figure 6: Optimal behavioral response to an environmental condition according to the its predictability.
This figure is extracted from the article of Riotte-Lambert and Matthiopoulos (2019) in *TRENDS In Ecology and Evolution*. The environmental predictability (both spatial and temporal) is defined as a function of the environment constancy (the converse of the spatial and temporal variability) and the environmental contingency (the spatial and temporal autocorrelation). The small graphs included in the figure give an example of the spatiotemporal environmental variation for given levels of constancy and contingency. Social information use is expected to occur for low environmental predictability, even though too unpredictable environment could not be foresight by using social information as they evolve too rapidly for the social information to be efficiently used.

individual costs (Rieucau and Giraldeau 2011, ‘costly information hypothesis’) as with habitats connectivity (*e.g.* pheromone trail in ants: Sumpter and Beekman 2003), risk of predation (*e.g.* Webster and Laland 2008), parasitism (*e.g.* Expósito-Granados et al. 2017), estimating dominance status before antagonistic interactions (*e.g.* Lopez and Martin 2001), or estimating mate quality before reproducing (*e.g.* Jones and Duval 2019). Third, such information, when co-existing with personal information, allows an individual to confirm its private information or even to complete it (Aguiñaga et al. 2021, *e.g.* Czaczkes et al. 2011, Throgood and Davies 2016, Winandy et al. 2021), and could also allow him to reject existing private information when there is conflict and when the personal information is of low reliability or costly to obtain compared to the social information (*e.g.* Kendal et al. 2004, Webster and Laland 2008, Smolla et al. 2016, Feyten et al. 2021).

The particular case of spatial decisions

Using social information during movements should be particularly profitable as it could allow an individual to have access to information on surrounding habitats through the arrival of immigrants before moving (Chaine et al. 2013, *e.g.* Jacob et al. 2015b, Cote and Clobert 2007a), to have access to information on habitats in which it travels (*e.g.* particularly high importance of social cues during migration movements, Nemeth and Moore 2007, 2014, or for nomadic species, Teitelbaum and Muller 2019), or to settle without exploring them in detail (reducing the cost associated with habitat selection: Delgado et al. 2014, *e.g.* rapid assessment of the predation or parasitism risk: Mönkkönen et al. 2009, Martin et al. 2010, Forsman et al. 2013, Tolvanen et al. 2017). Social information might also allow an individual to orientate in space, by using gradients (*e.g.* perceptible chemical cues with chemotaxis, Hellung-Larsen et al. 1990, Wadhams and Armitage 2004, pheromone trails in ant or other insects, Farkas and Shorey 1972, Morgan 2009, or sound localization, Erulkar 1972) or observing an individual behavior in space (bee waggle dance: De Marco and Menzel 2005, honey-guide birds, also called indicator birds: Spottiswoode et al. 2016, compass rafts in birds: Weimerskirch et al. 2010). Finally, there is also a possibility that individuals acquire social information about the difficulty related to displacement or reaching a given habitat (matrix resistance or connectivity, Cote and Clobert 2010, habitat distance, with the example of the bee waggle dance: De Marco and Menzel 2005, or of sounds localization: Naguib and Wiley 2001, risks of predation: Nemeth and Moore 2007).

Such precise knowledge of the environment should facilitate matching habitat choice or other strategies maximizing the individual's fitness gain (Cote and Clobert 2007a, Jacob et al. 2015b; Forsman et al. 2007 for an observed fitness gain following social information use for habitat selection), resulting in directed gene flow with important consequences on a population dynamics and evolution (Clobert et al. 2009, Chaine et al. 2013, Gil et al. 2018, Schmidt and Massol 2018, *e.g.* Ponchon et al. 2015, Fronhofer et al. 2017a). In particular, it should lead to convergence toward ideal free distribution as suggested by Cote and Clobert (2007a) or Nocera et al. (2009), by allowing a more accurate estimation of the quality of the surrounding patches. Studying the use of such social information in space could be central to better understanding how individuals will distribute in presence of other conspecifics, and how an individual could perceive its spatial environment, as social information may play a major role in an individual knowledge of its surroundings. As a consequence, this study field could have major practical application for better understanding the response of reintroduced individuals in a novel environment (as already highlighted by the study of temperaments: McDougall et al. 2006) and specifically to understand how such individuals will react to translocation in term of movements (Stamps and Swaisgood 2007, Le Gouar et al. 2011).

The use of social information is well-evidenced for decisions related to habitat selection (*e.g.* Danchin et al. 1998, Doligez et al. 2002, Szymkowiak 2013, Buxton et al. 2020), or emigration (*e.g.* Clobert et al. 2012, Le Galliard et al. 2012, Cayuela et al. 2020). Yet, social information use is quite overlooked when studying the precise conspecifics' social landscape (Wey et al. 2015) with relatively few information other than the presence, density, or reproductive success of other individuals taken into account (very few studies on the use of other social cues for estimating a habitat quality, but see Vercken et al. 2012, Endriss et al. 2018, Morinay et al. 2020a), and with an obvious lack of comprehensive studies, taking into account multiple social parameters, from multiple sources of information.

Handling multiple sources of information

The well-studied case of concurrent personal and social information

In most natural cases, individuals have access to multiple sources of information concurrently. In particular, the concurrence of personal and social sources of information is well documented (Kendal et al. 2009). In most cases, a prioritization over personal information has been observed as such information is very likely to be more reliable than social information. Yet, when personal information acquisition, is costly, uncertain, outdated, unreliable, or dissatisfied, the social information might be preferred ("when strategies"). In the same way, when social information is particularly repeated and constant, or conveyed by successful, older, or dominant individuals, it might also be preferred ("who strategies").
Cases of multiple sources of social information from different origins, that could conflict between them, are quite scarce in the current literature (*e.g.* Coolen et al. 2003, Drullion and Dubois 2008, Pilon 2020; Jaakkonen et al. 2015, Romero-Gonzalez et al. 2020 for comparisons between conspecific vs. heterospecific social information), and are almost non-existent when considering movement responses (except Chaine et al. 2013 for a theoretical framework, Stienessen and Parrish 2013 under experimental conditions in a socially foraging species). Nonetheless, the same hypotheses may be applied in the case of multiple social information sources.

On the importance and use of multiple social information sources

Here, we aimed to tackle the relative absence of information about how are used multiple social information sources for movement decisions using experimental designs and monitoring in natural conditions.
First, we focused on the use of local social information from multiple sources (in the natal area of a focal individual) by considering multiple components of the social context at the same time (sex ratio, age structure, density, body condition of conspecifics), to validate previous isolated experimental results (Chapter 1). This first study allowed us to precise the importance of such local social context for natal dispersal, and specifically to compare the importance of this social information use with other dispersal factors, by ranking their relative importance. We also tested the dependence of such social information

use on the individual phenotype. Natal dispersal was expected to be multi-determined, especially with several elements of the social context impacting the dispersal concurrently. We also expected social information to be used according to the individual's abilities, with a match between individual competitiveness and its use of social information (e.g avoidance of competitive context as dense habitats for individuals with low competitive abilities).

Second, we considered the concurrent arrival of conspecifics informants in the home area of a focal individual (Chapter 2). By using an adequate experimental design, we wanted to test the ability to orientate when being confronted with multiple social information sources. This experiment also allowed us to better understand how was used such information from concurrent sources, by testing the influence of averaged information and contrast between information sources on movement decisions. We expected averaged information to be used as information on the individual's surroundings, and the contrast in information to be also used as information on the signal variability and for orientation in space.

Third, we explored the use of such immigrants-based information in nature (Chapter 3). The aim was to better understand how such information was precisely used, *i.e.* whether it depended on the local experienced context and/or the phenotype of the focal individual (context- and phenotype-dependence of the use of immigrants-based information), and whether it depended on the distance, variability, and the number of information sources. We expected the immigrants-based information to be used accordingly to the individuals' needs (defined by their phenotype and actual context), and the information to be used only when not too costly (*e.g.* accessible in terms of distance) or too uncertain (too variable or conveyed by too few immigrants).

Finally, we more precisely investigated how conflictual social information sources were used depending on local context, using a microcosm experimental settings on *Tetrahymena thermophila*, a unicellular ciliate (Appendix 3). We confronted focal individuals to two sources of informants having dispersed under different temperatures (same ones or in conflict), and let them disperse at different possible temperatures. We found no effect of social information on temperature and therefore we could not explore the use of conflictual social information sources. Yet, we observed important effects of informants' traits (movement characteristics, cells' shape and size; potentially reflecting their physiological state) and their variance on dispersal responses, suggesting an information transfer on other environmental parameters, that remains to be explored.

We can sum up the previously described objectives of each chapter by the following question:

Is there a use of multiple sources of local social information in natural conditions? Does it depend on the individual phenotype? How important is it compared to other dispersal factors?

Can this use be generalized to individuals not originally from the local environment? Is the contrast between such non-local multiple sources used by the individual, especially for orientation?

Is this immigrant-based information used under natural conditions? Is it used in relation to local social information, to the individual phenotype? Does this use depend on the nature of the information, *i.e.* its

reliability or the cost of using it?
When two such sources of information conflict, how are they used? Is only one component of the information used, an average of the two, or neither? Does it depend on the local context? Is this information conveyed through the individual traits of the immigrants?

Model species and experimental/field designs

Biology of the common lizard

The common lizard (*Zootoca vivipara*, Jacquin 1787; Figure 7) is a small ground-living lizard of the Lacertidae family (snout-to-vent length: 40 to 60 mm on average, Horváthová et al. 2013, Khodadoost et al. 1987; 59 mm ± 5 SD in our long-term monitoring). This species is mainly encountered in wetlands (bogs, peatlands), but also in heathlands, grasslands, and wood edges, and is mainly distributed in northern Europe and Asia, from sea level up to 2900m height (Farren et al. 2010, Aghasyan et al. 2019). It feeds on small invertebrates (Avery 1966, Pilorge 1982, Khodadoost et al. 1987), and can be predated by various bird species and other reptiles (Steen et al. 2011, Antczak et al. 2019, Thoen et al. 1986, Bestion et al. 2014). This species is parasitized by various ectoparasites (ticks and mites: Sorci and Clobert 1995, Uller and Olsson 2004) and blood parasites (Sorci et al. 1996, Majláthová et al. 2010, Williams et al. 2020). Individuals can share their habitats with other non-avian reptiles (Strijbosch and Creemers 1988, Pilorge 1982, McInerny 2016). This ectothermic species is particularly sensitive to water restrictions (Lorenzon et al. 1999, Rozen-Rechels et al. 2018) and can endure cold temperatures (Costanzo et al. 1995, Grenot et al. 2000, Voituron et al. 2000, 2002). It has a temperature preference of about 31°C, with some variation according to environmental conditions or physiological state (Gvoždík and Castilla 2001, Le Galliard et al. 2003b, Trochet et al. 2018, Rozen-Rechels et al. 2021). Its critical temperature minima and maxima have been respectively estimated at 2 and 44°C (Gvoždík and Castilla 2001).

Individuals could live up to 10 years (Massot et al. 2011) and live 3-5 years on average (Strijbosch and Creemers 1988, Avery 1975), with particularly high mortality during their first year of life (about 60% mortality, Heulin et al. 1997, Le Galliard et al. 2010, up to 90%, Avery 1975) and a better life expectancy for females (Strijbosch and Creemers 1988, Le Galliard et al. 2010). Sexual maturity is acquired in the second year of life (Pilorge and Castanet 1981, with some exceptions in warm habitats as in low altitudes, Heulin 1985). Sexually mature individuals are referred to as adults, one-year-old individuals are referred to as subadults, and individuals in their first year of life are referred to as juveniles. Two forms of reproduction co-exist in this species with both oviparous and ovoviviparous populations (Surget-Groba et al. 2001). This species is polygynous and androgynous, with a same female mating with several males in the same season and males mating with several females (Fitze et al. 2005). Males are competing for females (Pilorge et al. 1987), and present important antagonistic interactions between them (Heulin 1988) and with females (Le Galliard et al. 2005a,b, 2008) during mating periods. Gestating females reduce movements during gestation to avoid predation risks (Bauwens and Thoen 1981). Clutch size varies from 1 to 11 neonates (4 to 8 on average, Pilorge 1987, Bauwens and Verheyen 1987, Horváthová et al. 2013; 4.6 ± 1.9 SD in our long-term monitoring) and neonates are independent of their birth.

The home-range of an individual is about a 15m radius with some variation with age and sex (Massot and Clobert 2000, Lecomte et al. 1994, Massot 1992a). This is a non-territorial species, with important overlapping among individuals' home ranges (Massot et al. 1992, Lecomte et al. 1994). Natal dispersal is particularly well described in this species: about 34% of neonates disperse during the long-term monitoring, while up to 60% disperse in experimental conditions (Massot and Clobert 1995, Lena et al. 1998a, De Fraipont et al. 2000, Cote and Clobert 2007a). Dispersal takes place on the 10 first day after birth (Massot 1992a,b, Léna et al. 1998a). The dispersal threshold is about 30m (Clobert et al. 1994, Massot and Clobert 1995, 2000, Massot et al. 2002, Cote and Clobert 2007a) with no return of dispersers to their initial home-range beyond this threshold (Clobert et al. 1994, Massot and Clobert 1995, 2000). It results in no overlap between the mother home range and the individual home range after dispersal, dispersal distance could reach up to a hundred meters (Chamaillé-Jammes et al. 2006; up to 152m in our long-term monitoring). These dispersal decisions are dependent on the phenotype and the environmental context (next sections for details). Adults or subadult dispersal also exists, but is much less frequent (Massot 1992a,b, Clobert et al. 1994, Sorci et al. 1994), and was not studied during this thesis.

A thirty year monitoring of a common lizard study site

We monitored the same study site for thirty-four years (from 1989 to 2022), in the Mont-Lozère (Cévennes national park, France, 44°30'N, 3°45'E, 1420m height; Figure 8) but only the data from 1989 till 2019 where used (because of time needed for data checking). We used a mark-recapture method, with a toe-clipping marking (approved by an ethical committee, DAP #5897-2018070615164391 v3), with no impact on their life-history traits and movements (Massot et al. 1992, Chamaillé-Jammes et al. 2006). The study site was delimited by natural boundaries such as forest or roads, and was about 18,370 m^2 (minimum convex polygon containing all captures over the thirty years). This study site is not particularly dense in predator or potential competitors (potential bird predators, particularly for juveniles, few snakes observed, few sand lizards, few occurrences of predation by frogs, Clobert pers. Comm.), but was relatively dense in ectoparasites (2.1 mites per adult or subadult individual ± 3.8 SD, up to 38 mites on the same individual). The density of this study site was estimated at 430 to 700 individuals per hectare depending on the studied zone (Clobert et al. 1994), the density was rather constant across years (Le Galliard et al. 2010). The survival rate of juveniles in their early life was estimated at 0.42 (Le Galliard et al. 2010), and we estimated a life expectancy of 1.7 years ± 1.1 SD (age at last recapture

Figure 7: Photographs of common lizards (*Zootoca vivipara*).
This figure is extracted from the article of Bonte et al. (2012) in *Biological reviews*. The top photograph displays an adult male common lizard taken in England (Credits: By Charles J. Sharp - Own work, from Sharp Photography, sharpphotography, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=57630280). The bottom picture was taken during the 2019 field session, just after the parturition of a female, all these neonates are from the same litter. For scale, adult males are about 55mm in snout-to-vent length and juveniles about 20mm.

during our long-term monitoring) for individuals having reached subadult age. Individuals present an ovoviviparous mode of reproduction in this study site and all other sites present in the same mountain range (Massif-central, Surget-Groba et al. 2001). Adults emerge in April and May and parturition occurs between mid-July and mid-August (Bleu et al. 2012).

Each summer, we performed capture sessions mainly in June (from June the first to July the fifteenth).

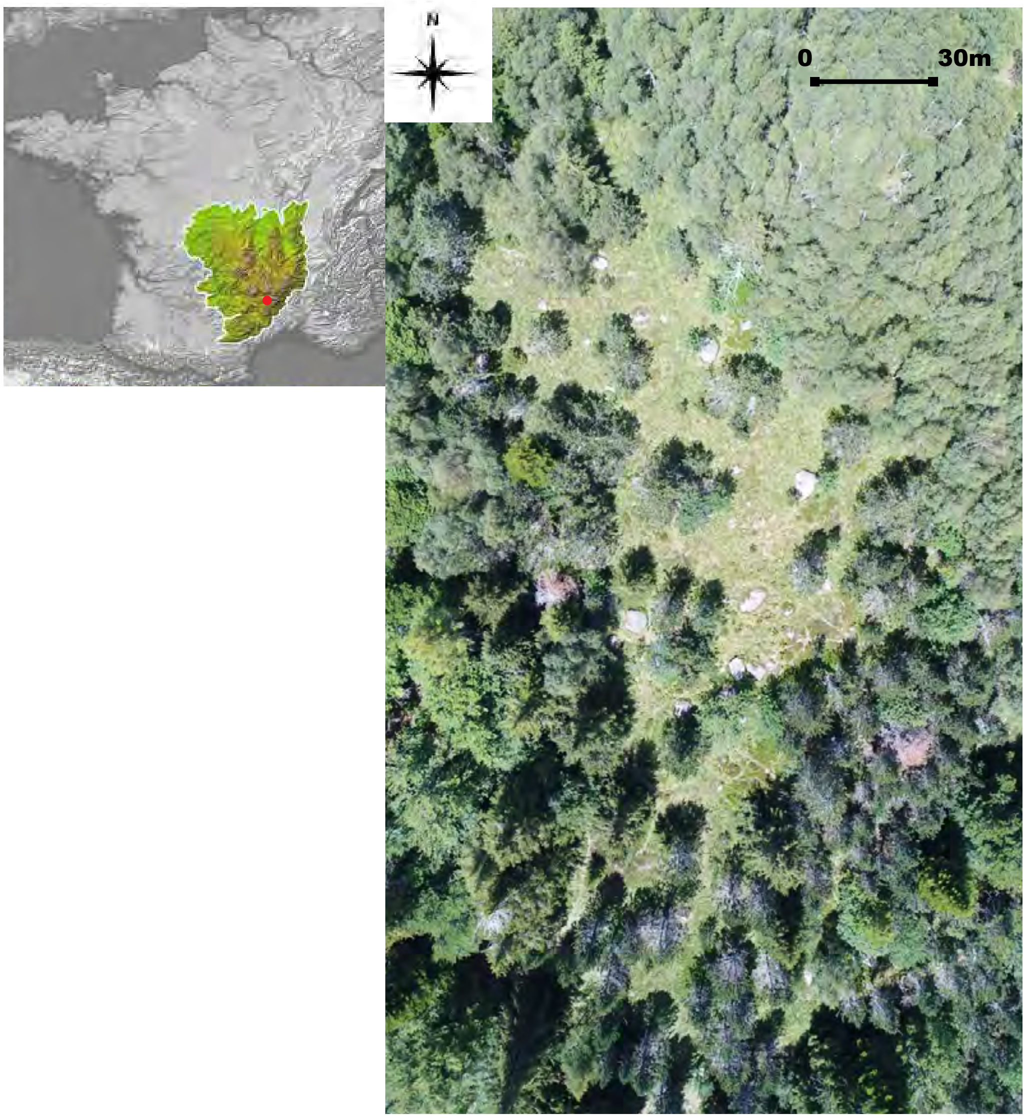


Figure 8: Location and aerial photograph of the studied area.
The study site is located in France, in the Massif-Central mountain range (colored on the left map), at the Mont-lozère (44°30’N, 3°45’E, 1420m height, red dot on the left map). It is located in a clearing, and the nearby undergrowth (right aerial picture).

Additionally to these capture sessions, recapture sessions were performed from late July (from July the nineteenth) to early October (to October the sixth), between 1989 and 2011. Additional capture sessions without captures of gestating females also took place during the first years of the monitoring, right after the mating period in April and May (in 1990, 1994, and 2004) or during the parturition period in July (between 1990 and 1995). Sampling varied over years, with 4 days of capture to 101 days of capture in one year, and 289 subadults or adults captured each year ± 150 SD. For each capture day, the number of samplers varied (from 2 to 8) but the time spent in the field on one day was relatively constant (approximately from 10 a.m. to 6 p.m., except in case of insufficient sunlight). We only sampled the population on sunny days. Over years, the sampling effort was rather stable: 35 ± 16% of individuals were recaptured in the same year in the field (without taking into account mothers, brought to the rearing facility, and juveniles, inconsistently recaptured over years). During these thirty years, 1,397 gestating females were captured (62 gestating females captured each year ± 19 SD), these females gave birth to 8,960 neonates (marked the day after their birth). We also captured 5,389 individuals (of all ages and sex) which were not born in the rearing facility (these individuals were marked at their first capture). All positions of captured individuals were recorded using a GPS device (meter precision). Pregnant females were brought to a rearing facility, where they were maintained until parturition. They were brought in an individual terrarium of dimension 18.5 x 12 x 11 cm, with a shelter and a 2 cm substrate of sterilized soil (Massot and Clobert 2000). Terrariums were placed under an incandescent bulb of 25W providing light and heat for 6 hours a day to allow basking (from 9 a.m. to 12 p.m. and from 2 p.m. to 5 p.m.). Terrariums were moistened three times a day with a water spray and females were fed at least once a week. Mothers and their litters were then released in the study site, at the precise location where the mother was captured. This method allowed us to access the dispersal status of each individual recaptured after its first year of life (1,562 individuals). All captured individuals were measured in the field: they were sexed (presence of the hemipenis), aged (depending on their morphology: adults or subadults), sized (snout-to-vent length, *i.e.* SVL, and total length), weighed (body mass, *i.e.* BM). We also measured their ventral coloration (using a gradient of color categories, Vercken et al. 2008), their dorsal melanic pattern (absent, linear, or reticulated, Lepetz et al. 2009), and counted the number of ectoparasites (mites and ticks) they carried. Females brought in the rearing facility were de-parasitized and more precisely weighed at their arrival (milligram precision). Measures were also performed just after parturition: we immediately weighed the mother, counted and weighed aborted eggs and stillbirths, separated the neonates from the mothers, and measured them the day after (SVL, total length, BM, sexed using Lecomte et al. 1992 method).

In 2019 and 2020, all captured individuals were brought back to a rearing facility near the study site. We performed then complementary standardized measurements on these individuals. First, we let these individuals have 48h to accommodate in their terrariums (same characteristics as those of pregnant females, except that the substrate was replaced by absorbent paper, terrariums were opaque, and there were two shelters in each terrarium, with a piece of absorbent paper inside each). After this time we replaced their substrate with new absorbent papers, that we retrieve 48h later and stocked in hermetic vials at -20°C to analyze the secreted and excreted chemical components of each individual later on (Appendix 2 for details). The next day, we measured their behavior (Figure 9), by using a 90 minutes

Figure 9: Photographs of an adult male during the behavioral monitoring.
The followed individual is located in its opaque home terrarium, with two shelters and a paper absorbent substrate, that will be collected to analyze the individual's excreted or secreted chemicals compounds. A camera is located above the terrarium to record its behavior. Another followed subadult individual appears at the left of the picture. For scale, adult males are about 55mm snout-to-vent length.

video tracking of individuals in their terrarium during which absorbent papers in shelters were replaced by an absorbent paper with male odors (collected on the absorbent paper used as substrate in a terrarium containing 3 males, from another close study site, left together for 48h) and an absorbent paper with no odor to test their social tolerance (based on Aragon et al. 2006c, Cote and Clobert 2007b, Appendix 1 for details). During this period, we also measured the individual's activity, boldness (using Cote et al. 2008a,b metrics), escaping attempts (using Aragon et al. 2006a metric), and tongue-flicking (perception of chemical components, Cooper 1994). We also performed measures of the individuals' aggressiveness, by presenting a small stick to each individual (3 back and forth movements in front of their snout) and registering their response (no movement, dodging, biting the stick). Three replicates of this measure were performed for each individual (when captured, right after the behavioral monitoring, when released). Preference for shelter containing males odor or not was also tested overnight, after the behavioral monitoring (survey of the shelter chosen for the night, before dawn). Same measurements (except sampling of chemicals excreted and secreted) were performed for neonates three days after their birth.

In 2019, we also brought 20 pregnant females from eleven different sites across Massif Central. The neonates from these females were then used in an experimental setting (Figure 10) where a focal neonate was confronted with two others which experienced contrasted environments in terms of food availability (Chapter 2 for details).

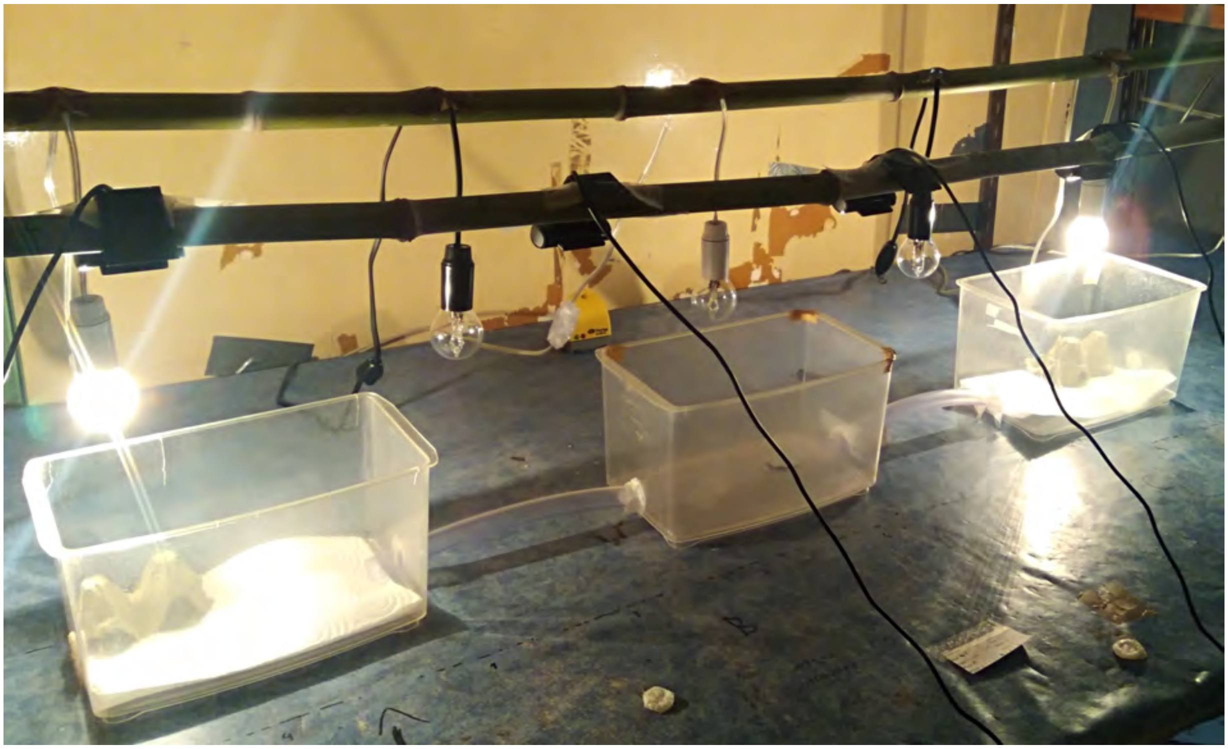


Figure 10: Photographs of the connected experiments performed in 2019.
The focal neonate appears at the center of the middle terrarium (*i.e.* its home terrarium). It is given the choice to move to two peripheral terrariums, after having been confronted with two other juveniles (each coming from one of the peripheral corridors) which have since been removed from the central terrarium. More details can be found in Chapter 2. For scale, juveniles are about 20mm snout-to-vent length.

Movement in the common lizard: the well-studied case of natal dispersal

Natal dispersal has been particularly well-described in this species, with numerous studies on the dispersal determinants (Clobert et al. 2012 and Cote et al. 2012 for reviews). The dispersal was observed to be often phenotype-dependent (partially reviewed in Cote et al. 2012). First, dispersal was found to be male-biased (Massot 1992a, Sorci et al. 1994, Le Galliard et al. 2003a, 2005a), in accordance with Greenwood's hypothesis (1980) in the case of a polygynous species where males compete for mates. Second, dispersal was sometimes conditioned by a sufficiently high body condition (Léna et al. 1998a, Meylan et al. 2002), suggesting that only the best competitors and/or individuals with the largest reserves dispersed. Finally, dispersers frequently displayed specific behavioral traits: they display different foraging techniques and success compared to philopatric individuals (Meylan et al. 2009, depending on the individual's sex), they are more active as subadults (in the absence and presence of conspecific scents, Aragon et al. 2006a, Clobert et al. 1994), suggesting that dispersers might have specific personality traits influencing their propensity to disperse (Cote et al. 2010). The individual's phenotype often interacted with other dispersal determinants, as described below.

Dispersal in this species also depends on the habitat quality (partially reviewed in Clobert et al. 2012). First, it is affected by the abiotic characteristic of the habitat, such as temperature, with a dispersal decrease with pre-natal temperature (Massot et al. 2008, opposite direction for post-natal temperature) and a match between temperature preferences and temperature of habitat for dispersal decisions (Bestion et al. 2015). An effect of habitat humidity was also observed (Massot et al. 2002), with a direction depending on the timing of variation (*i.e.* pre-natal or post-natal), in interaction with the temperature during gestation. Lastly, dispersal depends on habitat connectivity, with a decrease in dispersal when connectivity decreases (Boudjemadi et al. 1999, Cote and Clobert 2010).

Second, dispersal was found to depend on biotic factors, with an avoidance of the predation risk (Bestion et al. 2014, maternal exposure to predator cues), variations in dispersal depending on the substrate cover (preference of grassland over forest clearance, Boudjemadi et al. 199, Lecomte et al. 2004), avoidance of low availability of resources (food availability right after birth: Massot and Aragon 2013), and influence of parasites presence (Sorci et al. 1994, when the mother is parasitized dispersal increase in males and decrease in females). Many effects related to intra-specific competition have also been described, with an influence of density (positive density-dependence, potentially reflecting the avoidance of crowded habitat: Clobert et al. 1994, associated to grassland habitat in contrast to woodland, Cote and Clobert 2007b, in interaction with the individual's personality, Léna et al. 1998a, females density only), body condition of non-kin conspecifics (Léna et al. 1998a, body condition of a familiar female), and possible effects of the conspecific sex ratio (Le Galliard et al. 2005b, only observed for adult females, with an increase in dispersal in female-biased patches). Finally, a particularly well-described dependence on kin competition or inbreeding avoidance (through the presence and/or condition of kin) was frequently demonstrated. Thus, dispersal is influenced by the mother's presence (Cote and Clobert 2010, Léna et al. 1998a: increase of dispersal with the body mass or condition in presence of mothers; Le Galliard et al. 2003a: females dispersed more in presence of mothers), or more broadly of the relatedness level in the living area (Cote et al. 2007, when there is high relatedness dispersal increase with the neonate's body size). Moreover, dispersal also depends on the condition of the mother, such as its stress or body condition: it decreases when the mother is inoculated with corticosterone, a stress hormone (De Fraipont et al. 2000), dispersal of neonate females with a high corpulence increase when their mothers are stressed (Meylan et al. 2004), dispersal increased with the stress of mother with a low corpulence and decreased with the stress of mothers with a high corpulence (Meylan et al. 2002), dispersal increased with mother's body size, and decreased with it when treated with corticosterone (Meylan et al. 2002, 2004), and increased when the mother's body condition increase (Léna et al. 1998a). In the same way, dispersal depends on the mother's age (Ronce et al. 1998, the maternal senescence promotes philopatry in female neonates), or maternal feeding (Clobert et al. 1994, Massot and Clobert 1995, 2000, dispersal increases when the mother is well-fed). Lastly, it was influenced by the reproduction mode (Laloi et al. 2009, less dispersal in polyandrous litter with low litter success), and the litter's sex ratio (Massot and Clobert 2000, females dispersal increases with the proportion of males in the litter, Vercken et al. 2007a, dispersal increases or decreases with the litter's sex ratio when the mother is respectively exposed to a short- or long-term corticosterone exposure).

Dispersal was also found to be similar among siblings (family effect: Clobert et al. 1994, Léna et al. 1998b, Massot and Clobert 2000, Massot et al. 2002, Cote and Clobert 2010; Laloi et al. 2009: less similarity in dispersal decisions in monoandrous family compare to polyandrous ones), probably because they share the same natal environment, the same maternal effects, and close genetic determinism. Dispersal also varied among study sites (Clobert et al. 1994, Massot and Clobert 2000, Massot et al. 2002, Meylan et al. 2007) that could be related to variation in habitat characteristics such as temperature, humidity, or substrate coverage.

Use of social information during common lizards' movements

The use of social information for dispersal decisions was also particularly well-evidenced in this species. A negative density-dependence of dispersal was recurrently observed, and potentially reflects the use of density as a social cue for habitat quality (Le Galliard et al. 2003a, Cote and Clobert 2007b in interaction with the individual's sociability, Meylan et al. 2007, Léna et al. 1998a for density of males, Lecomte et al. 2004 when habitats are connected, or Massot et al. 1992 as suggested by a low emigration rate in high-density habitats). The average ventral coloration of females also influenced dispersal (Vercken et al. 2012): neonates disperse less from high yellow-morph frequency habitats and those who disperse settle more in such habitats (in interaction with the ventral coloration of their mothers), reflecting an attractivity toward the morph reflecting the highest dominance status. Despite the aggressiveness of such dominant individuals, it could be a cue for high environmental quality. The presence of the mother or kin is also used as a cue for kin competition (Le Galliard et al. 2003a, Cote et al. 2007, Cote and Clobert 2010), the condition of the present mother could further inform the level of kin competition but also on the habitat quality (De Fraipont et al. 2000, Meylan et al. 2002, 2004: trade-off between kin competition and environmental quality, represented by both the stress level and physical condition of mothers). Finally, there was evidence for immigrant-based information use, with an effect of the density of the immigrants' habitat of origin on dispersal (in interaction with the individual's body condition, Cote and

Clobert 2007a), but also an effect of the arrival of immigrants in a focal area (informing about habitat connectivity, Cote and Clobert 2010 in interaction with the individual's body mass).

Social information influence on space use has also been studied in other experiments. In particular, previous studies investigated the role of conspecific's behaviors (Cote et al. 2008a, effects of time spent moving by conspecifics on the time an individual spent basking), dispersal status of conspecifics (Aragon et al. 2006b affects the latency to leave home cage and time spent with intruders, Meylan et al. 2009 affects the time spent attempting to escape the area and activity, in interaction with its dispersal status), the density of the original area of intruders (Cote et al. 2008a influence on time spent moving, in interaction with the time spent moving by intruders, and on time spent hidden), or antagonistic interactions (Vercken and Clobert 2008, avoidance movements when confronted to some color morph associated with higher aggressiveness, with more biting and individuals of better physical condition). Particular attention was paid to the information provided by the chemical components perceptible by olfaction. Odors of conspecifics were found to often influence space use, as the time spent moving and attempts to escape the area (Aragon et al. 2006a, with variation in odor donors number, in interaction with the individual's dispersal status), the selection of nocturnal shelter (Aragon et al. 2006c, in interaction with individual's sex and body condition), the avoidance or attraction toward conspecifics' odors depending on the individual's condition and the environmental condition (Sorci et al. 1997 attraction toward patches visited by conspecifics, Meylan et al. 2017, avoidance of conspecific odors for males with a low corpulence and a hormonal treatment, Winandy et al. 2021 avoidance of conspecifics confronted to predator cues when personally confronted with predator cues, converse if conspecifics not confronted to predator cues). Odors of heterospecifics were also used as social cues, with possible avoidance of predator cues (Teyssier et al. 2014, Bestion et al. 2014: increase of activity in presence of predator cues), or competitors cues (Williams et al. 2020, avoidance of scent cues of potential heterospecifics competitors). All these results suggest that many different social cues could be used for movement decisions.

Biology of *Tetrahymena thermophila*

Tetrahymena thermophila is a unicellular eukaryote organism, about 50μm long and 20μm large (Frankel 1999, Figure 11). The cell surface is covered with cilia that allow directed movement of the cell (*e.g.* Leik et al. 1994). These organisms are found in natural conditions in freshwater ponds and streams, in North America; and mainly fed on bacteria or nutrients available in water (Doerder and Brunk 2012). Hunger may induce the production of a specialized posterior cilium, allowing long-distance movements (Nelsen 1978). Such condition was never induced during our experimental setting. Movements, and more specifically dispersal, were extensively studied in controlled experimental conditions in this species (see next section for details).

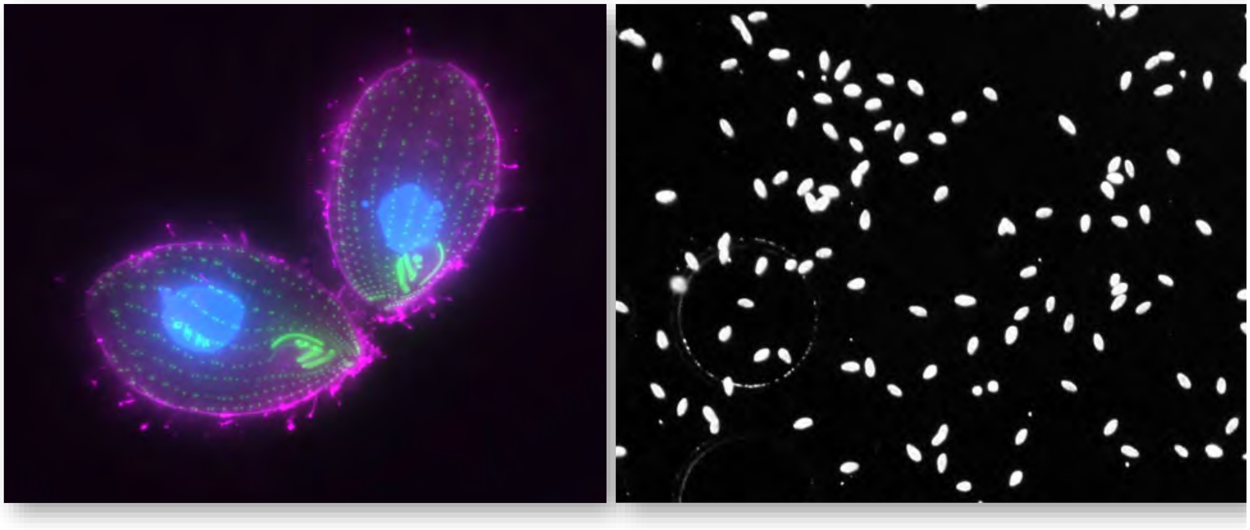


Figure 11: Microscope photographs of *Tetrahymena thermophila* cells.
The right picture display two cells in which DNA (in blue), basal bodies (in green) and microtubules (in purple) were marked. Cilia are visible on the surface of the cells (in purple). The left picture was taken after a microcosm experiment in our lab, on a Kima plate. For scale, a cell is about 50μm long. Photographs credits: Alex Stemm-Wolf (left picture), Staffan Jacob (right picture).

The dispersal in this species was found to depend on abiotic conditions, such as temperature (Jacob et al. 2017, 2018) or connectivity with other habitats (Jacob et al. 2019b, Laurent et al. 2020), on heterospecifics presence, with avoidance of predation risk (Hauzy et al. 2007), and dependence on heterospecific competition (Fronhofer et al. 2015a). Dispersal also depended on conspecifics presence, with avoidance of intraspecific competition (Jacob et al. 2018: competition for temperature niches, Hauzy et al. 2007, Fronhofer et al. 2015b, Fronhofer et al. 2017b: density-dependent effects), but also with social facilitation (cooperation level: Schtickzelle et al. 2009, Chaine et al. 2010, Jacob et al. 2016a, Allee effects: Pennekamp et al. 2014a, Fronhofer et al. 2015b). Finally, dispersal correlates with physiological traits in this species (Fjerdingstad et al. 2007, Pennekamp et al. 2014a, Pennekamp et al. 2019, Jacob et al. 2019a), with different observed dispersal syndromes implying movement abilities (velocity and linearity in movement), and cells dimensions (shape and size).

Use of social information occurs during movements in this species (Jacob et al. 2016b, Fronhofer et al. 2015a,b, Hauzy et al. 2007), with, in particular, the use of heterospecific or conspecific cues to orientate cells' movement through chemotaxis (Almagor et al. 1981, Hellung-Larsen et al. 1986, 1990, Leick et

Figure 12: Experimental system for the study of dispersal in *Tetrahymena thermophila*.
Experimental system for the study of dispersal in *Tetrahymena thermophila*. Dispersal systems were made of two Eppendorf tubes (here 5mL capacity, but we used smaller ones of 1.5mL capacity during this thesis experiments) and a corridor in flexible plastic (here 5cm long, but we used shorter ones, 2.5 cm long, during this thesis experiments). The cells were introduced in one of the two patches (*e.g.* left patch in the picture), dispersal initiation is retained by a clamp at the corridor beginning (green clamp in the picture). Cells are then let disperse by removing the clamp. To end dispersal movements two clamps are added at each extremity of the corridor (or one at the beginning of the corridor in a smaller system like the one we used during this thesis).

al. 1988, 1994). Social information appeared to be used locally (Fronhofer et al. 2015b, 2017a) and through immigrants (Jacob et al. 2015b) for dispersal decisions.

Microcosm experimental settings

Cells dispersal was studied experimentally using microcosm settings (*e.g.* Jacob et al. 2015b, 2016a, 2017, 2018, 2019a,b). To do so, different clonal strains (provided by Doerder et al., Doerder and Brunk 2012) were maintained in a pressurized laboratory, at a constant temperature of 23°C. These strains were weekly transplanted into new media to be maintained. Manipulation of strains was always performed in a sterile environment, under a laminar flow hood. Culture media is constituted of a mix of Difco proteose peptone (2%) and yeast extract (0.2%). The precise control we have on abiotic and biotic conditions allows us to investigate their role in dispersal dynamics, through controlled environmental treatments. Dispersal was studied in small microcosms (Figure 12), made from Eppendorf tubes (*i.e.* two patches), connected by a small plastic tube. Once inoculated in the departure patch the cells were let disperse in the system, dispersal movements were stopped by using clamps to close the corridor after a sufficient time (superior to three hours to be able to observe sufficient dispersal movements, Laurent et al. 2020, and inferior to the latency time for growth initiation after transplantation, Jacob et al. 2019b; dispersal timing between 4 to 6h are usually used: Jacob et al. 2015b, 2019b, Laurent et al. 2020). Cells density was then measured in departure and arrival patches using photos and videos of cells placed on Kima plates (Pennekamp and Schtickzelle 2013, Figure 11) and subsequently analyzed through the BEMOVI software (Pennekamp et al. 2014b, 2015), to obtain the initial concentration of cells in each patch and the cells traits (morphology: size, shape, and movement: linearity, velocity). Traits associated with dispersers and dispersal rate were then analyzed in function of performed treatments (previous section for examples).

Chapter 1

Multi-determinism and phenotype-dependence of dispersal in nature: insights from a 30-year long-term study

M. Brevet[1,2], S. Jacob[1], M. Massot[3], M. Richard[1], A. Rutschmann[1,4], M. Renoirt[5], D. Rozen-Rechels[3], J.F. Le Galliard[3], J. Clobert[1]

[1]Station d'Ecologie Théorique et Expérimentale (SETE), UAR 2029, CNRS, 09200, Moulis, FR

[2]Université Toulouse III Paul Sabatier, 31062, Toulouse, FR

[3]Institut d'Écologie et des Sciences de l'Environnement (IEES) de Paris Sorbonne Université, CNRS-UMR 7618, Paris, FR

[4]School of Biological Sciences, University of Auckland, Auckland, NZ

[5]Centre d'Etudes Biologiques de Chizé (CEBC), UMR7372, CNRS, 79360 Villiers-en-Bois, FR

En préparation pour une soumission dans la revue Ecology

Présentation et résumé du Chapitre

Dans ce premier chapitre, nous avons explorés comment étaient utilisées des informations sociales locales provenant de sources multiples (*i.e.* les congénères présents dans la zone natale d'un individu focal). Pour cela, nous avons considéré plusieurs composantes du contexte social simultanément (sex-ratio, structure d'âge, densité, condition corporelle des congénères), afin de valider des résultats précédemment mis à jour expérimentalement dans d'autres études, qui dans la plupart des cas testaient pour l'effet de paramètre seul. Cette première étude nous a permis de préciser l'importance du contexte social local pour la dispersion natale et plus particulièrement de comparer l'importance de cette utilisation de l'information sociale avec d'autres facteurs de dispersion (phénotype individuel, caractéristiques abiotiques de l'habitat, compétition entre apparentés) et de classer leur importance relative, ainsi que de tester la dépendance de cette utilisation au phénotype individuel. Nous nous attendions à ce que la dispersion natale soit multi-déterminée, en particulier avec plusieurs éléments du contexte social ayant un impact simultanés sur la dispersion. Nous nous attendions également à ce que l'information sociale soit utilisée en fonction des capacités de l'individu, avec une correspondance entre la compétitivité de l'individu et son utilisation de l'information sociale (par exemple, l'évitement d'un contexte compétitif comme les habitats denses pour les individus ayant de faibles capacités compétitives).

La dispersion dépend de différents facteurs, soit internes (dépendance au phénotype), soit externes (dépendance au contexte). Si les effets de ces facteurs ont souvent été étudiés individuellement, on sait peu de choses sur leurs interactions et leurs importances relatives lorsqu'ils sont considérés simultanément. Afin de déterminer quels sont les facteurs phénotypiques et environnementaux (facteurs maternels, contexte social et caractéristiques du substrat) de la dispersion, nous avons utilisé un suivi par marquage-recapture sur trente ans d'un site d'étude de lézards vivipares (*Zootoca vivipara*). Les captures et les naissances ont été suivies dans l'espace, permettant de définir le statut de dispersion natale des individus. Nous avons trouvé, en accord avec les études expérimentales et les attentes théoriques, que la dispersion dépendait du phénotype personnel (sexe, corpulence), du contexte social (sex ratio, densité, corpulence et âge des adultes) et des caractéristiques du substrat (couverture végétale et température) dans la zone natale. Le contexte social interagi avec le phénotype de l'individu focal pour façonner les réponses de dispersion dans la plupart des cas. Nous avons également constaté une importance relative élevée de ces variables significatives, notamment en comparaison des facteurs maternels et de certaines autres dimensions du contexte social (taille du corps de l'adulte, corpulence des nouveau-nés, proportion de subadultes). Nous avons particulièrement observé une importance majeure du sex-ratio des congénères pour la dispersion chez cette espèce.

Cette étude suggère que les mouvements de dispersion résultent de décisions basées sur une évaluation individuelle de l'environnement local à la fois physique et social. Elle souligne ainsi la nature multi-déterministe de la dispersion dans des conditions naturelles et l'importance de considérer les interactions entre le contexte social et le phénotype individuel pour bien comprendre les mouvements de dispersion.

Abstract

Dispersal has been found to depend on different factors, either internal (phenotype-dependence) or external (context-dependence). If the effects of such factors have been often studied one at a time, little is known about how they interact and what is their relative importance when considered concurrently. To investigate what are the phenotypic and environmental (maternal factors, social context, and substrate's characteristics) drivers of dispersal, we used a thirty-year mark-recapture monitoring of a common lizard (*Zootoca vivipara*) study site. Captures and birth were spatially monitored, allowing defining the natal dispersal status of individuals. We found, in agreement with experimental studies and theoretical expectations, that dispersal depended on personal phenotype (sex, corpulence), social context (sex ratio, density, adults' corpulence and age) and substrate's characteristics (vegetation cover and temperature) in the natal area. The social context interacted with the focal individual's phenotype to shape dispersal responses in most of the cases. We also found high relative importance of the previously described significant variables compared to maternal factors and some other social context dimensions (adult's body size, neonates' corpulence, proportion of subadults). We especially observed the major relative importance of the conspecifics' sex ratio for dispersal in this species.

This study suggests that dispersal movements result from decisions based on an individually-based assessment of both the physical and social local environment. It thus highlights the multi-deterministic nature of dispersal in natural conditions and the importance of considering the interactions between the social context and the individual phenotype to properly understand dispersal movements.

Keywords: Natal dispersal, Dispersal determinism, Social information, Phenotype-dependence, Context-dependence

Introduction

Dispersal can be defined as a movement of an individual from one location to another that can potentially affect gene flow (Ronce, 2007). It could be described in three phases: the departure, the transience, and the settlement of the individual (Ronce, 2007). The individual's phenotype (internal factors) and its environmental context (external factors) can both influence dispersal (Bowler and Benton 2005, *e.g.* Clobert et al. 2009, 2012). Two categories of external factors can be distinguished. First, factors related with avoidance of kin competition or inbreeding cued by the presence, physical condition, sex, or age of kin (*e.g.* Zedrosser et al. 2007). Second, environmental factors, being either abiotic, such as weather or physicochemical characteristics of the habitat (*e.g.* Legrand et al. 2015), or biotic. Biotic factors can then be further sub-categorized between heterospecifics and conspecifics factors (the social context). The heterospecific context can affect dispersal through the avoidance of predation, competition, or low resource availability based on cues such as densities of competitors, predators, or preys (*e.g.* Erm et al. 2019). The presence of conspecifics can affect intra-specific interactions, with dimensions known to potentially affect dispersal such as conspecific density, age, physical condition, sex ratio, or social status (*e.g.* Behr et al. 2020). Obtaining information about all these external factors might allow organisms to mitigate the costs of dispersal (Bonte et al. 2012), by reducing the uncertainty linked to dispersal decisions (Dall et al. 2005). The individual phenotype can also influence dispersal decisions (Bowler and Benton 2005, *e.g.* Clobert et al. 2009, 2012). Not all individuals have the same ability to compete, find resources, avoid predation, or endure environmental stress (depending on traits such as physical condition, sex, age, personality), which may explain differences between individuals in dispersal response to the local conditions (Kisdi et al. 2012).

Phenotypic and environmental factors have been shown to influence dispersal either through observational or experimental studies on a variety of species ranging from unicellular organisms (*e.g.*, Jacob et al. 2015b) to vertebrates (*e.g.*, Clobert et al. 2012). Most of these studies examined only one or a few factors at a time (with the notable exceptions of Legrand et al. 2015, Behr et al. 2020, and Suh et al. 2020). However, all these factors are known to concurrently influence dispersal (Dobson and Jones 1985, Matthysen et al. 2012), which raised the question of how they interact and what is their relative importance for dispersal decisions (Ronce 2001). Furthermore, the few studies examining several factors at the same time led to contrasting conclusions. Legrand et al. (2015) found the environmental factors to be more influential than internal factors, and abiotic environmental factors to be more influential than biotic ones (as theoretically predicted by Gandon and Michalakis 2001). Other studies highlighted the importance of inbreeding avoidance and competition for resources or mating (Behr et al. 2020, Long et al. 2008) or kin competition (Zedrosser et al. 2007). Matthysen (2012) reviewed the causes of dispersal and concluded that the main drivers of dispersal are habitat quality, population density, and kin interactions, followed by individual variation in dispersal decisions.
In addition, the individual phenotype has both theoretically (Kisdy et al. 2012 and Matthysen 2012) and experimentally (Bowler and Benton 2005, *e.g.* Baines et al. 2019) be demonstrated to influence the use of information on the local environmental context. Dispersal decisions can therefore be influenced by the interaction between the environmental context and the individual phenotype. Such interactions have been found with kin competition (Zedrosser et al. 2007, Cote et al. 2012), the social (Behr et al. 2020, Legrand et al. 2015, Cote et al. 2012), and abiotic environments (Legrand et al. 2015), but most of these findings were experimentally based. In fact, little is known about how common and important, relatively to other dispersal drivers, are these interactions in natural conditions.

Here we aimed at investigating the relative importance of dispersal factors and their interactions in natural conditions. To do so, we used data from a thirty-year mark and recapture monitoring on a common lizards (*Zootoca vivipara*, Jacquin 1787) study site, specifically designed for the study of natal dispersal in natural conditions (Methods for details). What we considered here could be viewed as realized dispersal, including both the dispersal of focal neonates and the neonates' mortality. Indeed, our study design did not allow us to access information about individuals who did not survive during their first year of life but made a dispersal decision. As a result, the observed effects on dispersal could correspond to effects on the actual dispersal decision and/or on the survival difference between individuals that dispersed or not during their first year of life. We specifically investigated whether the local conditions experienced by an individual and its phenotypic traits affect its dispersal decisions, meaning focusing on the emigration phase. To do so, we quantified multiple components of the individual phenotype, the social environment (including maternal factors) and the substrate's characteristics in the natal area, potential drivers of dispersal that were chosen according to the existing literature about the phenotype- and context-dependence of dispersal in this species (Clobert et al. 2012, Cote et al. 2012, effects that were showed mostly experimentally). Furthermore, we aimed at quantifying their relative importance as well as how some of them interacted. We specifically focused here on the interactions between the social context and the individual's phenotype, to better comprehend how widespread is the phenotype-dependent use of social information.

Based on earlier experiments and theoretical works, we expected the different factors (individual's phenotype, maternal factors, social context, and substrate's characteristics) to affect dispersal in natural conditions. We predicted that dispersal should depend on these multiple environmental factors concurrently (Clobert et al. 2012). The social context effects should also depend on the individual phenotype (Kisdi et al. 2012, *e.g.* Cote and Clobert 2007a). By ranking factors by their relative influence on dispersal, we also aimed to see which factors are the most important. As theorized in Gandon et al. (2001) and experimentally observed in Legrand et al. (2015), we could expect the abiotic environment (*i.e.* substrate's characteristics here) to be more influential than biotic ones. According to Matthysen (2012), we could also expect a higher effect of kin competition and density of conspecifics, followed by individual phenotype.

Materials & Methods

Model species and study site

The common lizard (*Zootoca vivipara*, Jacquin 1787) is a small ovoviviparous Lacertidae feeding on small invertebrates in wetlands. The study site is located in the Massif Central (France) mountain range (44°30'N, 3°45'E, 1420m height, Mont-Lozère in the Cévennes National Park). This site is covered by diverse substrates (forest, grass, heather, bilberry, rock, Figure S1 for details). Substrates coverage was obtained from previous studies (Rozen-Rechels et al. 2020, improved by A. Rutschmann). In this study site, mating occurred between March and April and parturition occurred from mid-July to mid-August (Massot et al. 1992). The juveniles emerge in the first few hours after hatching. The dispersal process is mostly completed within the 10 first day after birth (Massot 1992a, b).

Field monitoring

The site has been monitored for thirty years from 1989 to 2019. Each summer, capture sessions were performed, mainly in June. During these sessions, all gestating females were brought to a rearing facility close to the capture site. Additional capture sessions had been performed in July and September or in April and May between 1989 and 2011. Sampling effort was maintained over the years despite some variability resulting from logistical complexities or bad sampling weather conditions. This resulted in 35% ± 16 SD of individuals recaptured a second time during the same year (without taking into account gestating mothers).

During the monitoring period, a total of 1,397 gestating females were captured (62 gestating females captured each year ± 19 SD), these females gave birth to 8,960 neonates. An additional amount of 5,389 individuals (of all ages and sex) which were not born in the rearing facility were captured during the monitoring. All individuals were marked using a toe-clipping method that did not impact their survival, probability of recapture (Massot et al. 1992), or locomotor performance (Chamaillé-Jammes et al. 2006). All capture locations were recorded using Thales GPS ProMark3, with a horizontal precision of one meter for dynamic measures (see reference manual).

All individuals were immediately measured at capture. We measured their snout-to-vent length (SVL) using a ruler (millimeter precision), their body mass (BM) using a spring balance (precision to the half decigrams). Captured individuals were also sexed and aged (one year old, referred to as subadults further on, or more than one year old, referred to as adults further on). Only two experimenters performed these measures, as well as the measures performed in the rearing facilities, during the whole thirty years. They calibrated their measures by both measuring all individuals during a whole year.

Rearing condition

Pregnant females were kept in the rearing facilities until parturition. They were maintained individually in plastic terrariums (of dimension: 18.5 x 12 x 11 cm). Each terrarium contained a shelter made from two slots of a cardboard egg-box and a 2 cm substrate of sterilized soil (Massot and Clobert 2000). Terrariums were placed under an incandescent bulb of 25W providing light and heat for 6 hours a day to allow basking (from 9 a.m. to 12 p.m. and from 2 p.m. to 5 p.m.). Terrariums were moistened three times a day with a water spray and females were fed at least once a week.

Right after parturition, neonates from the same litter were isolated in a small plastic terrarium covered with two layers of paper towels, and the mother was immediately weighed using a precision scale (milligram precision). This weight was used for the subsequent analyses as it did not correlate with the corpulence of the neonates contrary to the measurements performed in the field before parturition (respectively, p=0.82 and p=0.002). The neonates were measured the day after their birth. We measured their SVL (millimeter precision), their BM (milligram precision) and we sexed them using the Lecomte et al. (1992) method. All individuals (neonates and mothers) were released at the mother's capture location (referred to as the natal location further on) two to four days after the parturition.

Dispersal distance and home range

We studied the natal dispersal of all individuals born in the rearing facility and recaptured as subadults or adults (1,562 individuals). We computed the distance between their natal location and the barycenter of their recapture location as subadult or adult. Following previous work on this species, we considered that natal dispersal occurred when this distance was superior to thirty meters (Clobert et al. 1994, Massot and Clobert 1995, Massot and Clobert 2000, Massot et al. 2002, Cote and Clobert 2007a). The diameter of an individual's home range was indeed previously estimated to be about thirty meters (Massot and Clobert, 2000, Lecomte et al. 1994, Massot 1992a). Beyond this threshold, there was no return of dispersers in their original area (Massot and Clobert 1995, Clobert et al. 1994). We nevertheless quantified home-range size in this study by computing home ranges using a kernel method ("adehabitatHR" R package, Calenge et al. 2006). We applied this method on all adults' or subadults' capture locations pooled, after scaling coordinates per individual (and thus making all individuals sharing the same home range barycenter). As expected, we found that the mean home range size estimate was similar to estimations (Figure S2): 30m diameter for an 85% kernel. We therefore kept a 15m radius home range for the definition of dispersers and residents to be consistent with previous studies. The natal area was considered as the size of a home range centered on the neonate natal location. It should correspond to the perceptual range of a neonate as most of the conspecifics it could encounter should be included in such an area (Lecomte et al. 1994).

Factors influencing dispersal

Retained variables

We chose the analyzed variables according to prior experimental or theoretical studies on the dispersal drivers in this species. We retained the individual's sex and corpulence at birth (Léna et al. 1998a, Cote and Clobert 2007a, Cote and Clobert 2010, Le Galliard et al. 2003a, Le Galliard et al. 2005c) for testing the phenotype-dependence of dispersal; the body size and the corpulence of its mother for investigating the effect of maternal factors on dispersal (Meylan et al. 2002, 2004); the substrate's nature (vegetation coverage, temperature, and humidity: Massot et al. 2002, Massot et al. 2008, Zajitschek et al. 2012, Boudjemadi et al. 1999, Lecomte et al. 2004), the density (Meylan et al. 2007, Le Galliard et al. 2003a, Léna et al. 1998a, Cote and Clobert 2007a, b, Cote et al. 2008a), sex-ratio (Le Galliard et al. 2005b, Léna et al. 1998a), average age (individuals are predicted to favor philopatry when being in aging local patches, Ronce et al. 2000), body size and corpulence (Cote and Clobert 2007a, Léna et al. 1998a) of conspecifics in the natal area for testing the context-dependence of dispersal. We distinguished body condition and sex-ratios for each age class (neonates or adults) as competition between age classes is expected to differ (Polis 1984, Ebenman 1987), as it was previously experimentally demonstrated

(Massot et al. 1992). We did not consider the subadult age class as the asymmetry of competition has been mostly described between juveniles and adults in our species (Lecomte et al. 1994, San-jose et al. 2016). Maternal factors (maternal body size and corpulence) could reflect both kin competition and information about habitat quality (Meylan et al. 2002, 2004), we cannot distinguish between these two here. We considered these latter metrics with a quadratic component because the intensity of kin competition is decreasing when the mother is senescent (Ronce et al. 1998).

Some other significant variables were not used here because they were not collected during the long-term monitoring or presented a too important amount of missing data such as for heterospecific factors like food availability, Massot and Clobert 1995, predation risk, Bestion et al. 2014, and parasite load, Sorci et al. 1994; other maternal factors as mother's stress, Meylan et al. 2002, 2004 and Vercken et al. 2007a, mother's age, Ronce et al. 1998, and litter sex ratio, Massot and Clobert 2000 and Vercken et al. 2007a; reproductive strategies in the surroundings, Vercken et al. 2012; or focal individual's personality traits, Cote et al. 2012.

All observations for which we had missing data for at least one of our variables were removed (N=117).

Social context metrics

For each juvenile, we computed precise estimates of the social context in its natal area the year of its birth. We considered that an adult, subadult, or another neonate was present in the home range when it was captured at least one time or released in this area during the year of interest. To ensure that they were likely to be present when the focal individual was released, the presence of conspecific neonates in the natal area was only considered if they were born at most 10 days after the focal neonate (*i.e.*, before the dispersal decision of the focal neonate was taken, Massot 1992 a,b, Léna et al. 1998a) and at least 10 days before birth for conspecific neonates that emigrated (*i.e.*, before these neonates dispersed from the focal natal area). Immigrant neonates (born in another patch and arrived in the focal natal area before the focal individual dispersed) were not considered because we could not know precisely when they arrived in the focal natal area.

We computed the overall density of conspecifics in each natal area by counting the number of conspecifics present the year the focal individual was born. We then described the natal area age structure as the proportion of subadults in the area compared to overall density, and the average age for adults only. We also measured the adult and neonate sex ratios in the natal area (number of males divided by the number of individuals for which we knew the sex). Finally, averaged adult physical condition in the natal area was defined as average SVL and average corpulence (computed as the residuals of the regression between SVL and BM, Figure S3). For average neonate physical condition in the natal area, we only used corpulence, since neonate SVL show very low variability compared to the precision of the measure when taken just after birth (21.6 mm ± 1.4 SD). When computing the neonates' sex ratio and corpulence in the natal area, we excluded siblings of the focal individual because siblings' physical condition was highly correlated (corpulence: Pearson correlation: 0.78; $p<0.001$).

Substrate's characteristics

To estimate the non-social environment around the focal neonates, we used the previously produced map of the substrates in the studied site (Figure S1) and temperature measurement led in parallel on the different substrate types. These measures on the cover and temperature of substrates were performed between 2016 and 2018 (Rozen-Rechels et al. 2020). As the site landscape only vary slightly during the monitored thirty years (Clobert pers. obs.), we assumed these estimates to be representative of the area's spatial structure over the whole monitoring period. Substrates were classified into four categories: forest cover, grasslands, bush or assimilated (heather and bilberry), naked surfaces (including rocks, dead trees). The proportion of these substrate categories in the natal area, as well as the mean and standard deviation of substrate temperature (computed with the same method as in Rozen-Rechels et al. 2020), were combined using a principal component analysis (using the "FactoMineR" R package, Lê et al. 2008; Figure S4). The first axis explained 67.1% of the variance and was used for the subsequent analyses as the variable describing the substrates' characteristics. When PC1 scores increased, it meant an increase in the mean and standard deviation of temperature, a decrease in forest cover, and an increase in grasslands and bush covers.

Data analyses

Analysis of dispersal responses

All statistical analyses were performed with R software (R Development Core Team, 2020, version 3.6.3). Graphs were produced using the package "ggplot2" (Wickham 2016).

We implemented a mixed logistic regression (using "lme4" package, Bates et al. 2015, with a logit link function) to test if dispersal depended on environmental context (social context and substrate's characteristics, as defined previously), maternal factors (mother's physical condition, *i.e.* SVL and corpulence, including their quadratic component) and focal individual's phenotype (individual's sex and corpulence). All variables were scaled before implementing the logistic regression. We also included all interactions between personal condition and the social context. We used a bound optimization by quadratic approximation for the optimizer function of the regression to avoid convergence issues (Powell 2009).

A year random effect was also implemented to take into account possible annual variation in uncontrolled variables (such as weather or prey availability) and to take into account the variation in sampling efforts. This random effect was tested before implementing the regression and appeared to be significant (analysis of deviance test between null models with and without random effects; $p < 0.001$) and was therefore kept in our model. The 2010 field session (N=12) was removed from our analyses since an error occurred for the release of neonates during this year: newborns were mistakenly released in the wrong locations. Finally, we removed all field sessions with insufficient data (N<11 in one year, occurred in 1990, 2011, 2018). The final sample size was 840 individuals (33.6 individuals per year ±

11.9 SD).

We checked for multi-collinearity using the variance inflation factor ("car" R package, Fox and Weisberg 2018): the obtained value was sufficiently low to avoid multicollinearity bias (1.78). Estimation of the model's coefficient of determination (Nagakawa and Schielzeth, 2013) was also used to measure the model fit. The model was diagnosed using an analysis of deviance for testing the effects of the variables (likelihood-ratio tests, "car" R package, Fox and Weisberg 2018). The stability and robustness of our model were tested through bootstrap resampling (Royston and Saurbrei 2009) with 1000 iterations (using "boot" R package, see Canty and Ripley 2020). The bootstrap was used on p-values statistics (Figure S8) and variables effects size (Figure S9).

Treatment of potential statistical biases

Siblings shared the same natal environment and maternal condition, and have very close phenotypes and dispersal responses (Massot et al. 1994). Therefore, to avoid pseudo-replication, we only used one juvenile per clutch. Thus, in the clutches where several individuals were retained for analyses (391 among the overall 988 clutches), we retained randomly one individual within the clutch. To check for sensitivity to this random selection process, we performed a 1,000 times resampling of randomly selected individuals over all of these clutches. We then use different statistical metrics distribution (p-values and effect sizes) to compare them with the original model and test for the stability of our effects to the difference in dispersal responses among siblings (Figures S10 and S11).

Ranking of dispersal factors

We ranked the retained variables by computing the odds ratio of each fixed term (exponential of each regression coefficient). We convert this metric in Cohen's d (Cohen 1988) by using the "effectsize" R package (Ben-Shachar et al. 2020), to be able to measure the magnitude of our effects size. We also performed a coefficient of determination (referred to as r-squared subsequently) partitioning using the Nagakawa and Schielzeth method (2013, "partR2" R package, Stoffel et al. 2021), to estimate all parameter relative importance, including interactions.

Results

Among all retained 840 individuals, for which we were able to define the dispersal status, 35.1% (*i.e.*, 295) dispersed during their first year of life. Our model, exploring the phenotype and environmental correlates of dispersal, has marginal (fixed effects only) and conditional (including the random effect) r-squared of respectively 0.106 and 0.176. Overall, we found that dispersal in this species depended on the substrate's characteristics and the social context in the natal area, often in interaction with individual phenotype for the latter.

Phenotype- and context-dependence

We found the dispersal probability to be dependent on the environmental context (Table 1) with significant effects of the substrate's characteristics and several social context elements (adults' and neonates' sex ratios, adults' age, and adults' sex ratio in the natal area), often in interaction with the focal individual's phenotype. The dispersal probability decreased when open landscape proportion, the mean and the standard deviation of the substrates' temperature increased (Figure 1-B). Dispersal probability decreased when the adults' age in the focal neonate's natal area increased (Figure S6-B) but only for focal individuals with low corpulence; the converse was observed for focal individuals with a high corpulence (Figure 1-C,D). The dispersal probability increased when the proportion of male adults and neonates in the natal area decreased (*i.e.* when their respective sex ratios decreased, Figure 1-A,F). The latter relationship between the neonates' sex ratio in the natal area and the dispersal probability was only observed when the focal neonates had a sufficiently high corpulence (Figure 1-F). We also found that the dispersal probability increased with adults' corpulence in the natal area for female focal neonates, while the inverse relationship was observed for male focal neonates (Figure 1-E).

Our bootstrap resampling revealed that the previously described effects are stable as all their p-values were included in the 95% percentile intervals obtained from the bootstrap resampling and the median of the p-values obtained after the resampling remained significant or marginally significant (Figure S8). When considering the sensitivity of our analysis to differences observed in dispersal responses within a litter (Figure S10), we found that the above results were also rather stable relatively to which neonate was selected within the same clutch. Indeed, all p-values were included in the 95% percentile intervals obtained from the resampling and most of the median of the p-values obtained after the resampling remained significant or marginally significant. Yet, the interactive effect of the adults' age and the focal neonates' corpulence was poorly reliable (the median of the resampled p-values did not remain significant).

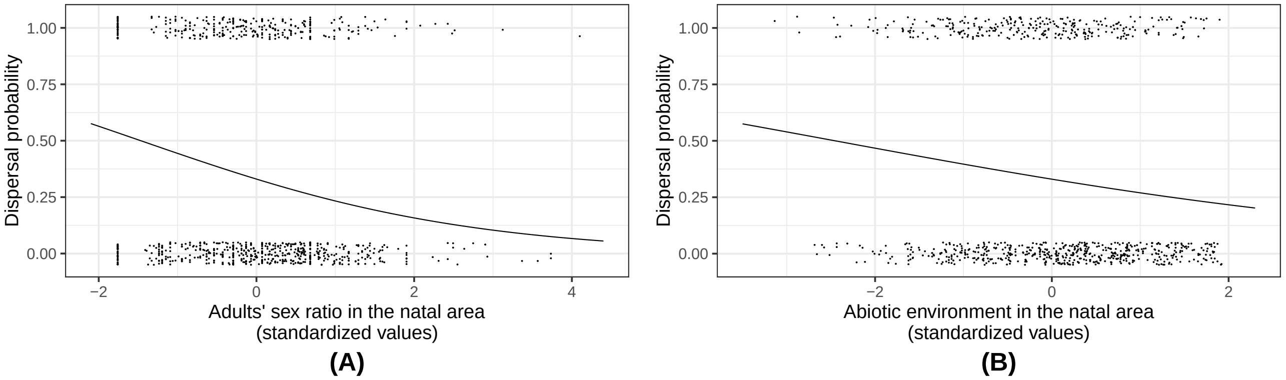
Variables ranking

The variable importance ranked in the following order (Figure 2): the largest effect size was attributed to the adults' sex ratio in the natal area (Cohen's d > 0.2), followed by the focal individuals' sex, the neonates' sex ratio, the substrate's characteristics, the density and the adults' corpulence in the natal area (0.2 > Cohen's d > 0.1), and by adults' size and age, neonates' corpulence in the natal area, focal individuals' corpulence and the body size of the focal mother (0.1 > Cohen's d > 0.05). All others variables' effect sizes were negligible. When considering the partial coefficients of determination for each variable (Table 1), we observed approximately the same ranking among fixed effects, except for the adults' age in the natal area with a relatively high proportion of variance explained (percentage of contribution to the r-squared of 12.7%, versus 15.3% for the adults' sex ratio) and for the adults' corpulence in the natal area with a negligible contribution to the explained variance (<1%). For interactions,

	Parameter	Coefficient	SE	df	χ^2	P-value	Partitioning of R-squared (%)
Individual's phenotype	**Sex (baseline level: female)**	**0.334**	**0.179**	**1**	**3.671**	**0.055•**	**8.6**
	Corpulence	0.121	0.124	1	0.025	0.875	0.2
	Corpulence x Sex	-0.321	0.190	1	2.376	0.123	4.7
Mother's phenotype	Mother's SVL	0.107	0.104	1	1.062	0.303	1.3
	Mother's SVL (squared)	-0.078	0.067	1	1.402	0.236	2.5
	Mother's corpulence	0.004	0.113	1	0.001	0.97	<0.1
	Mother's corpulence (squared)	0.005	0.056	1	0.007	0.932	0.8
Social context	Density	-0.194	0.140	1	2.005	0.157	4.2
	Adults sex-ratio	**-0.483**	**0.155**	**1**	**8.495**	**0.004****	**15.3**
	Neonates sex-ratio	**-0.299**	**0.124**	**1**	**3.169**	**0.075•**	**7.5**
	Adults' corpulence	0.185	0.146	1	0.001	0.978	<0.1
	Neonates' corpulence	0.148	0.137	1	0.507	0.476	1.2
	Adults' SVL	-0.154	0.166	1	0.416	0.519	0.5
	Adults' age	**-0.144**	**0.122**	**1**	**4.666**	**0.031***	**12.7**
	Proportion of subadults	-0.017	0.133	1	0.045	0.832	0.9
Abiotic environment	**Substrate features**	**-0.289**	**0.104**	**1**	**7.681**	**0.006****	**6.3**
Phenotype by social context interactions	Density x Sex	0.072	0.183	1	0.156	0.693	<0.1
	Density x Corpulence	**-0.138**	**0.125**	**1**	**2.766**	**0.096•**	**<0.1**
	Density x Corpulence x Sex	-0.045	0.188	1	0.057	0.812	0.2
	Adults sex-ratio x Sex	0.286	0.204	1	1.890	0.169	2.6
	Adults sex-ratio x Corpulence	0.099	0.142	1	0.316	0.574	<0.1
	Adults sex-ratio x Corpulence x Sex	-0.089	0.213	1	0.175	0.675	0.5
	Neonates sex-ratio x Sex	0.221	0.189	1	1.574	0.210	1.4
	Neonates sex-ratio x Corpulence	**-0.172**	**0.104**	**1**	**5.322**	**0.021***	**<0.1**
	Neonates sex-ratio x Corpulence x Sex	-0.100	0.186	1	0.291	0.589	0.3
	Adults' corpulence x Sex	**-0.427**	**0.181**	**1**	**5.850**	**0.016***	**5.6**
	Adults' corpulence x Corpulence	0.134	0.119	1	0.009	0.925	<0.1
	Adults' corpulence x Corpulence x Sex	**-0.328**	**0.190**	**1**	**2.979**	**0.084•**	**6**
	Neonates' corpulence x Sex	-0.201	0.192	1	1.096	0.295	1.6
	Neonates' corpulence x Corpulence	-0.0002	0.109	1	0.016	0.898	<0.1
	Neonates' corpulence x Corpulence x Sex	0.037	0.187	1	0.038	0.845	<0.1
	Adults' SVL x Sex	0.126	0.198	1	0.445	0.505	0.4
	Adults' SVL x Corpulence	-0.055	0.140	1	0.055	0.815	<0.1
	Adults' SVL x Corpulence x Sex	0.065	0.200	1	0.104	0.747	0.3
	Adults' age x Sex	-0.114	0.179	1	0.401	0.526	0.4
	Adults' age x Corpulence	**0.219**	**0.127**	**1**	**3.982**	**0.046***	**<0.1**
	Adults' age x Corpulence x Sex	-0.063	0.191	1	0.110	0.740	0.2
	Proportion of subadults x Sex	-0.057	0.186	1	0.087	0.768	0.1
	Proportion of subadults x Corpulence	-0.070	0.117	1	0.285	0.594	<0.1
	Proportion of subadults x Corpulence x Sex	0.057	0.199	1	0.081	0.776	0.3

Table 1.1: Logistic regression on natal dispersal decision.
Results of the logistic regression on natal dispersal decision along with environmental context, individuals' phenotype, and the phenotype of their mother. We displayed here the regression coefficients and their standard errors (SE). The results were then analyzed through an analysis of deviance, for which we displayed here the chi-square statistics and their associated p-values. All significant ($p<0.05$) or marginally significant ($0.05<p<0.1$) variables are in bold font. We also displayed the partitioning of the coefficient of determination (r-squared, using "partR2" package), with the percentage of contribution to the r-squared for each variable (semi-partial r-squared divided by the model r-squared). This partitioning was computed with main effect priority (Stoffel et al. 2021 for details). • : $0.05<p<0.1$, * : $0.01<p<0.05$, ** : $0.001<p<0.01$, *** : $p<0.001$

Environnmental context



Environnmental context x Focal individuals' phenotype

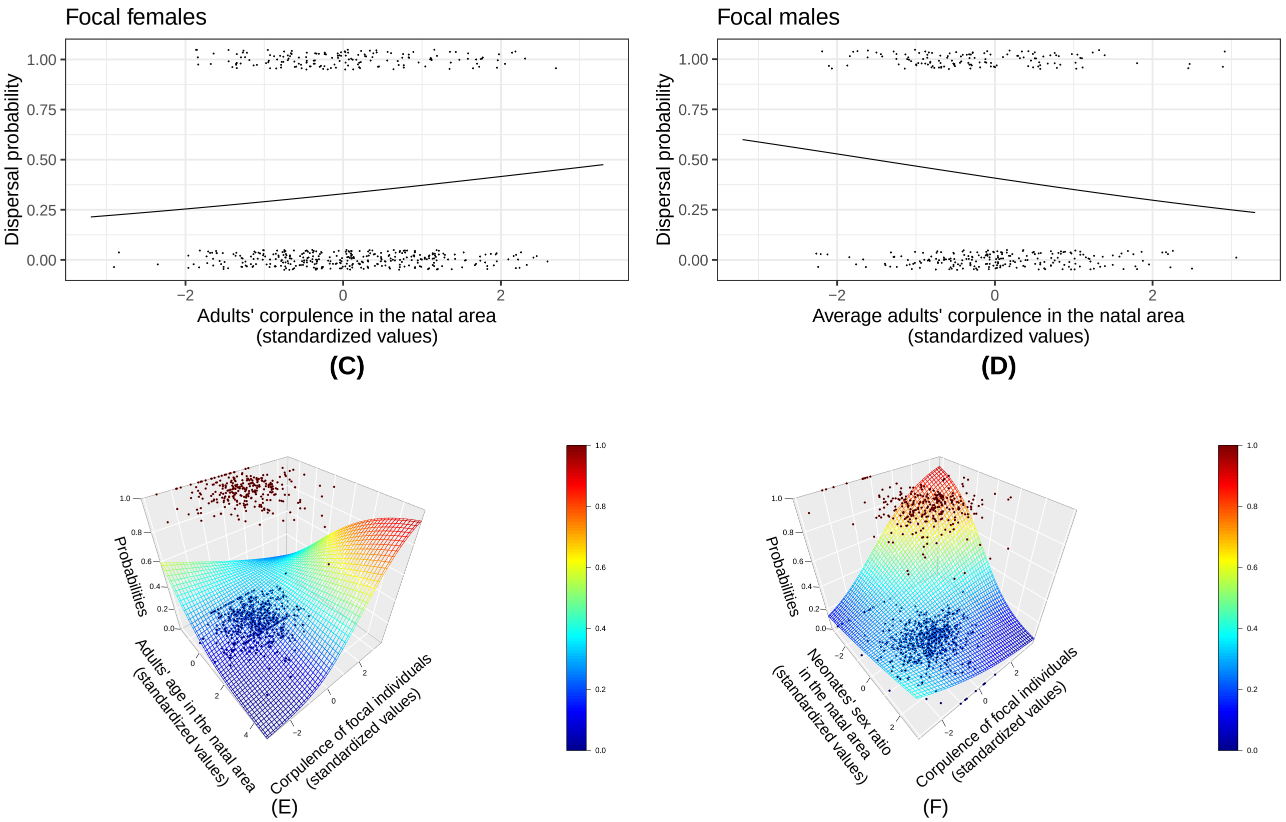


Figure 1.1: Significant correlates with the natal dispersal response in the studied site of common lizards.
We looked at the distribution of focal individuals' dispersal predicted probability as a function of the significant determiners (focal individuals' phenotype, environmental context in the natal area, and their interactions). We only displayed the highest degrees effects (graphs of lower degrees significant effects are displayed in Supplementary materials). Plots were obtained from the logistic regression results (Table 1) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). Effects degree of significance is displayed in Table 1. Black dots display observations from all retained neonates: a dot around the 0% probability line corresponds to an individual which did not disperse, a dot around the 100% probability line corresponds to an individual which dispersed. These dots were jittered (vertically for quantitative variables, horizontally and vertically for qualitative variables) to gain in readability.

we only found relatively high importance of the interactions between the adults' corpulence in the natal area and the focal individuals' traits (sex and corpulence) and the interaction between the sex and corpulence of the focal individual (percentage of contribution to the r-squared between 4,7 to 6%), all others interaction explained a low proportion of variance (contribution to the r-squared <2.6%).

Effect sizes from the bootstrap kept approximately the overall same relative order compared to the original model, the same was observed for effect sizes obtained from the sensitivity analysis (figure S9 and S11).

We found no relationship between the variables' absolute values of effects size and their temporal (F-value=0.0003, p=0.99) or spatial autocorrelation (F-value=0.361, p=0.58, Supplementary materials for details).

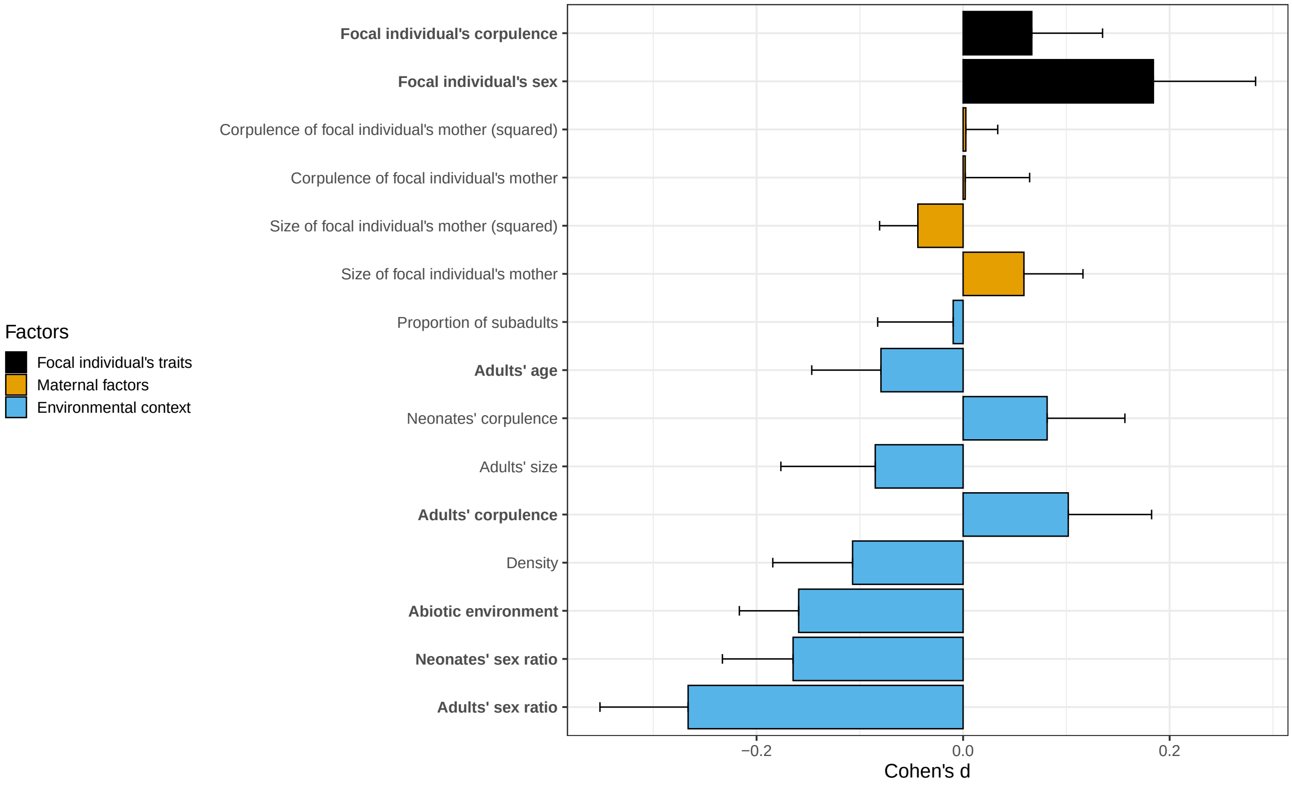


Figure 1.2: Effect size estimates for retained dispersal factors.
The Y-axis displays the fixed terms used in the logistic regression (Table 1). Variables in bold on the Y-axis have significant effects or are involved in significant interactions (Table 1). The method used to calculate effect sizes (Cohen's d) is described in Mat&Met. Error bars were obtained from the standard deviation of each regression coefficient, to which we applied the same transformation as above for estimating effect sizes.

Discussion

By considering multiple potential dispersal drivers at the same time in nature, we tested the extent to which dispersal was multi-determined and what was the relative importance of these different factors. We also specifically examined whether the use of information about social context depended on individual phenotype. We found realized dispersal, including both dispersal decisions and mortality differential between dispersers and non-dispersers, to be both phenotype- and context-dependent (with dependence on both social and non-social context), confirming previous experimental findings and coining for the importance of multi-determinism for dispersal. Individual sex and environmental context, including conspecifics' sex ratios, adults' corpulence and age, density, and substrate's characteristics in the natal area, revealed to be the most important correlates of dispersal in this system. Finally, most of the effects of social context depended on the individual's phenotype, highlighting the importance of considering the receiver phenotype for social information use.

Multi-determinism of dispersal

As we originally hypothesized (Clobert et al. 2012 in the common lizard, but also Suh et al. 2020 , Morales-Gonzales et al. 2021 in other species), dispersal in natural conditions is multi-determined. We observed concurrent dependence on the individual's phenotype and many components of the local context. We particularly confirmed many experimentally demonstrated findings on the dispersal determinism (Léna et al. 1998a and Le Galliard et al. 2005b on avoidance of adults' females, Boudjemadi et al. 1999, Lecomte et al. 2004 on avoidance of forest cover, Meylan et al. 2007, Le Galliard et al. 2003a on density negative dependence of dispersal; see subsequent sections for interpretations and details), while including in our present study the mortality differential in the first year of life following dispersal decision (by staying in the natal area versus during dispersal or at and after settlement). This absence of difference while including mortality was somehow expected here since survival rates were not influenced by the dispersal status in a long-term experiment (Le Galliard et al. 2005a). This is also likely that mortality differential reflects dispersal decisions here in case of adaptive decisions, with high relative mortality of individuals making irrelevant decisions (by staying in a natal area with poor environmental conditions or leaving a natal area with good conditions) compared to the other individuals. Some new factors have also been found to correlate with natal dispersal (age structure and physical condition of adults in the natal area), which were theoretically expected (Ronce et al. 1998, Léna et al. 1998a). The use of contextual information in our study could be interpreted in terms of avoidance of competition (*e.g.* avoidance of too high females proportion) or of too low habitat quality (*e.g.* avoidance of covered and cold substrates). The use of multiple cues could then allow an individual to get precise information on its environment, these cues being potentially complementary (different aspects of competition, resource availability, abiotic habitat quality, Clobert et al. 2009, 2012), or could confirm one another (*e.g.* Czaczkes et al. 2011, Damas-Moreira et al. 2018, Endriss et al. 2018), a process that may be central in our species considering the limited time prior the dispersal decision (Massot 1992a, b).

Yet, not all included factors correlated with dispersal. Surprisingly, we found no dependence on maternal physical condition (contrary to what was observed in Meylan et al. 2002, 2004, Léna et al. 1998a). The importance of such maternal effects could be minor compared to the others presented here or not very well described in this analysis. It is probable that we missed important markers of kin competition here (such as mother's age, Ronce et al. 1998, or maternal stress, Meylan et al. 2002, 2004), and interactions between them. For example, female conditions and stress interact to shape the response to kin competition (Meylan et al. 2002, 2004), but such a fine description was not available here.

More broadly, the relatively low r-squared obtained for our model advocate for the intervention of other factors shaping dispersal decisions, such as heterospecific or particular abiotic factors like prenatal or post-natal temperature and humidity (Clobert et al. 2012), the focal individuals' personality traits (Clobert et al. 2009, Cote et al. 2012), or females' reproductive strategies in the natal area (Vercken et al. 2012). We also probably missed interaction effects between the considered local context variables, as the interaction effect experimentally observed between the density and the adults' sex ratio (Léna et al. 1998a), or the influence of the immigrants-based information (Cote and Clobert 2007a). Finally, we also lack information on the potential heritability of the dispersal behavior (*e.g.* Greenwood et al. 1979) and the importance of randomness in such a response.

Ranking of dispersal factors

We found the focal individual's sex and the environmental context to be of major importance in the dispersal process of this species. The effect size of adults' sex ratio was particularly high, with a greater order of magnitude than the other ones (Cohen 1988, Gignac and Szodorai 2016, for interpretations on effects size magnitude) and a contribution to the r-squared largely superior to the others. We also found that the neonates' sex ratio, the adults' age, the density, the substrate's characteristics, and the adults' corpulence in the natal area were all having high relative importance (Table 1 and Figure 2), especially when in interaction with the focal individual's phenotype for the latter one (Table 1).

The above hierarchy of variables was somehow surprising compared to what was found in previous theoretical and empirical studies (Legrand et al. 2015, Behr et al. 2020, Matthysen 2012, Gandon and Michalakis 2001). However, these differences in the factors' ranking were somehow expected since different species are most likely to not present the same sensitivity to their external environment. Indeed, the ranking of factors across species might depend on the species' cognitive abilities (determining its ability to process the information on their close environment, Nathan et al. 2008, Riotte-Lambert and Matthiopoulos 2019), its biology (*e.g.* sensitivity to environmental change, the importance of the intraspecific competition in the species, social structures or the species position in the food web, Ronce et al. 2001) or its environmental context (*e.g.* quantity of resources, predators or competitors; temporal and spatial predictability of their environment, Duputié and Massol 2013, Riotte-Lambert and Matthiopoulos 2019).

The common lizard is inhabiting wetlands within which the habitat characteristics might be less variable (although some significant variation in substrate characteristics is quite important for dispersal, Massot et al. 2002), resulting in potentially less important use of information about abiotic habitat characteristics. In this case, the social context could have a more important role in determining an individual's fitness due to a greater influence of intraspecific competition (as theorized by Lee et al. 2016). The common lizard is also likely to have good cognitive abilities (Wilkinson and Huber 2012) and so perhaps have a higher ability to collect information on its surrounding environmental context via social cues (Varela et al. 2019), compared to other studied species (as butterflies in Legrand et al. 2015). There is also the possibility that we missed here important dispersal determinants as information on heterospecific factors such as predation and parasitism (Bestion et al. 2014, Sorci et al. 1994) or kin competition factors such as mother's age, stress, or siblings sex ratio (Clobert et al. 2012).

We did not observe any relationship between effect sizes and the predictability of environmental factors (either spatial or temporal, Supplementary materials). Spatial or temporal autocorrelation of some characteristics of the environment might determine the use of information: it should be valuable if informing on sufficiently predictable dimensions, to be useful for decisions with imprecise spatial location and/or long-term consequences (Doligez et al. 2003, Heinen and Stephens 2016), but also sufficiently unpredictable to be of interest with respect to personal information (Deygout et al. 2010, Riotte-Lambert and Matthiopoulous 2020). For these reasons, this absence of either spatial or temporal autocorrelation effects on the use of information is quite surprising, especially considering the deleterious effects of environmental unpredictability on the survival and growth rate of individuals in this species (Masò et al. 2019, 2020), that could have been hindered by appropriate use of information about the most unpredictable environmental dimensions (less important use of outdated information, Kendal et al. 2009). It could therefore underline the importance of the local habitat characteristic during the early step of life, the dispersal decision being made in function of these immediate local conditions.

Local context-dependence of dispersal

As expected (Bowler and Benton, 2005, Clobert et al. 2012), dispersal initiation depended on various elements of the environmental context in the natal area (both social and non-social). We found a strong dependence on the substrate's characteristics in the natal area, with a decreased dispersal probability in open and warm environments covered by grass or grass-like substrate. Such environments could represent an advantage in terms of thermoregulation and perhaps prey availability (Lecomte et al. 1993). Better survival and growth rate were indeed found in warmer dry environments (Lorenzon et al. 2001). Poor habitat (with shorter grass on the soil, as found in the woody parts of our study site) could also impact the individuals' stress level (Josserand et al. 2017), by possibly impacting resources accessibility or thermoregulation possibilities. This result is consistent with previous experimental findings (Lecomte et al. 2004 and Boudjemadi et al. 1999 for the importance of substrate features, Massot et al. 2002 for the importance of substrate temperatures).

Local social factors seemed to be of primary importance for natal dispersal in this species. We observed correlations of several local social factors (like the sex ratio, age structure, density, and the average conspecifics' body condition in the natal area) with the dispersal probability.

Neonate dispersal was negatively correlated with the proportion of males in the natal area (partially consistent with Le Galliard et al. 2005b, in which the relationship was found only for the emigration of adult females). Males often display aggressive behavior and were found to outcompete females (Lecomte et al. 1994, Pilorge et al. 1987) and to impact their survival (Le Galliard et al. 2005b, 2008). We should therefore have observed an opposite trend if competition with males was the driver of neonate dispersal. We hypothesized that adult males do not enter directly in competition with neonates such that the presence of males potentially constitutes a cue for better environmental quality further reinforced by their short life expectancy (males have a lower survival rate than females, Le Galliard et al. 2010). Alternatively, these results could be interpreted as an avoidance of adults females because they were found experimentally to be in direct competition with juveniles for foraging sites contrarily to males (Lecomte et al. 1994). Such an adult sex-dependent trend in neonates' dispersal had been observed experimentally in Léna et al. (1998a). At last, we know that male-biased populations could display an overall lower level of sexual competition (Dreiss et al. 2010), potentially also explaining such influence on natal dispersal. A similar result has also been found for the neonates' sex ratio in the natal area but only in the case of corpulent neonates. The relationship is less intense (Figure 1-F), and, as above, can either reflect the avoidance of a future high proportion of females or more simply a higher competitive ability of neonate females.

An increase in the average adult age in the natal area was associated with a reduction in natal dispersal (Figure S6-B). The extent to which this reflects kin competition (Ronce et al 2000) or the expectation of a decrease in competition with adults (because of aging, Massot et al. 2011) is unknown. This trend was however reversed in the case of neonates in high body condition (Figure 1-E). Individuals in good physical condition may avoid competition with these older adults that are potentially high competitors since they probably have better access to reproduction (Dreiss et al. 2010, Massot et al. 2011) and more competitive offspring (Massot et al. 2011). Yet, this interaction effect was more sensitive to the resampling among siblings (Figure S10) than the other significant effects and should be considered with caution. Finally, we found a slight local negative density-dependence of dispersal (Table 1, Figure S7-C; as in Le Galliard et al. 2003a, Meylan et al. 2007, Léna et al. 1998a) but only for corpulent focal neonates. Density is perhaps considered here as a cue for environmental quality, high densities being associated with high resources and/or low competition (Léna et al 1998, Stamps 1991, Le Galliard et al. 2003a, Clobert et al. 1994, Boudjemadi et al. 1999), or a dilution of infestation risk for neonates (Mugabo et al. 2015). Moreover, the increase in density is associated with an increase in juveniles' survival (Mugabo et al. 2013, Meylan et al. 2007 for females only), even if the proximate cause underlying such increase in survival is still poorly understood (Mugabo et al. 2013). The social fence hypothesis

(Hestbeck, 1982) is unlikely to occur here as the increase in local densities did not impact juveniles' emigration rate (Massot et al. 1992), nor its locomotor abilities (Meylan and Clobert 2004) and was associated with an increase of neonates' movements (Cote et al. 2008a). The stability of this effect is however questionable since the resampling among siblings only marginally supported it (see Figure S10).

The use of social metrics could be here understood either as a direct cue on the competitiveness of the environment (*e.g.* females proportion) or on the contrary as a cue of habitat quality (e.g density), as already observed in other studies (Cote and Clobert 2007a, Brevet et al. 2022 in prep.). Further investigations are needed to precisely understand which cues on social contexts are used for which dimension of the habitat. For example, the use of information on density could depend on behavioral modification of individuals according to their habitat densities (as suggested in Cote and Clobert 2007b, Cote et al. 2012), and individuals could have access to information on densities or sex distribution through odors (Aragon et al. 2006 a, c).

Phenotype-dependence and the use of social information in dispersal

As expected, we found dispersal to be phenotype-dependent (Bowler and Benton 2005, Clobert et al. 2009) with a tendency for male-biased dispersal (Table 1, Figure S5) as found in Massot (1992b) and Le Galliard et al. (2005a). As this species is polygynandrous (Fitze et al. 2005) with males competing for reproduction and resources and females for resources only (Pilorge et al. 1987, Massot et al. 1992), greater movement of males is probably related to the search for mates, as predicted by the Greenwood's hypothesis (1980).

Most of the time, neonates' dispersal depended on the interaction between their phenotype and social factors (except for the effect of the adults' sex ratio). Such phenotype-dependence has been observed in some experiments (Cote et al. 2012) and has been found in a few other species as well (*e.g.* Parejo et al. 2007, Baines et al. 2019). Yet, no study tried to comprehensively test for the phenotype-dependence use of social information in natural conditions and to what extent this was the rule rather than the exception. First, the neonate sex also influenced dispersal in interaction with the adults' corpulence in the natal area: females were leaving areas with high adults' corpulence and males areas with low adults' corpulence. In this species, adults' corpulence correlates with resources availability (Mugabo et al. 2010, 2011, Le Galliard et al. 2005d) and is likely related to some higher competitive abilities (see Mugabo et al. 2010, 2011) since such corpulent individuals could withstand higher energy expenditure (Kooijman 2000, *e.g.* Bystorm and Andersson 2005). As males are dominant over females in this species (Lecomte et al. 1994, Pilorge et al. 1987, see also Le Galliard et al. 2005b, 2008 for males aggression) and, therefore, probably less sensitive to competition than females, adults' corpulence could be used as a cue for expected competition level by females (positively influencing their dispersal) and as a cue for the availability of resources in males (negatively influencing their dispersal).

Second, we found, for the most corpulent neonates, the correlation between dispersal and most of the local social factors to be more intense (Figures1 and S7; for the effects of the neonates' sex ratio, adults' age, density, but also the interaction between the adults' corpulence and the neonates' sex, although not strongly supported, Figure S10). Physical condition is associated with an increase in neonates' survival rate (Le Galliard et al. 2010, 2013) or physical performances (Le Galliard et al. 2004, Meylan and Clobert 2004), potentially reflecting higher competitive abilities (*e.g.* Garland et al. 1990, for an effect of locomotor abilities) in such individuals. It is also associated with the presence of important reserves (Olsson et al. 2002). Such interactions could then indicate that dispersal is accessible mostly to individuals with the ability to endure the costs of dispersal (Léna et al. 1998a, Cote et al. 2012), *i.e.* having sufficient reserves for displacement costs and/or competitive abilities to settle in a novel environment. Corpulent neonates dispersal would be a way for such individuals to settle in better habitat quality, even if these habitats are more competitive (Léna et al. 1998a), as for example reflected by their density (Massot et al. 1992, Lecomte et al. 1994, Dreiss et al. 2010, Mugabo et al. 2013).

To explain such widespread phenotype dependence of the social context, we hypothesized two non-exclusive mechanisms. First, the individual's phenotype could reflect the ability a neonate has to endure dispersal cost to escape a local context somehow disadvantageous. Second, the individual's phenotype could reflect neonates' ability to compete and establish in a better habitat, even if more competitive, having then access to more resources or mates. The fact that dispersal strategies depend on individual phenotype could then have important implications for meta-population dynamics (Clobert et al. 2009).

Conclusion

Dispersal in the common lizard appeared to correlate with multiple factors linked to the local environmental context and the individuals' phenotype. Most of the findings confirmed earlier results on the use of the social context obtained in experimental conditions in enclosures and/or small-scale set-ups (Léna et al. 1998a, Le Galliard et al. 2003a, Lecomte et al. 2004, Boudjemadi 1999, Galliard et al. 2005b). The social and non-social context (substrate's characteristics), especially the adults' sex ratio in the natal area, had major relative importance in our model. Interestingly, many factors describing the local social context were used concurrently in natural conditions, possibly indicating that the information content of each of them is complementary or that a certain level of redundancy is necessary to ensure the quality of the information. Neonate dispersal also depended on the interactions between the neonates' phenotype and many social factors, probably meaning that the information content of these factors is differently translated by each neonate depending on its competitive ability. Such phenotype-dependent dispersal decisions raise the question of the evolution of plasticity in the use of social and non-social information and its multi-determinism. For example, the use of indirect social cues for assessing the quantity of resource (as adults' corpulence) might depend on the overall availability of resources in the environment (*e.g.* Wurtz et al. 2021) assessed directly by the individual and/or the respective cost of accessing information (*e.g.* Wray et al. 2012). Such multiple context-dependence could then influence the hierarchization of social information for dispersal decisions (Rushing et al. 2015). Better understanding information integration processes for movement decisions (Nathan et al. 2008, Riotte-Lambert et al. 2020), could be a way to better apprehend the evolution of the phenotypic and context-dependent variability in such decision processes (Cauchoix et al. 2020).

Author contribution

MB, SJ and JC defined the research questions. JC and MM designed the field monitoring. JC and MM mostly collected the data, all the other authors participated substantially but to a lesser extent to the field monitoring. MRi, MB, AR, DRR and MRe prepare the dataset for analyses. MB performed all the statistical analyses. MB, SJ and JC conducted the writing and all the other authors significantly helped revising it.

Funding

This work was supported by the Agence Nationale de la Recherche (ANR-17-CE02-0013) and TULIP (Laboratory of Excellence Grant ANR-10 LABX-41).

Acknowledgements

We gratefully thank all interns who contributed to the field monitoring work over the thirty years and for their precious help to manage the rearing facility. We thank the Parc National des Cévennes for allowing us to use the study site. This work beneficiated from the scientific environment of the Laboratoire d'Excellence entitled TULIP (ANR-10-LABX-41). The 'Office Nationale des Forêts', the 'Parc National des Cévennes', and the regions Auvergne, Rhône Alpes and Languedoc Roussillon delivered permits to capture and handle lizards (last permits: 81-17 2013-05; 2013274-0002, 2013/DREAL/259). The used monitoring method was validated by an ethical committee (DAP #5897-2018070615164391 v3). No conflict of interest has to be declared.

Supplementary Materials

Spatial and temporal autocorrelation

For each environmental variable (social and non-social), we measured the spatial autocorrelation in the whole study site. To do so, we divided the area including all capture locations in the study site in rectangles with the same area as an individual home range (figure S1). We computed the social and the substrate's characteristics over the thirty years of capture in each of these polygons in the same way as previously described. Then, we computed Moran's I (Moran 1948, index for the spatial autocorrelation) for each variable (using "spdep" R package, Bivand and Wong 2018). We also computed the temporal autocorrelation of all social variables (not applicable to the substrate's characteristics as we did not have access to temporal series), by considering the annual temporal series (from 1989 to 2019) over the whole study site ("acf" R function). We computed the autocorrelation coefficient considering a one-year step. For the adults' sex ratio and the subadult proportion we did not have any data in 1998 (there was no capture of adult males or subadults this year), so we considered two temporal series (from 1989 to 1997 and from 1999 to 2019) and averaged the obtained autocorrelation coefficients. We did not compute the temporal autocorrelation estimates for the density as it would be biased due to the variation in sampling effort between years.

We then tested whether the effect sizes of variables describing the environmental context in the natal area were explained by their spatial and temporal autocorrelations. To do so, we performed a linear regression between the effect size (in absolute values, to ignore the direction of effects) and spatial and temporal autocorrelations of each variable. The regression results were analyzed using an analysis of deviance (likelihood-ratio tests, "car" R package).

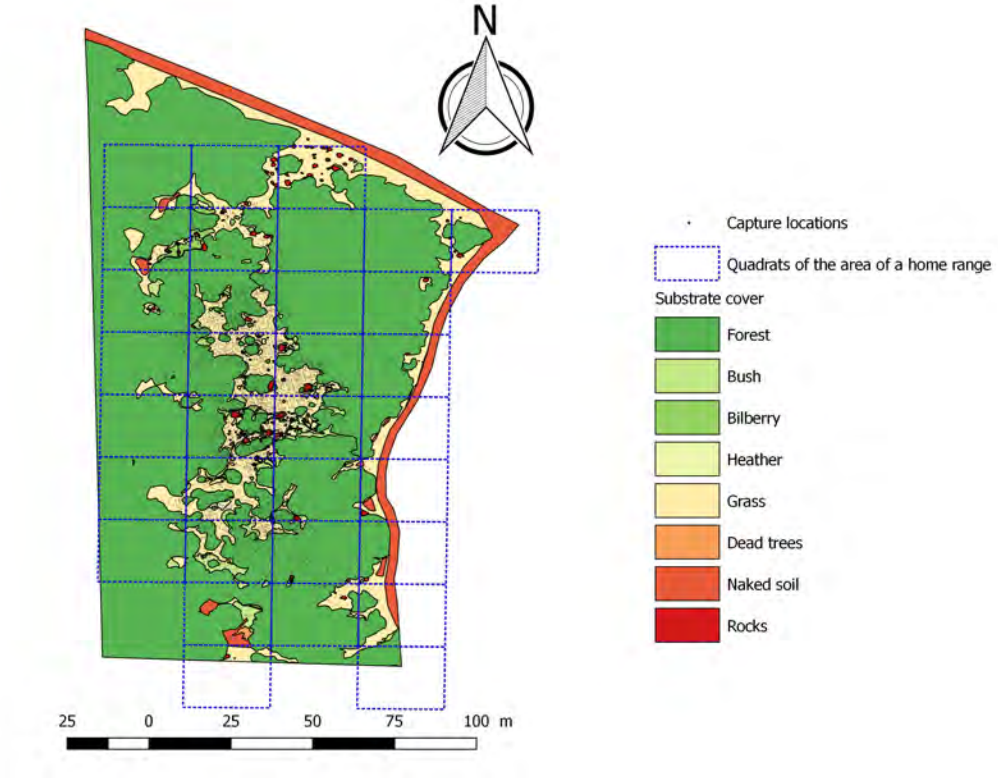


Figure S1: Substrate cover in the studied site.
All capture locations throughout the thirty-year monitoring are displayed by tiny points. The map division used for the calculation of spatial autocorrelation (for a quadrat size of 707 m^2, equivalent to the area of a 15m radius home range) is indicated by the blue dashed line. The map was produced with QGIS 2.18.25.

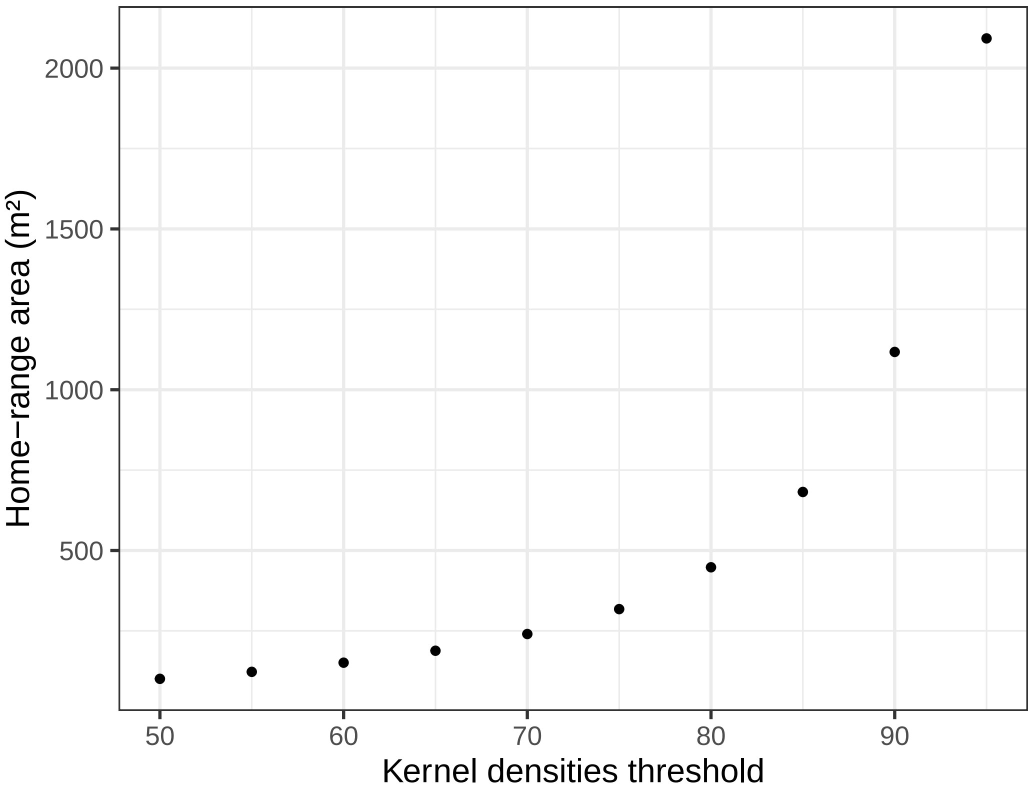
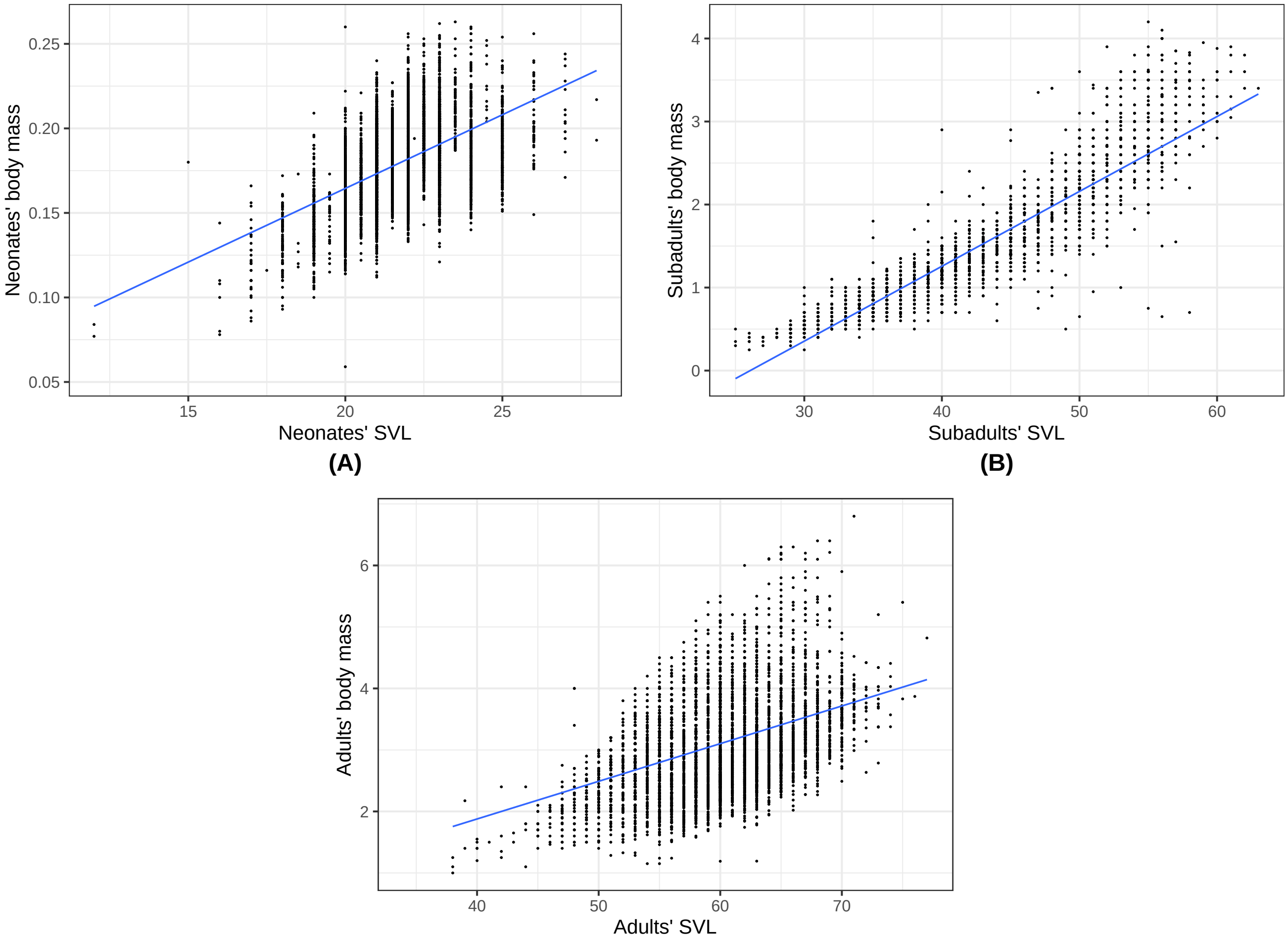


Figure S2: Home range estimates obtained from the kernel density method.
The 85% kernel estimate is about 682 m^2 (equivalent to the area of a circle with a radius of 14.73 m). The 75% and 90% kernel estimates are respectively about 318 and 1117 m^2 (equivalent to the areas of circles with respective radii of 10.06 m and 18.86 m).



(A) **(B)**

(C)

Figure S3: Regressions between body size and body mass to estimate the focal individuals' corpulence.
SVL refers to the snout-to-vent length. Regressions are performed on all captured individuals. Each capture occurrence is associated with a black dot on the graph. The line represents the linear regression slope between the body size and the body mass.
A- Regression for neonates' traits.
B- Regression for subadults' traits.
C- Regression for adults' traits.

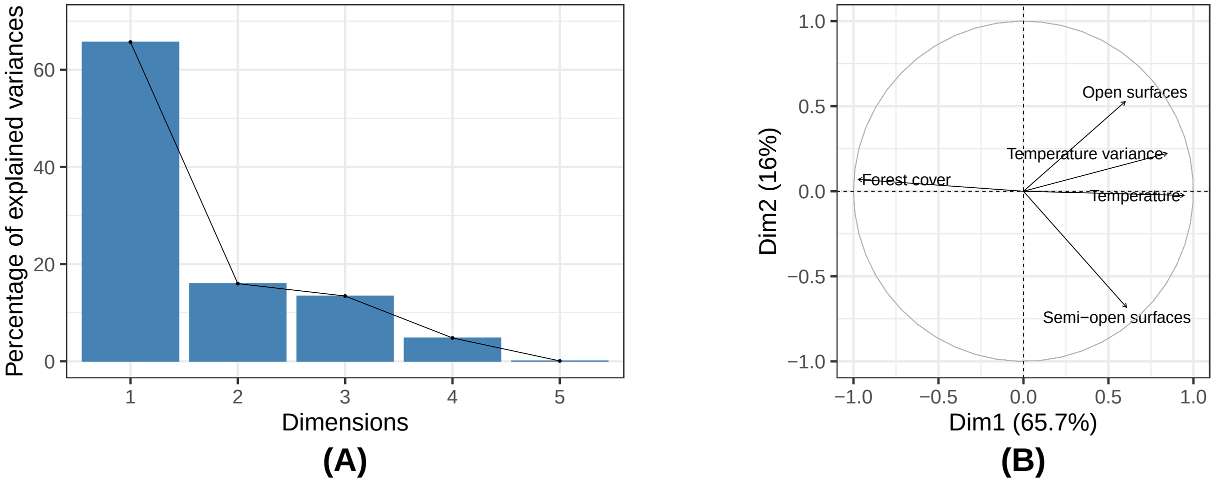


Figure S4: Substrate characteristics PCA graph of variables.
A- Explained variance of the PCA components.
B- PCA graph of variables (first and second axes). All used variables are described in Mat&Met. Each arrow is associated to a behavior displayed at their extremities. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on x-axis and y-axis (percentages).

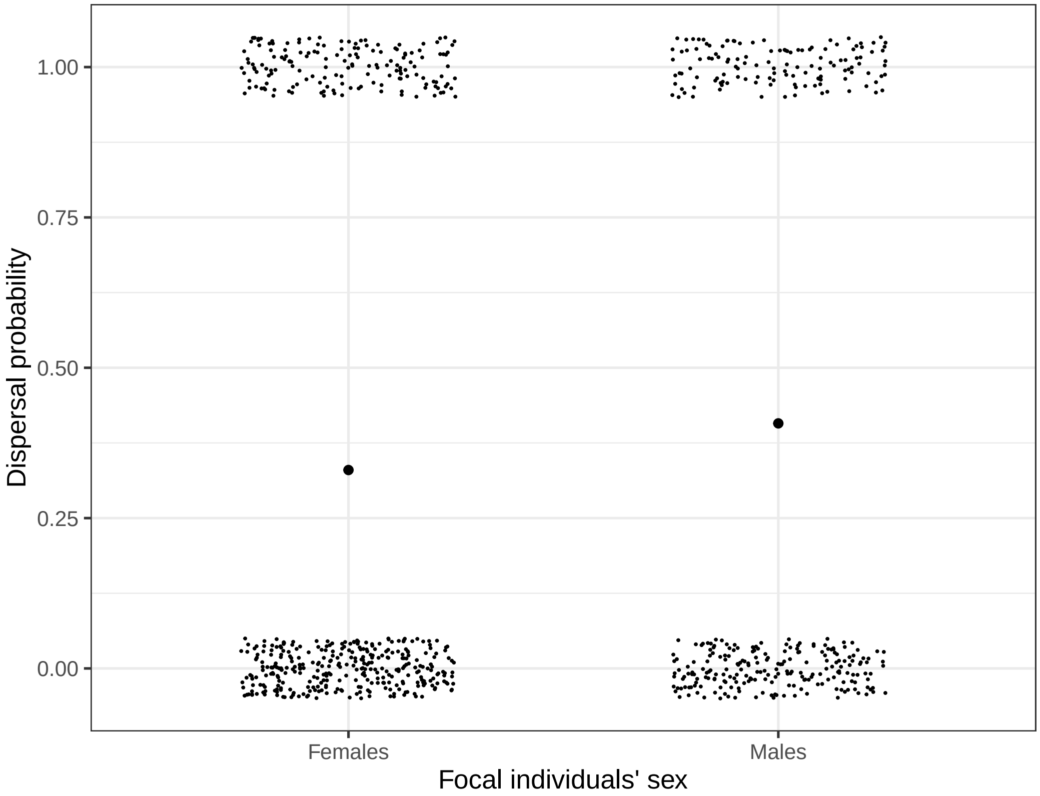


Figure S5: Phenotype-dependence of dispersal (focal individual's sex marginal effect on its dispersal probability).
We looked at the distribution of focal individuals' dispersal predicted probability as a function of the focal individuals' sex. Plots were obtained from the logistic regression results (Table 1) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). The bold black dots display the effects at each possible level (female or male). On the x-axis, "0" refers to female individuals and "1" refers to male individuals. Small black dots display observations from all retained neonates: a dot around the 0% probability line corresponds to a philopatric individual, a dot around the 100% probability line corresponds to an individual who dispersed. These dots were jittered (vertically for quantitative variables, horizontally and vertically for qualitative variables) to gain in readability.

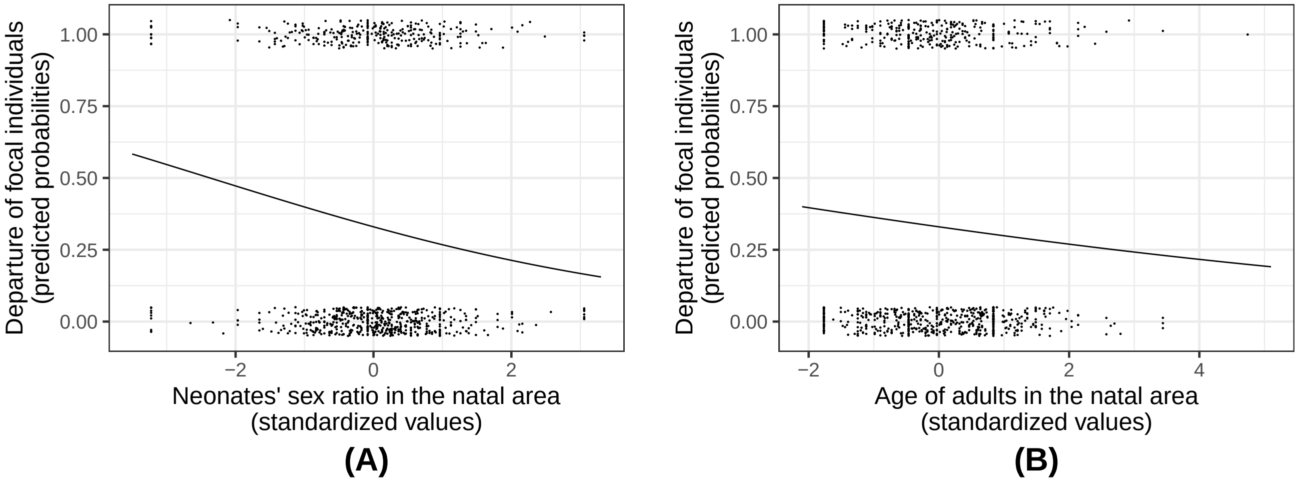


Figure S6: Context-dependence of dispersal.
We looked at the distribution of focal individuals' dispersal predicted probability as a function of the low-order significant (or marginally significant) environmental context elements. Plots were obtained from the logistic regression results (Table 1) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). Effects degree of significance is displayed in table 1. Black dots display observations from all retained neonates: a dot around the 0% probability line corresponds to an individual that did not disperse, a dot around the 100% probability line corresponds to an individual that dispersed. These dots were jittered (vertically for quantitative variables, horizontally and vertically for qualitative variables) to gain in readability.
A- Predicted probabilities of the individuals' dispersal as a function of the neonates' sex ratio in the natal area.
B- Predicted probabilities of the individuals' dispersal as a function of the adults' age in the natal area.

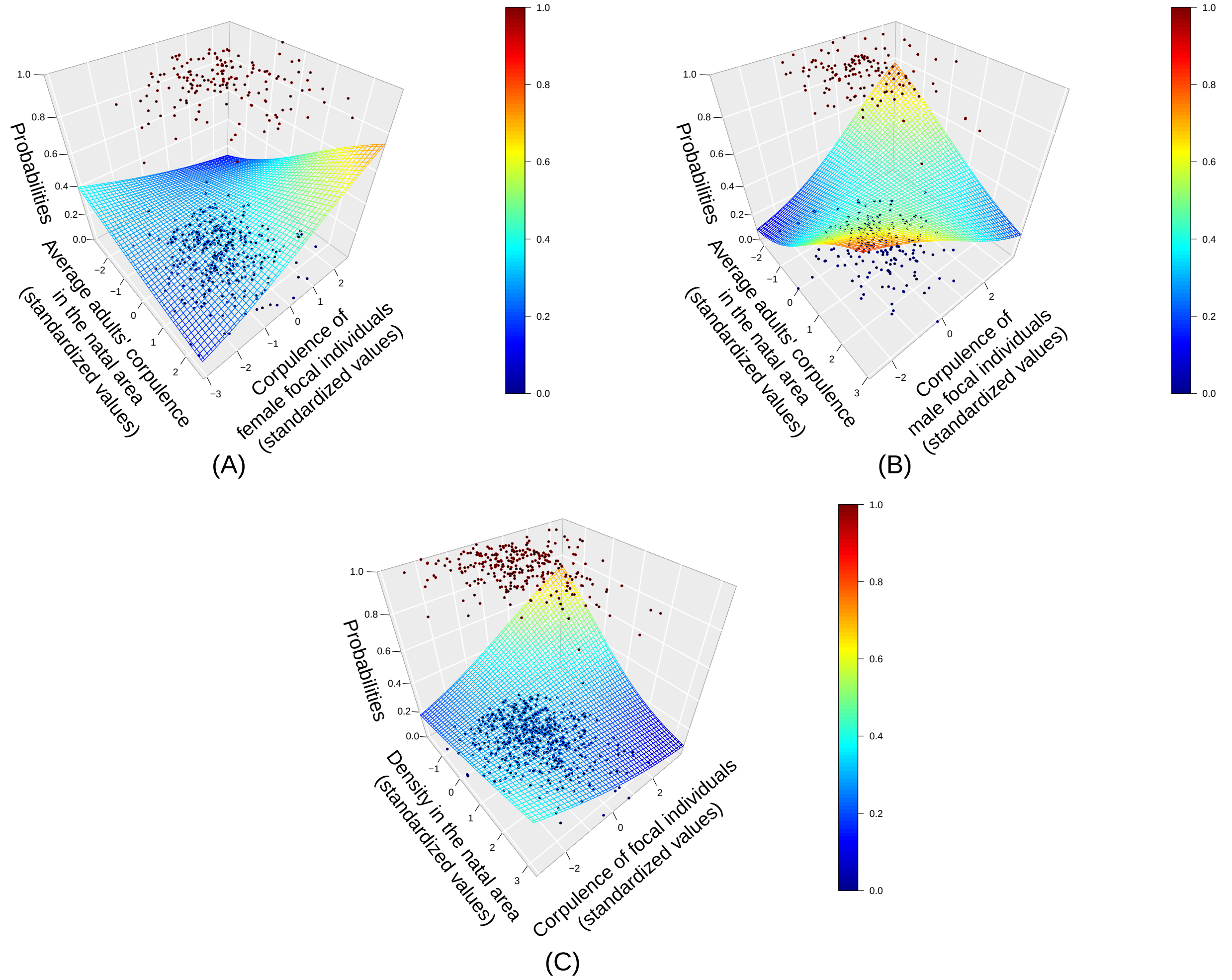


Figure S7: Phenotype-dependence of the use of social information.
We looked at the distribution of focal individuals' dispersal predicted probability as a function of the marginally significant interactions between the focal individuals' traits and the adults' corpulence in the natal area. Plots were obtained from the logistic regression results (Table 1) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). Effects degree of significance is displayed in table 1. Black dots display observations from all retained neonates: a dot around the 0% probability line corresponds to a philopatric individual, a dot around the 100% probability line corresponds to an individual who dispersed.

A- Joint effects of the adults' corpulence in the natal area and the focal individuals' corpulence on dispersal probability of females.

B- Joint effects of the adults' corpulence in the natal area and the focal individuals' corpulence on dispersal probability of males.

C- Joint effects of the density in the natal area and the focal individuals' corpulence on dispersal probability of focal individuals.

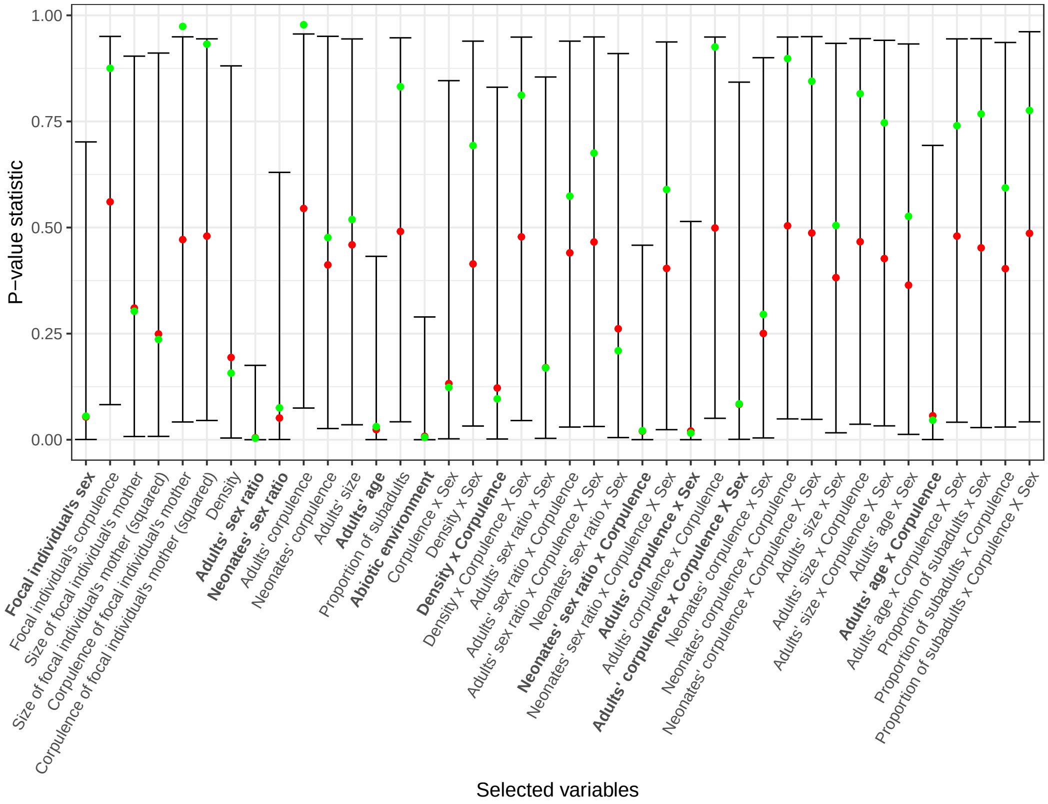


Figure S8: Bootstrap on the logistic regression p-values.

The X-axis displays the used variables in the logistic regression (Table 1), variables in bold on the X-axis have significant effects in the initial regression. For each variable, p-values are computed a thousand times from ordinary bootstrap resampling (used to run the same regression as previously described: p-values are obtained through an analysis of deviance). Grey bars display the 95% percentile interval obtained from all bootstrap resampling. Red dots are associated with the median values obtained from bootstrap resampling. Green dots refer to the original p-value obtained from the regression.

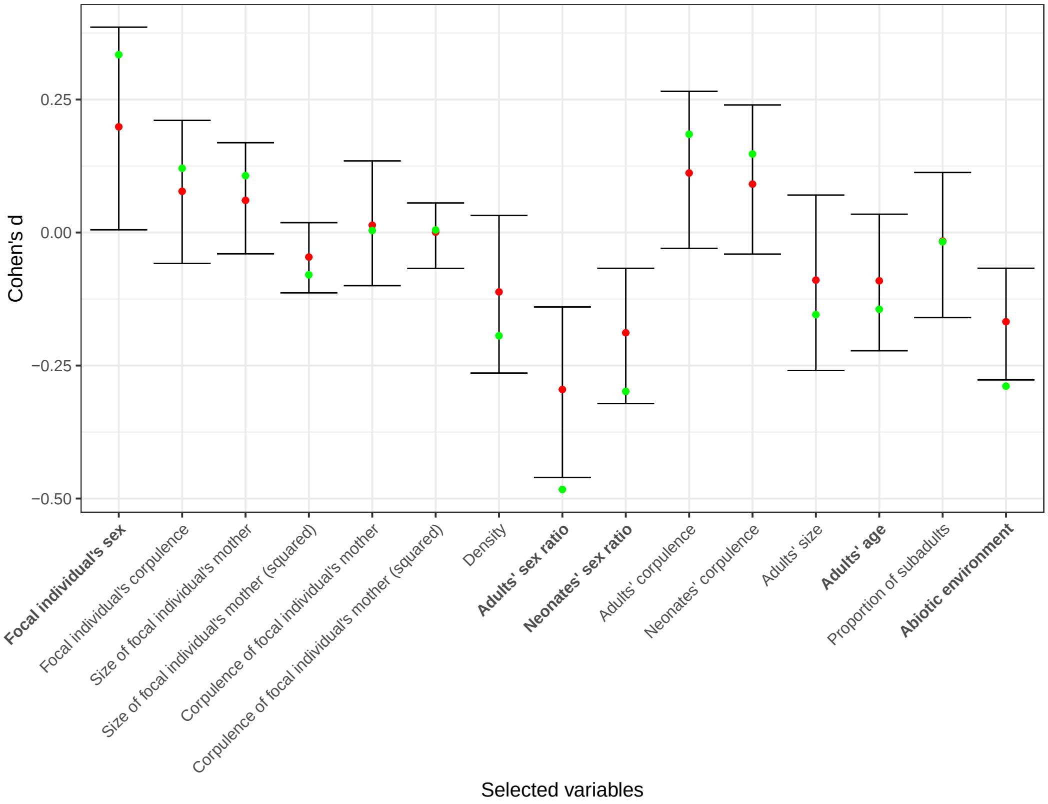


Figure S9: Bootstrap on the effect size estimates.
The X-axis displays the used variables in the logistic regression (Table 1), variables in bold on the X-axis have significant effects in the initial regression. For each variable, effects sizes are computed a thousand times from ordinary bootstrap resampling (used to run the same method as previously described in Mat&Met). Grey bars display the 95% percentile interval obtained from all bootstrap resampling. Red dots are associated with the median values obtained from bootstrap resampling. Green dots refer to the original p-value obtained from the regression. Green dots refer to the original p-value obtained from the regression.

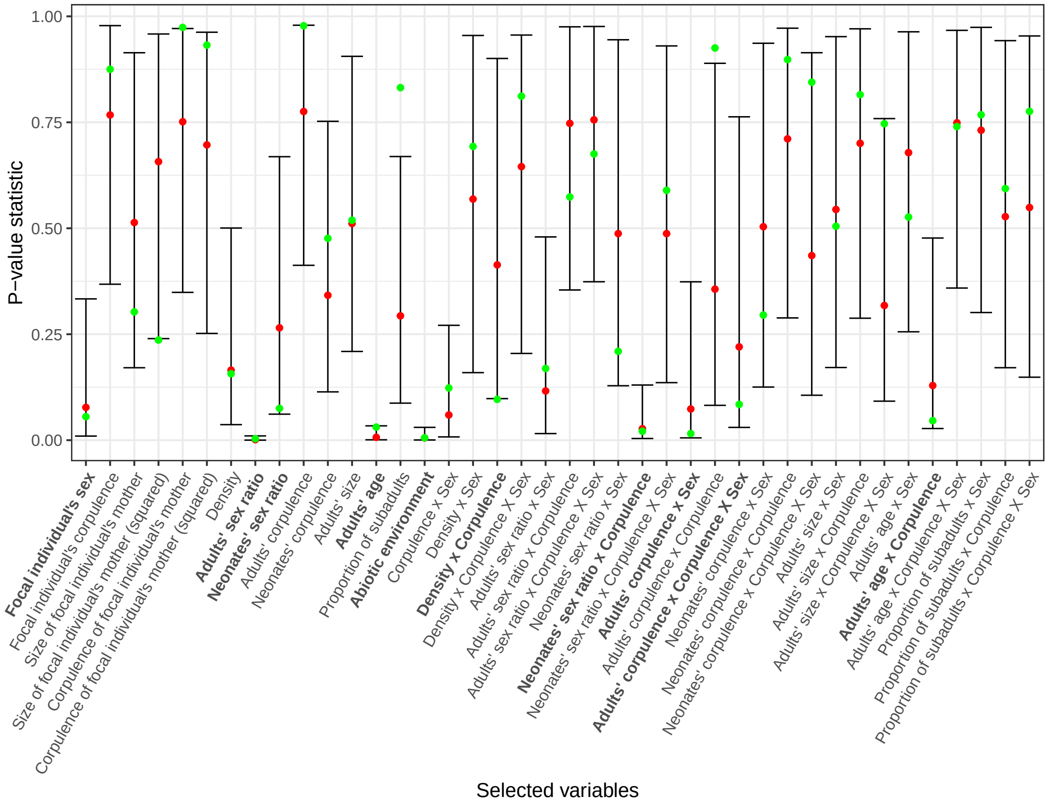


Figure S10: Resampling among siblings to re-estimate the logistic regression p-values.
The X-axis displays the used variables in the logistic regression (Table 1), variables in bold on the X-axis have significant effects in the initial regression. For each variable, p-values are computed a thousand times from a random resampling among siblings of a same clutch (used to run the same regression as previously described: p-values are obtained through an analysis of deviance). Grey bars display the 95% percentile interval obtained from all bootstrap resampling. Red dots are associated with the median values obtained from bootstrap resampling. Green dots refer to the original p-value obtained from the regression. Green dots refer to the original p-value obtained from the regression.

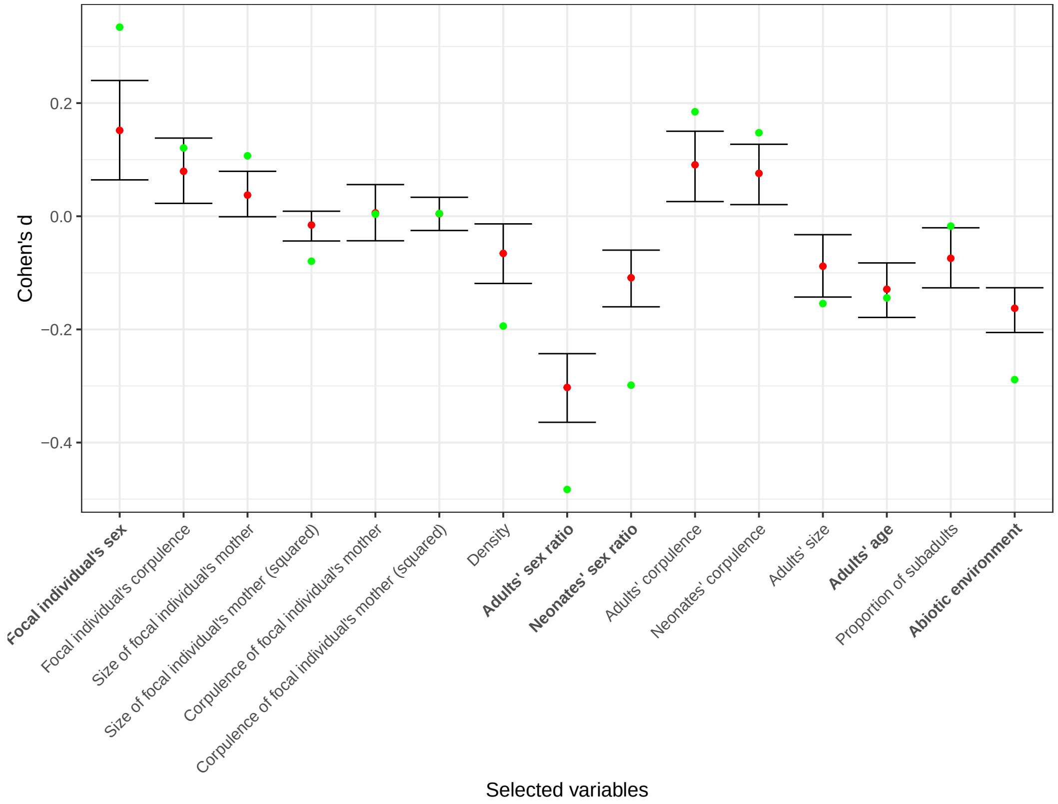


Figure S11: Resampling among siblings to re-estimate the effect size estimates.
The X-axis displays the used variables in the logistic regression (Table 1), variables in bold on the X-axis have significant effects in the initial regression. For each variable, effects sizes are computed a thousand time from a random resampling among siblings of a same clutch (used to run the same method as previously described in Mat&Met). Grey bars display the 95% percentile interval obtained from all bootstrap resampling. Red dots are associated with the median values obtained from bootstrap resampling. Green dots refer to the original p-value obtained from the regression. Green dots refer to the original p-value obtained from the regression.

Chapter 2

Social information use for spatial decisions in *Zootoca vivipara*

M. Brevet[1,2], S. Jacob[1], A. Rutschmann[1,3], M. Richard[1], J. Cote[2,4], J. Clobert[1]
[1]Station d'Ecologie Théorique et Expérimentale (SETE), UAR 2029, CNRS, 09200, Moulis, FR
[2]Université Toulouse III Paul Sabatier, 31062, Toulouse, FR
[3]School of Biological Sciences, University of Auckland, Auckland, NZ
[4]Laboratoire Evolution et Diversité Biologique (EDB), UMR5174, CNRS, 31062, Toulouse, FR

Soumis dans la revue Behavioral Ecology and Sociobiology

Présentation et résumé du Chapitre

Dans ce second chapitre, nous avons exploré, en condition contrôlée, comment était considérée l'arrivée simultanée d'informateurs conspécifiques dans la zone d'habitation d'un individu focal. L'objectif était de confirmer expérimentalement l'utilisation provenant de sources multiples et de préciser ses modalités d'utilisation. En utilisant un plan expérimental adéquat, nous avons voulu en effet tester la capacité à s'orienter lorsqu'on est confronté à de multiples sources d'informations sociales. Cette expérience nous a également permis d'explorer le mode d'utilisation précis de ces sources multiples, en explorant l'influence de la moyenne des informations et du contraste entre les sources d'information sur les décisions de déplacement. Nous nous attendions à ce que la moyenne des informations soit utilisée comme information sur l'environnement de l'individu, et que le contraste des informations soit également utilisé comme une information sur la variabilité du signal et pour l'orientation dans l'espace.

Les mouvements des individus sont conditionnés par l'acquisition d'informations provenant de sources personnelles ou sociales, mais on sait peu de choses sur la façon dont les mouvements des individus sont influencés par des informations sociales provenant de sources multiples. Ici, nous nous sommes attaqués spécifiquement à ce problème en testant expérimentalement (i) comment les informations sociales provenant de sources multiples sont utilisées pour prendre des décisions de mouvement, et (ii) si un contraste dans ces informations permet aux individus de s'orienter dans l'espace. À cette fin, nous avons mené des expériences répétées chez le lézard commun (*Zootoca vivipara*) dans lesquelles un nouveau-né focal recevait des informations de deux autres nouveau-nés provenant d'environnements périphériques, avant d'avoir la possibilité de se relocaliser dans l'un ou l'autre environnement périphérique.

Nos analyses ont révélé que le comportement des nouveau-nés, la morphologie de la mère des informateurs, ainsi que la qualité de l'environnement des informateurs, affectaient les décisions de relocalisation : la probabilité de relocalisation augmentait lorsque les informateurs présentaient des traits associés à de faibles ressources (pas de prise de nourriture, mauvaise condition maternelle) ou à une forte compétition (forte activité sociale). La condition physique des individus focaux conditionnait également la réponse aux informations sociales sur la prise alimentaire. En revanche, l'orientation spatiale n'était pas affectée par les différences de traits entre les informateurs ou par la variabilité spatiale de la disponibilité des ressources.

Cette étude met en évidence le fait que de multiples sources d'informations sociales peuvent être utilisées pour les décisions de déplacement, probablement parce que ces sources d'informations reflètent la qualité du milieu environnant (niveau de compétition ou disponibilité des ressources). Elle souligne également que l'utilisation des informations sociales pour les déplacements peut dépendre du phénotype de l'individu, afin de correspondre à ses besoins.

Abstract

Movements of individuals are conditioned by the acquisition of information from personal or social sources, but little is known about how individuals' movements are influenced by social information from multiple sources. Here, we specifically tackled this by experimentally testing (i) how social information from multiple sources is used to make movement decisions, and (ii) whether a contrast in this information enables individuals to orient themselves in space. To this end, we conducted repeated experiments in common lizard (*Zootoca vivipara*) in which a focal neonate received information from two other neonates coming from peripheral environments, before being given the opportunity to relocate to either peripheral environment.

Our analyses revealed that the neonates' behavior, the morphology of informants' mothers, as well as the quality of informants' environment, affected relocation decisions: the probability of relocation increased when informants exhibited traits associated with low resources (no food intake, poor maternal condition) or high competition (high social activity). The physical condition of focal individuals also conditioned the response to social information about food intake. In contrast, spatial orientation was not affected by trait differences between informants or by spatial variability in resource availability.

This study highlights the fact that multiple sources of social information can be used for movement decisions, probably because these sources of information reflect the quality of the surrounding environment (level of competition or resource availability). It also highlights that the use of social information for movement may depend on the individual's phenotype, to match the individual's needs.

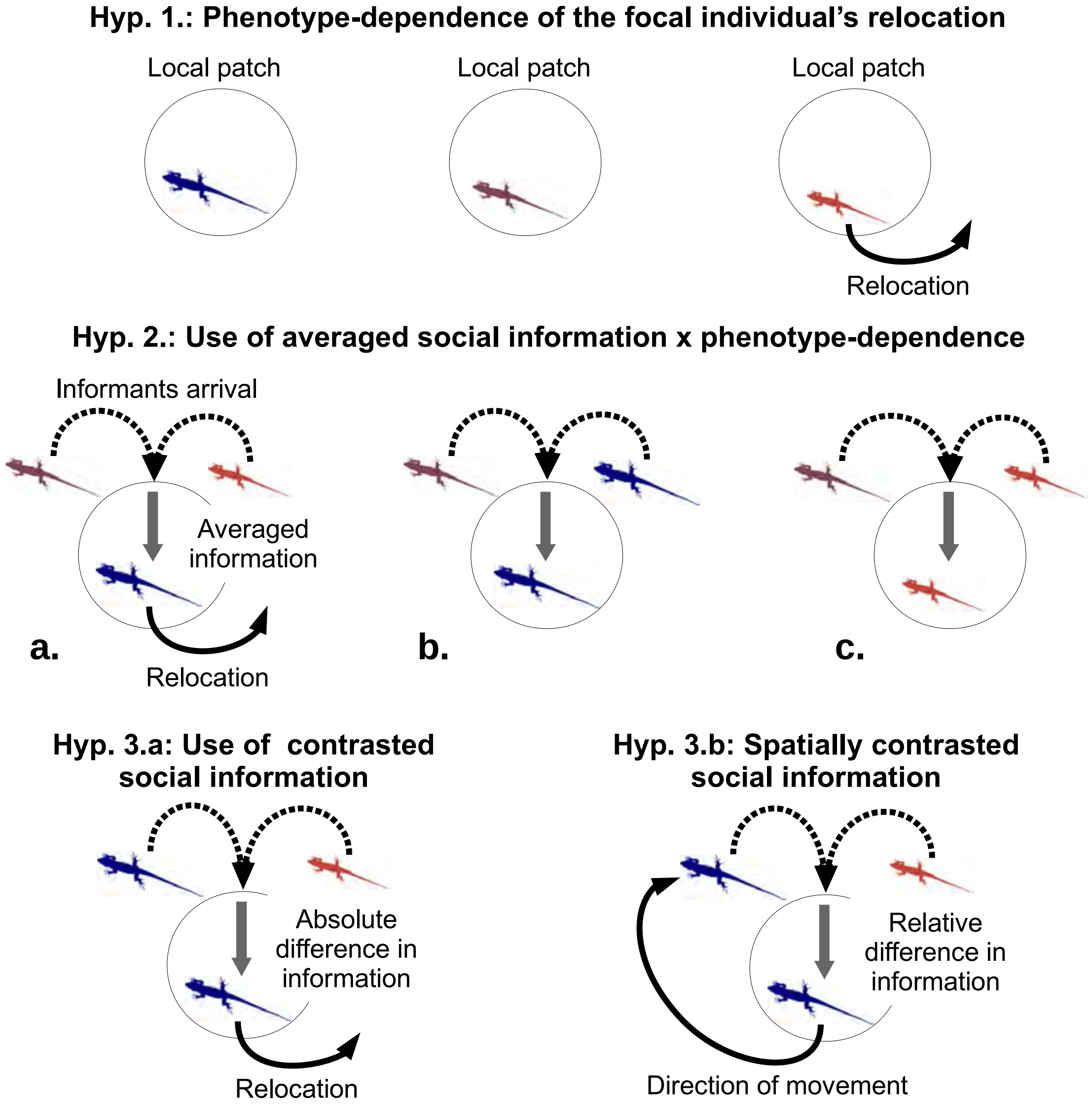
Keywords: Social information, Movement decisions, Spatial orientation, Common lizard, Information transfer, Information use

Introduction

Information acquisition is central for an individual to assess the quality of its environment and to take appropriate decisions to feed, survive and reproduce (Dall et al. 2005, Schmidt et al. 2010). Information can be obtained via personal interactions with the environment (*i.e.*, personal information, Dall et al. 2005) and/or via social interactions (*i.e.*, social information, Dall et al. 2005, Schmidt et al. 2010). Social information is acquired through the observation of conspecific's or heterospecific's detectable traits (*e.g.*, behavior, performance, body condition, odors; Moreira et al. 2008, Clobert et al. 2009) and can inform individuals about both abiotic and biotic characteristics of the local and distant environments such as breeding habitat quality (Doligez et al. 2002, 2004) or conspecific density and resource availability (Endriss et al. 2018). Social information can be intentionally transmitted by informant individuals through signals such as calls or territorial marking (Johnson 1973, Macedonia et al. 1993) but may also be inadvertently conveyed by cues (Danchin et al. 2004, Schmidt et al. 2010), as it is the case for breeding habitat quality, informed by reproduction performances in some bird species (Doligez et al. 2002, 2004).

Social information has long been recognized to be key in organisms' decisions to move through their

Figure 2.1: Experimental aims.
Graphical representation of the different hypotheses investigated in our experimental design. Individuals with different phenotypes are represented by different colors and sizes. Hyp.1 - Phenotype-dependence: relocation depends on the focal individuals' phenotype (*e.g.* only small/orange focal individuals relocate). Hyp.2 - Social information synthesis: relocation depends on averaged information gathered from conspecifics (*e.g.* relocation only occurs when averaged information about small/orange/brown conspecifics is provided, panel a. vs b.), possibly in interaction with the focal individuals' phenotype (*e.g.* only big/blue individuals relocate for such information, panel a. vs. c.). Hyp 3 - Contrasted social information: a) relocation would depend on the variability between information sources (*i.e.* absolute difference, *e.g.* individuals relocate when there is a high difference between information sources), b) direction of movement would depend on the relative difference between information sources (*e.g.* movement toward the origin of the big/blue informant).



environment and is notably known to influence the optimization of spatial decision making for microhabitat use (*e.g.*, Moreira et al. 2008), habitat selection (Doligez et al. 2002, 2004) or dispersal (Cote and Clobert 2007a, Jacob et al. 2015b). In spatially heterogeneous environments, social information is expected to be particularly useful for any movement decision. Indeed, in such environments, the social information is made of a mosaic of cues or signals carried by either local inhabitants or immigrants, respectively informing on the specificities of close and distant habitats (Cote and Clobert 2007a, Jacob et al. 2015b). With increasing heterogeneity, environmental predictability is expected to decrease and socially acquired information can increase an individual knowledge of the general environment, hence reducing the probability of erroneous decisions due to environmental uncertainty (Dall et al. 2005, Riotte-Lambert et al. 2020). In other words, informed individuals are more likely to make the movement decisions that maximize their fitness if they acquire knowledge about the suitability of surrounding habitats throughout social information, compared to when relying on their local prospects only, especially if their movement abilities are restricted.

Yet, little is known about the use of social information for movements decision when multiple sources of social information are simultaneously accessible to an individual (*i.e.*, multiple conspecifics reflecting different surrounding habitats). More specifically, two important questions have to be addressed. First, when multiple sources of information are available, how information sources are used to decide whether the individual should relocate or not? One may expect that the averaged information on surrounding habitats should prevail (Hyp. 2: Social information synthesis, figure 1, panel a. and b.): an individual would optimize its movement by synthesizing all sources of information available (*i.e.*, each social cue or signal among sources), whatever the quality and origin of the cue or signal, to get a global idea of the amount of resource and level of intraspecific competition in the vicinity (Stamps 2001, Clobert et al. 2004, Bowler and Benton 2005). The use of information on surrounding habitats could also depend on the phenotype of the informed individual, which would adjust movement decision to its condition and relocate only when necessary (Hyp. 2 in figure 1, panel a. vs. c.). Many examples in the literature illustrate such phenotype-dependent use of social information for spatial decisions, with dependence on personality (Smit and van Oers 2019, Morinay et al. 2020b), age and success (Parejo et al. 2007), or body condition (Cote and Clobert 2007a, Baines et al. 2019). One may also expect individuals to use the absolute difference between available information sources (Hyp. 3.a: Contrasted social information use, figure 1): by comparing the concordance or discordance of social cues or signals between sources, individuals might be able to assess information reliability or environmental variability in the vicinity. The importance of conflicting information for movement decisions has already been observed for conflicts between personal and social information (*e.g.*, Cronin 2013, Winandy et al. 2021), with prioritization of personal information in case of conflicts (Kendal 2009).

The second question lies in the spatial integration of information gathered from multiple sources coming from different locations: how does an individual use multiple sources of information to orientate, and therefore to choose a specific destination of relocation between alternative habitats? One likely hypothesis (Hyp. 3.b: Spatially contrasted social information use, figure 1) is that relative differences in information between multiple sources originating from different habitats allow spatial orientation for the information receivers. Such differences in information could indeed inform the individual on the direction of habitats with a higher fitness expectancy, since the surrounding habitats are possibly associated with different social information quality as a function of their fitness expectancy (Schmidt et al. 2010).

To investigate these questions, we used the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model species. This lizard is known to use social information in different contexts, and notably to acquire information about the dispersal status of conspecifics (Aragon et al. 2006b), the reproductive strategy and aggressiveness of other females from their ventral coloration (Vercken et al. 2012), or the population density in the surrounding habitats through immigrants (Cote and Clobert 2007a, Cote et al. 2008a). In this species, the use of personal and social information is also known to occur immediately after birth and to shape natal dispersal decisions (Clobert et al. 2012, Cote and Clobert 2012). Contrary to these previous studies, we aimed to test for the use of multiple simultaneous information sources for spatial decisions (relocation and orientation).

Specifically, we tested how common lizards used social information from two contrasted habitats, varying in food availability (present or not) and conspecifics traits (physical condition, behaviors, sex, physical condition of mothers), to take decisions of relocation from their local area in a reduced spatial scale. We also tested whether such information could influence movements' orientation when relocation occurred. To do so, we placed juvenile lizards (neonates from 2 to 4 days, born in our facilities from caught gravid females) in a three-chamber system (figure S1), where an information receiver (referred to as the focal individual further on) was confronted with two individuals coming from independent chambers (referred to as informants further on). One informant came from an experimental environment where food was provided, while the other came from an experimental environment where food was absent. The partially random choice of informants led to variable mean traits and variable differences in traits among informants pairs used experimentally (Methods for details). We hypothesized that informants could transmit social information through their phenotype (*e.g.*, behaviors, feeding, age, sex, or physical condition) but also through their mothers' condition (*i.e.*, maternal effects, Bernardo 1996). These phenotypic traits are known to be related with short term sexual and resource competition contexts (Massot 1992, Léna et al. 1998a, Galliard et al. 2005c for sex and physical condition; Lecomte 1994, Cote et al. 2008a for behaviors), or with the long-term environmental context through maternal condition effects (Sorci and Clobert 1997, Uller and Olsson 2005, Mugabo et al. 2011). Note here that these phenotypic traits do not only inform about the competition in the standardized experimental setup, but possibly also about the competition level present in the habitat of origin of the individuals.

Considering our hypotheses and the existing literature we expected that: 1) the relocation probability of the focal individual would vary with its phenotypic traits (Phenotype-dependence of movement, Hyp. 1 in figure 1; as already shown for body condition, Cote and Clobert 2007a, sex, Galliard et al. 2005c and

Aragon et al. 2006b, age, Massot 1992 and Léna et al. 1998a, behaviors, Cote et al. 2010, or maternal body condition, Léna et al. 1998a, Meylan et al. 2002), 2) the relocation probability of focal individuals would increase when information about high quality surrounding habitats is on average provided (Hyp. 2, figure 1; *i.e.* habitat with high resources and low competitors), with possible adjustment of the information use depending on the focal individuals' phenotype. Here we specifically investigated whether the phenotype of the focal individual influenced the use of social information about food availability in peripheral environments: we expected an increased probability of movements when focal individuals are in low condition and provided with information about a high amount of resources. As the absolute differences of traits between informants might reflect the heterogeneity of information on surrounding environments (Hyp. 3.a, figure 1), we expected individuals to 3) decrease their movements when heterogeneity of information about surrounding environments, and thus possibly information uncertainty, increases (Riotte-Lambert et al. 2020, *e.g.* Heinen and Stephens, 2006). Lastly, 4) focal individuals would adjust movement direction depending on social information relative differences between sources (Hyp. 3.b, figure 1), possibly moving towards the chamber of the informant having access to food, with a better physical condition, displaying low competitive behaviors, or being of the opposite gender.

Materials & Methods

Species and study sites

Zootoca vivipara (Jacquin 1787) is a small size ground-living species of the Lacertidae family. This species is widespread in Northern Europe and Asia and lives in heathlands, bogs, and wet meadows. Individuals used in this study have been sampled in seven populations located in the Massif Central mountain range (France). These sites range from 1000m to 1500m in altitude and cover the diversity of possible habitats in this region (Rutschmann et al. 2016). In the Massif Central, mating takes place just after individuals emerge from hibernation, between March and April. Parturition usually occurs between late June and late July, depending on temperature conditions (Rutschmann et al. 2016). In our sites the current mode of reproduction is ovoviviparity and juveniles emerge from the egg within a few hours after parturition. Some of the juveniles disperse from their natal site a few days after birth (Massot 1992).

Capture and rearing condition

Twenty pregnant females were captured at each site between June 12th and 24th, in 2019. These females were brought to a field laboratory, where we measured snout to vent length (SVL). Females were maintained in individual plastic terrariums (18.5 x 12 x 11 cm), containing a shelter made from two slots of a cardboard egg-box and a 2 cm substrate of sterilized soil (Massot and Clobert 2000). Terrariums were placed under an incandescent bulb of 25W providing light and heat for 6 hours a day to allow basking (from 9 a.m. to 12 p.m. and from 2 p.m. to 5 p.m.). Terrariums were sprayed with water three times a day. Females were fed with three mealworms, every second day.

After parturition (between July 2nd and 24th), juveniles from a same clutch were isolated from their mother in a terrarium (day 0). Females that just gave birth were immediately weighed. Juveniles' SVL and body mass (BM) were measured the day after their birth (day 1), before any feeding treatment. Sex was assessed following the method provided in Lecomte et al. (1992). The same day, juveniles were isolated to individual terrariums (25 x 15 x 15 cm), containing a shelter made from two slots of a cardboard egg-box and layered with two sheets of absorbent paper. Juveniles were left for another day (day 2) in their respective terrarium before experiments started on day 3, so they could consider this terrarium as their living area (Aragon et al. 2006b). All juveniles and mothers were fed and released at the mother's capture site on day 4.

Experimental design

The experiment aimed at testing if the spatial decisions of a focal individual were influenced by informants' phenotypes and food intake. Each of the 56 replicates of the experiment required three juveniles (one focal individual which was confronted to two informants). Each juvenile was tested once, there was no re-used of individuals among replicates. Multiple-individuals encounters are likely to occur in natural conditions, as this species is living in crowded habitats (Massot et al. 1992) with individuals sharing spatial resources for basking or sheltering (personal observations). Mark and recapture data also suggest that the number of neonate immigrants arriving in the natal area of a focal neonate rarely exceeds two individuals (immigrants number: 1.7 ± 2.1 SD, 2 immigrants or less in 78% of registered cases; Brevet et al. in prep.). As such, our experimental design reflects potential encounter, as likely to happen in natural populations.

For each replicate, juveniles were selected among clutches of mothers from the same capture site. When possible, informants had the same laying date. Most experimental replicates (n=37) took place 3 days after the birth of focal individuals but some replicates happened 2- (n=10) or 4-days (n=9) after birth when there were too few births on the same day. Similarly, 2 (n=10) and 4 days old (n=13) informants were used when necessary. There was an age difference between the focal individual and at least one of the informants in seventeen replicates. Focal individuals were always selected from different brood than the informants, but informants from the same brood were used in the same experimental replicate when there were too few births (n=19). Simultaneous encounters of related individuals are likely to occur in natural conditions as siblings often share similar dispersal behaviors (Massot and Clobert, 2000).

One day before the encounter between the focal individual and the informants, one of the two informants had access to food: three small crickets, from 3 to 5 mm, were introduced in the fed informant's terrarium. The number of consumed crickets (0 to 3) was counted just before the experiment (referred to as the fed informant's food intake further on). The focal individual was never fed before the experiment to increase the probability of responses to social information about food availability (Wurtz et al. 2021). To avoid any side-effects due to sex distribution, informants' sexes were orthogonally crossed with informants' access to food and the focal individual's sex. Each focal female (n=29) or male (n=27) was confronted with either two informant males, or two informant females, or one informant male and one informant female. These combinations were balanced between replicates within an experimental day. In the replicates with one informant male and one informant female, the fed informant was the male in nearly half of the replicates (n=14) and the female in the other half (n=16).

Replicates took place from July 5th to 27th between 7 a.m. and 8 p.m. We summed up the timing of experiments in a categorical variable, accounting for the lighting periods in the field laboratory, with four classes: early morning (7 a.m. to 9 a.m., n=13), morning (10 a.m. to 12 a.m, n=23), afternoon (1 p.m. to 4 p.m, n=13) and evening (5 p.m to 8 p.m, n=7).

By-products of experimental constraint (absolute difference in age between informants, informant kinship and time windows) had no significant effect on relocation probability when individually added in the selected model about relocation probability (respectively (z-value, p) = (-1.08, 0.28) / (-0.85, 0.39) / (from 0.26 to 1.22, from 0.22 to 0.80)). The relative difference in age between informants did not impact movement decision when added in the model about movement direction (χ^2 = 1.39, p = 0.24).

Experimental assay

The home terrarium of the focal individual was placed on an isolated table. Corridors (PVC tubes of 25 cm length and 16 mm internal diameter) were introduced at each side of this terrarium. Informants were placed in corridors' extremities and their arrival in the focal terrarium was synchronized by slightly brushing their tails (figure S1). We alternated the introduction position (left or right) of the fed informant and males and females between each replicate so that the position was not biased towards a treatment or an informant's sex. Once the informants entered the focal terrarium, exits were plugged. The dimension of the focal terrarium (25 x 15 x 15 cm) was sufficient to accommodate the three juveniles together while allowing them to avoid each other. The three juveniles interacted together for thirty minutes (figure S1). After that period, informants were put back in their respective terrariums. In the home terrarium, absorbent paper, shelter, and heat/light source were removed to promote departure (Aragon et al. 2006b). The focal individual was left five minutes in these conditions to acclimatize (figure S1). Then the corridors used previously were attached again at each extremity of the focal terrariums (without any modification since the informants' passage) and connected to two identical and clean terrariums. The focal individual was left thirty minutes in this system (figure S1). After this time, the experiment was stopped and we observed if the focal individual had left its terrarium and in which direction. All used side-terrariums were washed with water between replicates. Corridors were used only once. Experiments were entirely filmed with three webcams (Creative Live Camera Sync HD 720p) placed above each terrarium to analyze the three individuals' joint behaviors.

Data analyses

Retained variables

We chose to measure the focal individuals' and informants' traits that had been found to be influent for movement decisions in the common lizard (Introduction for details, Clobert et al. 2012, Cote et al. 2012 for reviews). Not all existing influent traits were measured, either because we did not have enough time to measure some of them (*e.g.*, individuals' stress level) as juveniles had to be released no later than 4 days after birth to avoid influencing their chances of survival, or because the information was missing for most individuals (*e.g.*, mothers' age and reproductive strategy, the litter sex ratio), or because our design prevented from testing their influence (*e.g.*, density, presence of kin, predators or parasites).

For the retained variables, the three juveniles had variable phenotypes that we did not control for in the preparation of our experiments. However, we analyzed their effects on movement decisions, since they displayed sufficient variability to be potential drivers of movements (juveniles' SVL: 20 ± 1 mm SD, juveniles' BM: 157.7 ± 18.2 mg SD, SVL of mothers: 62.2 ± 4.1 mm SD, BM of mothers: 3616 ± 566.7 mg SD). In particular, there was sufficient variability in the averaged traits of each informants pair used in experimental replicates (SVL: 20 ± 1 mm SD, BM: 157.7 ± 15.4 mg SD, SVL of mothers: 62.1 ± 3.6 mm SD, BM of mothers: 3605 ± 467.1 mg SD) and in the absolute differences between their traits (SVL: 1.05 ± 0.84 mm SD, BM: 17.3 ± 13.1 mg SD, SVL of mothers: 2.82 ± 3.02 mm SD, BM of mothers: 526.3 ± 508.6 mg SD), for them to be used as potential social cues or signals.

Table 2.1: Joint behaviors of the focal individuals and informants.

Behavior	**Description**	**Unit**	**Mean value**	**Sd**
Activity	Cumulative time spent moving by the three individuals (Aragon et al. 2006a, Cote et al. 2008a)	Seconds	949	389
Sheltering	Cumulative time spent sheltering by the three individuals (Cote et al. 2008a)	Seconds	1381	795
Escaping attempt	Time spent by at least one individual trying to escape the terrarium by scratching or climbing the walls (Aragon et al. 2006a)	Seconds	64.8	78.6
Boldness	Time spent by at least one individual basking above the shelter (Cote et al. 2008b)	Seconds	177	232
Non-aggressive proximity	Time spent motionless by at least two individuals in close proximity to each other, *i.e.* at a distance less than the approximate size of an individual (Aragon et al. 2006b)	Seconds	192	160
Competitive interaction	Number of contacts between two individuals leading to the flight of at least one individual (Aragon et al. 2006b)	Events count	3.61	3.86
Tongue-Flicking	Olfactory cues acquisition that could be interpreted as a chemical exploration or social assessment (Cooper 1994, Aragon et al. 2006b)	Events count	2.88	3.43

Description of the joint behaviors of the three juveniles, measured during the last twenty minutes of their confrontation (see Mat&Met). We did not use cumulative times for escaping attempts and boldness behavior because these behaviors were performed extremely rarely by several individuals at the same time (4% and 2.7% respectively). Bibliographic references used to define these metrics are cited in the description column. Mean and standard deviation have been computed over all experimental replicates.

Joint behaviors of focal and informant individuals

Behaviors of focal and informant juveniles were measured to test their impact on relocation decisions (Hyp. 1 and Hyp. 2, in figure 1). Due to technical constraints (*i.e.*, videos quality), we could not distinguish the behavior of informants and focal individuals. As a consequence, we analyzed the joint behaviors of the three juveniles together through the last twenty minutes of their confrontation, the first ten minutes being considered as an acclimation time (Cote et al. 2007, 2008a). We used BORIS software (Friard and Gamba, 2016) to quantify the following behavioral traits (the description and interpretation of behaviors are detailed in table 1): activity, sheltering, escaping attempt, boldness behavior, non-aggressive proximity, competitive interactions, and tongue-flicking. These behaviors were considered apart from other focal individuals' traits or informants' traits because they described the behaviors of both focal and informant individuals simultaneously and cannot individually be ascribed. To prevent any observer bias, we used blinded methods when the behavioral data were recorded (with no observer during the video recording) and analyzed (no knowledge of the treatments associated with the replicates during their analysis).

We synthesized behavioral information using a principal component analysis (PCA) (figure S3; all analyses were performed with the "FactoMineR" R package, Lê et al. 2008). Given the explained variance distribution (figure S2-A, computed from eigenvalues, with the same distribution) we retained the first axis, explaining 50.4% of the variance, for subsequent analyses. This axis could be described as the level of social interactions between the three juveniles, with non-negligible (loadings > 0.4, variables close to this threshold were also displayed) positive contribution of activity, competitive interactions, non-aggressive proximity and tongue-flicking behaviors, and a negative contribution of sheltering behavior (figure S2-B and table 2 for details). This axis will be subsequently referred to as juveniles' social activity. The second PCA axis (which mainly described the boldness behavior, figure S2-B) explained a non-negligible part of the variance (18.5%). Yet, when including this variable in our models we found no significant effects of this variable on focal individuals' relocation (z-value = -1.13, p = 0.26) and it did not change the other variables' significance.

Condition of informants and focal individuals

In our models, we considered three groups of variables describing informants' and focal individuals' condition (Table 2): the condition of focal individuals (age, SVL, BM, mother's SVL and BM; testing for Hyp. 1 and Hyp. 2 in figure 1), the condition of informants (mean age, mean SVL and BM, mean mothers' SVL and BM; testing for Hyp 2 in figure 1) and the absolute differences between informants' traits (SVL, BM, mothers' SVL and BM; testing for Hyp 3.a in figure 1). There was no correlation between the informants' condition and the absolute differences in informants' condition prior to the PCA analyses (Pearson correlation test; informants' SVL: p=0.10 / informants' BM: p=0.16 / SVL of informants' mothers: p=0.49 / BM of informants' mothers: p=0.39). Note that for the orientation decision (see later), the latter group of variables was replaced by the relative differences between informants'

Table 2.2: Variables describing the condition of juveniles.

Set of measured traits (in a same PCA)	PCA axes retained for analysis	Described traits (high contribution variables)	Explained variance
Joint behaviors of juveniles	Social activity	Activity (0.49) / Competitive interaction (0.43) / Non-aggressive proximity (0.42) / Tongue-flicking (0.38) / Sheltering (-0.44)	50.4%
Focal individual's condition	Morphology of focal individual's mother	SVL of focal individual's mother (0.63) / BM of focal individual's mother (0.68)	41.2%
	Focal individual's state	Focal individual's SVL (0.57) / Focal individual's BM (0.53) / Focal individual's age (-0.52)	31.3%
Informants' condition	Morphology of informants' mothers	SVL of informants' mothers (0.68) / BM of informants' mothers (0.68)	39%
	Informants' morphology	Informants' SVL (0.49) / Informants' BM (0.43)	31.3%
Absolute differences in informants' condition	Absolute differences in morphology of informants' mothers	Absolute differences in SVL of informants' mothers (0.62) / Absolute differences in BM of informants' mothers (0.62) / Informants' BM Absolute differences (0.46)	48.6%
	Absolute differences in informants' morphology	Absolute differences informants' SVL (0.83) / Absolute differences informants' BM (0.45)	29%
Relative differences in informants condition	Relative differences in morphology of informants' mothers	Relative differences in SVL of informants' mothers (0.63) / Relative differences in BM of informants' mothers (0.57)	48.5%
	Relative differences in informants' morphology	Relative differences in informants' SVL (0.59) / Relative differences in informants' BM (0.60) / Relative differences in informants' mothers' BM (0.44)	37%

This table presents most of the retained variables which describes the condition of the focal individual and informants, obtained by using PCA analyses to synthesize each set of correlated measured traits (first column). PCA axes are presented in their order of importance (in terms of explained variance), we attributed a name for each of them (second column). Traits with the most important contribution for each PCA axis were described in the third column, with their loadings displayed in brackets. A positive loading was associated with a positive correlation with the PCA axis and a negative one with a negative correlation.

traits (SVL, BM, mothers' SVL and BM, left informant minus right informant traits; testing for Hyp 3.b in figure 1), to spatially polarize the contrast between informants. To synthesize these variables we used a PCA and conserved the axes explaining most of the variance in each group (all selected axes explained > 70% of the variance, figures S3-A, S4-A, S5-A, and S6-A). All selected PCA axes and the respective part of explained variance are described in table 2.

Briefly, the first two axes of the focal individual's condition PCA (figure S3-B) resume the morphology (*i.e.*, SVL and BM concomitant variations) of the focal individual's mother and the focal individual's state (define as SVL, BM, and age concomitant variations). The first two axes of the informants' condition PCA (figure S4-B) resume the morphology of informants' mothers and informants' morphology. The first two axes of the absolute differences in informants' condition PCA (figure S5-B) resumed the contrast in the morphology of informants' mothers and the contrast in informants' morphology. Finally, the first two axes of the PCA on relative differences in informants' condition (figure S6-B) synthesized the differences in morphology of informants' mothers and differences in informants' morphology. In addition to these four PCAs axes, we also considered in our models the focal individual's sex, informants' sex ratio, and the fed informant's food intake (representative of the overall food availability as only one informant had access to food). Of note, there was no correlation between the fed informant's food intake and informants' morphology (Pearson correlation test, p = 0.54) or morphology of informants' mothers (Pearson correlation test, p = 0.48), and between sex and physical condition (Wilcoxon tests; focal individual's sex and state: p = 0.47, informants' sex-ratio and morphology: p= 0.42).

Statistical Analyses

All statistical analyses were performed with R software (R Development Core Team, 2008, version 3.6.3). Graphs were produced using the package "ggplot2" (Wickham 2016).

First, we analyzed the relocation probability of focal individuals after their confrontation with the two informants (Hyp. 1,2,3.a, figure 1). To do so, we used a Firth logistic regression (Firth 1993, 'brglm' function with a logit link, in "brglm" R package, Kosmidis and Firth 2021), a penalized likelihood regression method. This method was chosen to take into account data separation (Heinze and Schemper 2002), *i.e.* a predictor variable perfectly predicting the outcome variable (Albert and Anderson 1984), and quasi-separated data, that is likely present in our dataset given our sample size. We first tested for the population of origin as a potential random effect (Zuur et al. 2009). Note here that a daily effect was partially nested in the population variable as the different capture sites are associated with different hatching periods (Rutschmann et al. 2016) and as only one or two capture sites were used each day of experiments. The population random effect appeared non-significant (analysis of deviance test between null models with and without random effects, using standard logistic regressions; p = 0.47) and was dropped in our subsequent models. Then, we performed a model selection (Table S1) among the set of candidate variables, describing the informants and focal individual joint behaviors (social activity PCA axis; to test for Hyp. 1 and Hyp. 2), the focal individual's condition (morphology of focal individuals' mothers and focal individuals' state PCA axes, and focal individuals' sex; to test for Hyp.1), informants' condition (morphology of informants' mothers and informants' morphology PCA axes, informants' sex-ratio and the fed informant's food intake; to answer Hyp. 2), contrasts in informants' condition (absolute differences in the morphology of informants' mothers and absolute differences in informants' morphology PCA axes; to test for Hyp. 3.a) and the interactions between the fed informant's food intake and the focal individual condition variables (food intake with every three focal individuals' condition variables; to test for Hyp. 2). All used quantitative variables were scaled. This model selection was performed using the function 'dredge' (package MuMIn, Barton et al. 2009). Only one model appeared in $\Delta AICc < 2$ (threshold for the best models; Burnham and Anderson 2004), this model was used for all subsequent analyses.

The resulting model showed a sufficiently low variance inflation factor (maximal VIF of 1.71) for the interpretation of our statistical results (O'brien 2007). We measured the quality of our selected model by implementing a Nagelkerke pseudo-R-squared (Nagelkerke 1991). Effects of retained variables were tested through Wald tests on the selected model variables (since the model comparison approach on Firth's regression is still ongoing research, Kosmidis and Firth 2021). We also used partial Nagelkerke pseudo-R-squared on our model to rank variables by their level of explained variance and relative importance obtained from the model selection (sum of Akaike weights) to estimate all the variables' degree of importance (including the ones that did not appear in our selected model).

A second analysis was conducted to test which of the informants' traits influenced the direction of relocation (Hyp. 3.b, figure 1) when focal individuals left their terrarium (n=22). This time, we used simple logistic regressions with a binary response variable (leave toward left or right). In this model, we used the spatial distribution of male and female informants (female coming from the right and male coming from the left, male coming from the right and female coming from the left or the same sex left and right), fed informant spatial origin (coming from left or right), difference in informants' morphology (Table 2) and difference in morphology of informants' mothers (Table 2). The model was diagnosed as presented before, with an analysis of deviance instead of Wald tests for testing the variables' effects (likelihood-ratio tests, "car" R package, Fox and Weisberg 2018). Again, we obtained a sufficiently low VIF (maximum equal to 1.38) for the interpretation of our results.

Results

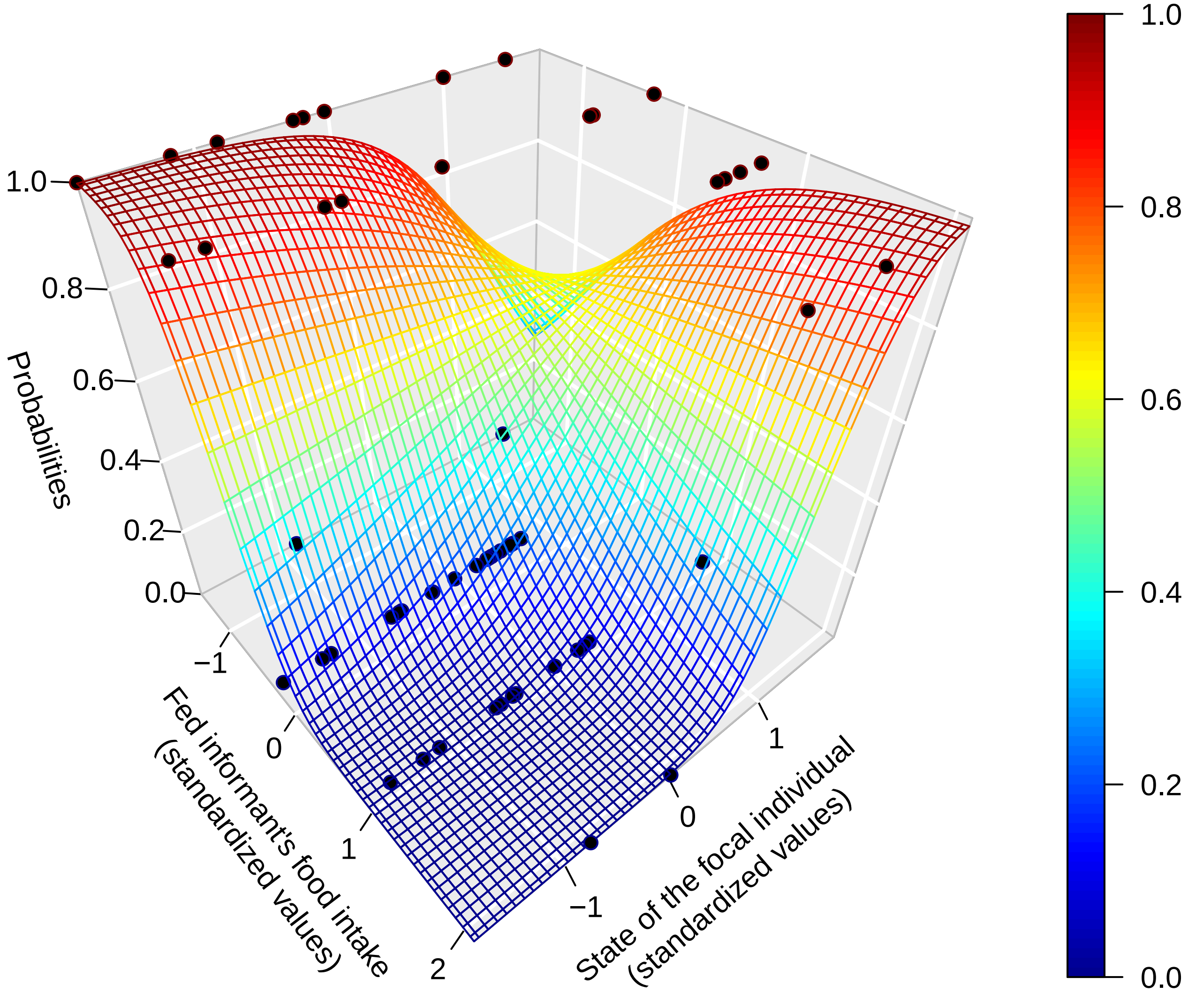
Table 2.3: Selected Firth's logistic regression about focal individuals' relocation probability.

	Parameter	**Coefficient**	**SE**	**z-value**	**df**	**P-value**	R^2
	Intercept	-0.46	0.53	-0.86		0.39	
Focal traits	Sex (male)	-1.86	0.92	-2.03	1	0.043*	0.21
	Individual's state (age/morphology)	0.85	0.49	1.75	1	0.081$^{\bullet}$	0.13
Informants' traits	Mothers' morphology	-0.87	0.42	-2.08	1	0.038*	0.22
	Fed informant's food intake	-2.26	0.77	-2.96	1	0.003**	0.49
Focal / informants interactions	Food intake x focal condition	1.91	0.66	2.87	1	0.004**	0.44
	Juveniles' social activity	1.59	0.6	2.67	1	0.008**	0.40

Analysis of the selected model (the only one in $\Delta AICc < 2$) is displayed here. For each retained variables (see Mat&Met) we displayed the average coefficient and its standard error. The partial Nagelkerke pseudo-R-squared (R^2) of each variable in the selected model were also displayed. Wald-tests were performed to test for the significance of each variable effect : we displayed here the associated statistics and p-values. Asterisks indicate the degree of significance. $^{\bullet}$: 0.05<p<0.1, * : 0.01<p<0.05, ** : 0.001<p<0.01, *** : p<0.001

Over the 56 experimental replicates, 22 focal individuals left their terrariums. The regression results revealed significant (p<0.05), or marginally significant (0.05<p<0.1), effects of focal individuals' state (age, morphology) and sex, informants' traits (maternal morphology, the fed informant's food intake), focal individuals' and informants' social activity, and the interaction term between the focal individual's state and the fed informant's food intake. All tests' statistics are available in Table 3. Shortly, the relocation probability of focal individuals decreased when the age of focal individuals increased and when their morphology decreased (figure S7-A), and was lower for males compared to females (figure S7-B). The relocation probability further decreased when the informants' maternal morphology decreased (*i.e.* lower mothers' SVL and BM, figure S8-B, table 3) and when the fed informant's food intake decreased (figure S8-A, table 3, representative of the overall food availability as only one informant had access to food). Relocation also depended on the social activity of focal and informant individuals (figure S9): it increased when the social activity increased, with higher levels of social interaction (non-aggressive

Figure 2.2: Joint effects of the fed informant's food intake and the focal individual's state on relocation probability of focal individuals.
The graph was produced by plotting the predicted probabilities as a function of the variable of interests' and the intercept's coefficients. Black dots display observations from all experimental replicates: a dot on the 0% probability surface corresponds to a focal individual who did not relocate, a dot on the 100% probability surface corresponds to a relocation.



proximity, competitive interactions, of tongue-flicking behaviors), higher activity level, and lower sheltering behaviors (Mat&Met, figure S2-B and Table 2). We also found that the food intake of the fed informant interacted with the phenotype of the focal individual to impact the focal individual's probability of relocation (figure 2): relocation probability increased for an informant with poor food intake confronted to a focal individual with a low score of individual's state (*i.e.* smaller morphological traits and older age) or for an informant with high food intake confronted to a focal individual with a high score of individual's state (*i.e.* larger morphological traits and younger age). Overall, the fitting quality of this model was good, with a Nagelkerke R-squared of 0.68.

We computed explained variance estimates for each variable included in the selected model by using Nagelkerke's partial R-squared (Table 3). Food intake of fed informants and joint behaviors had relatively high partial r-squared of 0.49 and 0.4; the sex of focal individuals and morphology of informants' mothers had respective r-squared of 0.21 and 0.22; the state of focal individuals (age and morphology) had an r-squared of 0.13. The r-squared of the interaction between the fed informants' food intake and the focal individual's state (0.44) was rather important relatively to the previously described values. The relative importance of all tested variables (obtained from model selection, Table S1) showed that the importance of the other non-selected variables was much lower (relative importance inferior to 0.27 for non-selected variables and superior to 0.84 for selected variables).

Table 2.4: Logistic regression on direction taking (analysis of deviance).

Parameter	χ^2	**df**	**P-value**
Fed informant origin	0.71	1	0.4
Sex contrast between informants	1.88	2	0.39
Morphologies differences between informants	0.004	1	0.95
Morphologies differences between informants' mothers	0.034	1	0.85

Results of the logistic regression on focal individuals' direction taking are displayed here. An analysis of deviance was performed to test for the significance of each variable effect (likelihood ratio tests). For each test, the chi-squared statistic and the associated p-values are displayed. Asterisks indicate the degree of significance. $^{\bullet}$: 0.05<p<0.1, * : 0.01<p<0.05, ** : 0.001<p<0.01, *** : p<0.001

We then analyzed the movement direction of the 22 focal individuals which left their terrariums; nine individuals went to the right and thirteen to the left. No significant effect was found among the tested variables, including the feeding treatment (Table 4, figure S10). Overall, we obtained a Nagelkerke R-squared of 0.15, suggesting a poor quality for the model.

Discussion

We experimentally investigated how social information is used for movement decisions when simultaneous sources of information (*i.e.*, informant individuals), coming from different environments, are available for decision making.

We found the relocation probability of focal individuals to be phenotype-dependent (in support of Hyp. 1: figure 1): relocation was more likely for females, for young individuals, and focal individuals with high morphology (high BM and SVL). We also found that the relocation probability of focal individuals increased when informants ate fewer available prey and originated from mothers with smaller morphological traits (low BM and SVL), suggesting the use of averaged social information for movement decisions (in support of Hyp. 2: figure 1). We further observed a phenotype dependence of the use of social information about food availability (in support of Hyp. 2: figure 1). We found no significant influence of absolute differences in traits between informants, potentially representative of information variability or reliability, on the relocation probability of focal individuals (contrary to the expectations from Hyp. 3.a: figure 1). Finally, when focal individuals left their terrarium, the position of the informant having access to food did not influence the direction of the movement, as for other relative differences in traits between informants (contrary to the expectations from Hyp. 3.b: figure 1).

Phenotype dependence of relocation

In many species, movement from one location to another can be related to environmental factors or the individual's phenotype (respectively context- and phenotype-dependence, Bowler and Benton, 2005). In the common lizard for example, dispersal is known to depend on the juvenile's phenotype such as its level of stress or its physical condition (Clobert et al. 2012). In our experiments, we further observed that the focal individual's state variable correlated with the relocation probability: it increased for focal individuals' with larger morphology (increase in BM and SVL) and lower age. The morphology of a neonate lizard, just after birth, directly reflects the amount of energetic reserve available from initial yolk reserves in the egg and therefore influences its performance in the early stage of life (Sinervo 1990, Olsson et al. 2002). As movements implied energetic cost (for displacement itself or potential interactions with competitors and predators, Bonte et al. 2012), larger reserves should provide an advantage for successfully relocating toward another habitat if necessary. Such a relationship between juveniles' physical condition and movements had already been observed in common lizards for natal dispersal (Meylan et al. 2002). Similarly, in the absence of any food intake, neonates only rely on the energetic reserves inherited from the eggs' yolk for early physiological performance. As a consequence, younger individuals may be more inclined to allocate such reserves towards relocation before these are consumed. It could be an advantage to rapidly use such natal reserves for displacement or exploration, especially as early-stage appeared to be central for future survival (Mugabo et al. 2010, Massot and Aragon, 2013). More generally, the youngest and smallest individuals are likely to be more sensitive to aggressiveness (Léna et al. 1998b) and could attempt to avoid it.

We also observed an effect of focal individuals' sex on their relocation probability: the propensity for juveniles to relocate was higher for females than for males. This is a surprising result as male-biased movements are often observed in lizard species (*e.g.*, Doughty et al. 1994, Schofield et al. 2012), including the common lizard (Le Galliard et al. 2005c). Yet, this result echoes what has been found in earlier experiments (Aragon et al. 2006b), where, when relocating after a confrontation with another neonate, female juveniles relocated with lower latency than males. Thus, it is likely that the observed female-biased movement would have disappeared if we had let the juveniles disperse for a longer period, to potentially give way to male-biased movements.

Use of social information from multiple sources

Our results suggest that focal individuals were able to integrate the averaged information from multiple sources to relocate or not from their initial location. Indeed, we observed that averaged informants' traits such as their mother's morphology and their food intake, as well as the juveniles' social activity, were significantly correlated with the relocation of focal individuals, while the differences in informants' traits were not used by focal individuals in our experiments. Our results also show that focal individuals modulate the use of social information according to their physical condition, with conditional use of social information about food availability depending on the morphology of the focal individual.

Social information that appeared to have a significant impact on the relocation of focal individuals (*i.e.*, informants' mother's morphology and food intake), explained a higher variance (Table 3) than the traits of focal individuals that had a significant impact on its relocation (sex, age and morphology). This suggests a prioritization of the surrounding social context over personal condition alone. This highlights the importance of context-dependence over phenotype-dependence for movement in our experimental setting. Such a result is not surprising given the fact that the main evolutionary factors driving movements are based on proximate or ultimate social contexts (Bowler and Benton 2005). Yet, the personal phenotype is still critical for determining movements when considering it in relation with the local or distant context (*e.g.* Léna et al. 1998a, Cote and Clobert 2007a), as suggested in our experiments by the important part of variance explained by the interaction between the focal individual state and the informants' food intake (Table 3).

Furthermore, different social cues appeared to have different importance for movement decisions: information about the immediate social environment such as food availability (displayed by food intake) or the informants' interaction behaviors (that could be reflected by juveniles' social activity) was more influential than social information such as conditions of informants' mothers which might depend on longer-term processes. One possible explanation is that information associated with immediate spatial or temporal context may be considered as more reliable, and/or pressing to consider, than long-term information (Seppänen et al. 2007, Spencer et al 2012). Since long-term context information can often prove unreliable due to changing environmental conditions, focusing on information about short-term context might prevent maladaptive decisions (Dubois et al. 2012).

To further explore the prioritization of information, better knowledge about the conflict between the different social cues is required. For example, it would be crucial to better understand how the information on long-term habitat quality conflicts with the information on immediate habitat quality. If information conflicts between personal and social sources are well-described in the literature (Kendal 2009), this is not the case for conflicts between different social cues.

On the meaning of informants' traits

In our experiment, interacting conspecifics might convey information about either the local or the distant habitat, or both of them. Distinguishing between these hypotheses would require further experimental investigation that is beyond the scope and the aims of this paper. Given our experimental design, we looked at spatial movement on a small spatial scale, potentially reflecting microhabitats selection.

We observed that focal individuals' relocation propensity increased when the morphology of informants' mothers decreased, and when focal lizards were facing fed informants who ate few or no crickets. These informants' traits could be indicators of low resource availability in a close environment, and therefore related to the avoidance of a poor environment by the focal individual, given the importance of resources for early-life survival (Mugabo et al. 2010, 2011, Massot and Aragon 2013). The physical condition of informants' mothers could also be representative more broadly of habitat quality as it could vary with other important environmental parameters as density (Massot et al. 1992) or abiotic parameters such as temperature (Chamaillé-Jammes et al. 2006). Focal individuals' avoidance of informants whose mothers were of poor physical condition could then reflect the avoidance of an environment of low quality. Such an avoidance had already been observed with dispersal increase in case of too high competition (Léna et al. 1998a, Cote et al. 2008a) or abiotic parameter that does not match energetic requirement (Bestion et al. 2015). Since the focal individuals did not encounter informants' mothers, the information about their condition may be conveyed by informant's phenotype measured not here (as odors, specific behavioral traits, locomotion abilities) and that correlates with the informants' mother condition due to genetic transmission or maternal effects (Meylan et al. 2002, 2004, Meylan and Clobert 2004, Meylan et al. 2007).

We also observed that relocation probability increased when the fed informant's food intake and the focal individual's physical condition were both low or both high. In the first case, individuals seemed to avoid an environment with insufficient resources given their conditions (low energetic reserves), while in the second case, they seemed to escape unnecessary competition for resources while having a good enough physical condition to relocate toward a less competitive habitat. Such results further suggest a phenotype dependence of social information use for movements, as it was observed previously (Cote and Clobert 2007a, Cote and Clobert 2010, but also Baines et al. 2019 in another species) but never with information on direct resources availability at stake.

Finally, we observed that relocation propensity increased when juveniles' (informants and focal individual) social activity increased. This effect is difficult to interpret, it might result from an assessment of competitiveness of informants by the focal individual as the presence of active and aggressive conspecifics is likely to reflect high levels of direct competition in the environment (Sih et al. 2004, *e.g.* Garland et al. 1990). It could also simply be due to the presence of an active and explorative focal individual, since such individuals should be more likely to leave their home environments (Cote et al. 2010). More knowledge about the individual behaviors of each juvenile would have helped to refine our interpretations. This variable is also likely to reflect the degree of interactions between informants and the focal individual, and as the behavior of an individual, and ultimately its space use, can be influenced by the behaviors of encountered conspecifics in this species (Cote and Clobert 2007b, Cote et al. 2008a) it could then reflect information transfer between these individuals. In addition, a measure of stress hormones (as corticosterone, see Belliure et al. 2004) would have been useful to precise the influence of informants' stress level on focal individuals' relocation.

Direction of movement

Previous findings have shown a limited but existing ability to orientate in space for the common lizard (Strijbosch et al. 1983), in accordance with the spatial cognition abilities of reptiles (Wilkinson and Huber 2012). In particular, there is accumulating evidence on various species of lizards highlighting important spatial memory abilities (Ladage et al. 2012), including for orientation (*e.g.* Zuri and Bull 2000, Day et al. 2003). Lizards have also long-term memory of encountered conspecifics (Korzan et al. 2007). For these reasons, we could expect lizards to be able to orientate from the cues obtained by social interactions. Yet, we found no effect of the relative differences between informants (including the difference in food access) on movement orientation when relocation occurred. Given the small sample size for direction analyses (22 replicates), we have to be very cautious about the validity of such effects. These results might suggest that focal individuals considered social cues or signals from present information sources as information about local conditions, for which no orientation is needed. It could reflect that rather than using information about each encountered individual, a juvenile could use a summary of all information for spatial decisions. Alternatively, individuals might not have had access to sufficient cues for visual orientation, the design being symmetrical and the arrival lasting a few seconds only. Decisions on direction would then mainly rely on informants' arrival with olfactory signals or cues left by informants in corridors (Aragon et al. 2006a, c). It is quite surprising that such olfactory cues were not used, as they have an important influence on the selection of an environment according to the conspecifics quality (Léna et al. 1998b, 2000, Aragon et al. 2006c). Perhaps the time spent by informants in the corridors was not sufficient for the focal individuals to link informants and their corridors of origin. Further experiments, focusing for example on pheromones carried by informants, would be necessary to make any conclusion on the actual use of these odors.

Conclusion

Our experiment showed that when an individual is presented with social information from multiple sources, the average of this information, in some cases interacting with the individual's phenotype, influences movement. Differences in information sources were not used in our experiments for relocation or orientation decisions. This use of information could reflect an assessment of the quality of the surrounding habitat, with the use of cues or signals on resource availability and the degree of intra-specific competition. We also showed that, for the common lizard, a hierarchy of information could occur, as information related to the immediate environment seemed to be of primary importance in explaining relocation responses.

Author contribution

MB, MR, JC, SJ and AR designed the experiment. MB, JC and AR performed the field work. MB performed all experiments and analyses. MB, MR, JC, SJ and AR wrote the manuscript.

Acknowledgements

We thank S. Liegeois, C. Fosse, A. Le Pajolec, C. Lauden and D.Miles for their help during experiments and field work. We thank the Parc National des Cévennes for allowing us to use the different sampled sites. We thank L.Lejeune and D.Miles for helpful comments on the manuscript. This work beneficiated from the scientific environment of the Laboratoire d'Excellence entitled TULIP (ANR-10-LABX-41). J. Cote is supported by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement n^{o} 817779). The 'Office Nationale des Forêts', the 'Parc National des Cévennes', and the regions Auvergne, Rhône Alpes and Languedoc Roussillon delivered permits to capture and handle lizards (permits 81-17 2013-05; 2013274-0002, 2013/DREAL/259).

Funding

This work was supported by the Agence Nationale de la Recherche (ANR-17-CE02-0013).

Competing interests

The authors have no competing interests to declare.

Ethical approval

The capture and rearing conditions have been validated by an ethical committee (DAP number 5897-2018070615164391-v3), to ensure the welfare of involved animals.

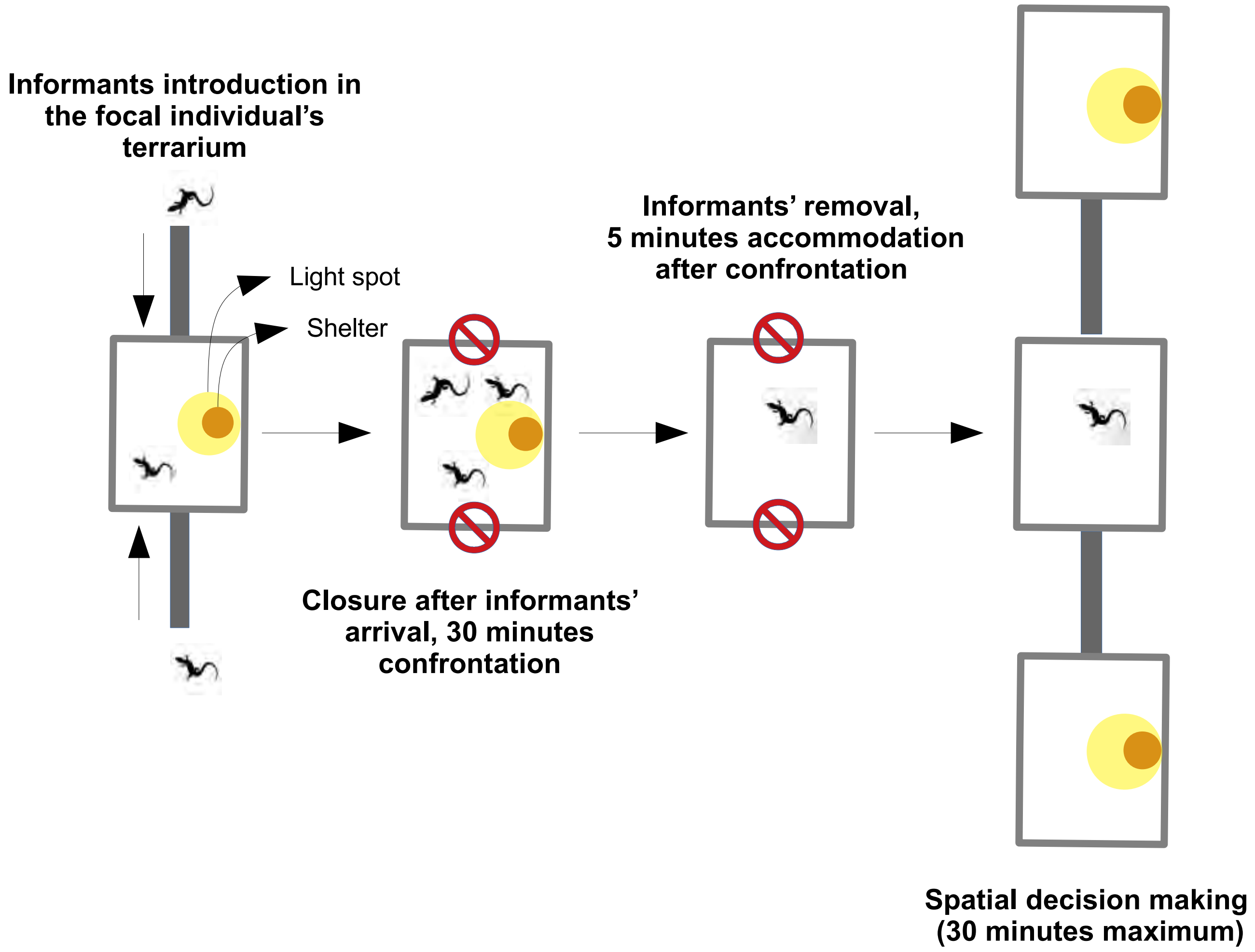
Supplementary Materials

Table S1: Model selection on Firth's logistic regressions (focal individual's relocation).

Parameters										Importance
Focal sex	+	+	+	+	+	+	+		+	0.84
Focal state	+	+	+	+	+	+	+	+	+	0.99
Focal mother's morphology							+			0.22
Informants' sexes		+							+	0.22
Informants' morphology				+						0.20
Morphology of informants' mothers	+	+	+	+	+	+	+	+	+	0.88
Fed informant's food intake	+	+	+	+	+	+	+	+	+	1
Social activity	+	+	+	+	+	+	+	+	+	0.99
Fed informant's food intake x Focal sex						+				0.15
Fed informant's food intake x Focal state	+	+	+	+	+	+	+	+	+	0.99
Fed informant's food intake x Focal mother's morphology										0.04
Absolute differences in informants' morphology			+						+	0.27
Absolute differences in morphology of informants' mothers					+					0.19
Model rank	1	2	3	4	5	6	7	8	9	
AICc	52	54.3	54.3	54.7	54.8	54.9	54.9	55.8	56.2	
$\Delta AICc$	0	2.27	2.31	2.75	2.83	2.94	2.95	3.85	4.21	
Akaike weight	0.181	0.058	0.057	0.046	0.044	0.042	0.041	0.026	0.022	

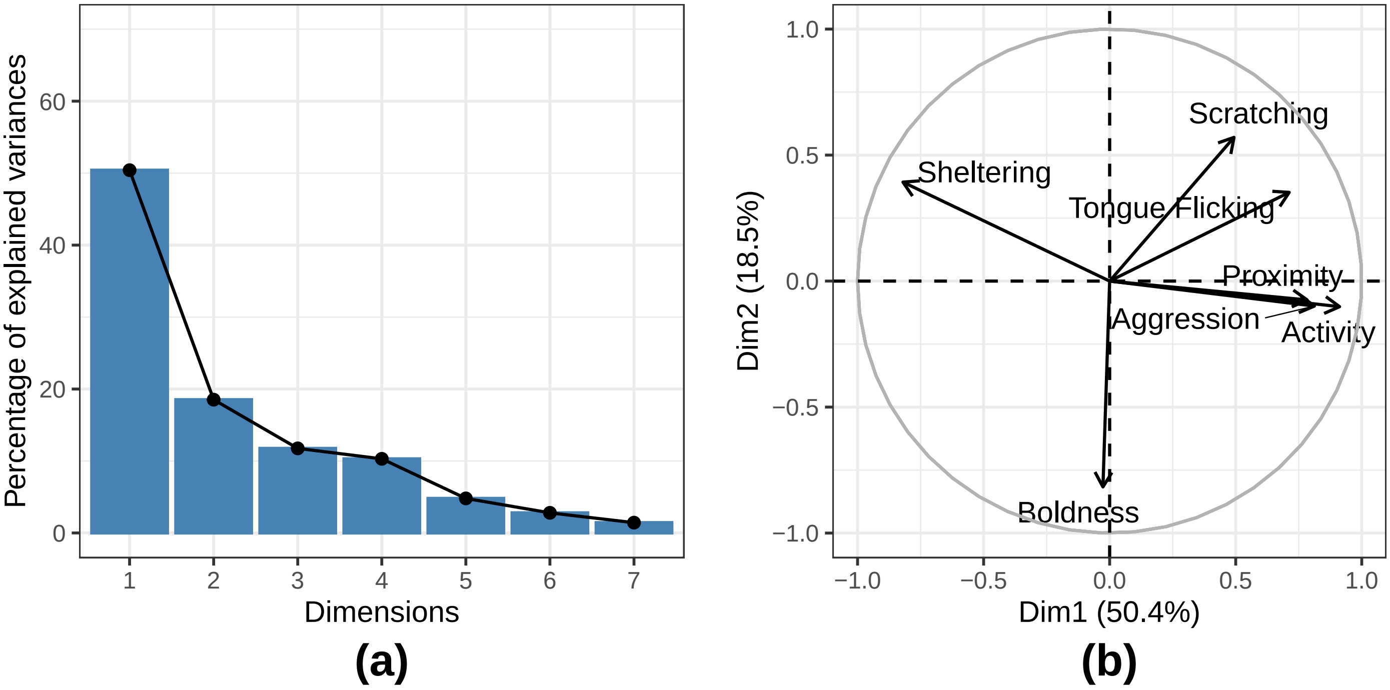
Results of the comprehensive model selection (performed with the 'dredge' function, "MuMIn" R package) on Firth's logistic regressions on focal individuals' relocation probability are displayed here (with all models in $\Delta AICc < 4$). All variables of interest (see Mat&Met) were included in the global model. These variables (in their order of appearance) could be grouped as focal individuals' traits, informants' traits, juveniles joint behaviors, interaction terms between informants and focal individuals (including interactions between the focal individual's traits and food intake of the fed informant) and informants' traits contrasts. Models are ranked according to the corrected Akaike information criterion (AICc), AICc differences between the best model and other ones are also displayed. For each model, the selected variables are indicated by a "+" symbol. Variables present in the selected model (only model in $\Delta AICc < 2$) are in bold. The importance (sum of models' Akaike weight) of each variable is given on the left.

Figure S1: Experimental design.



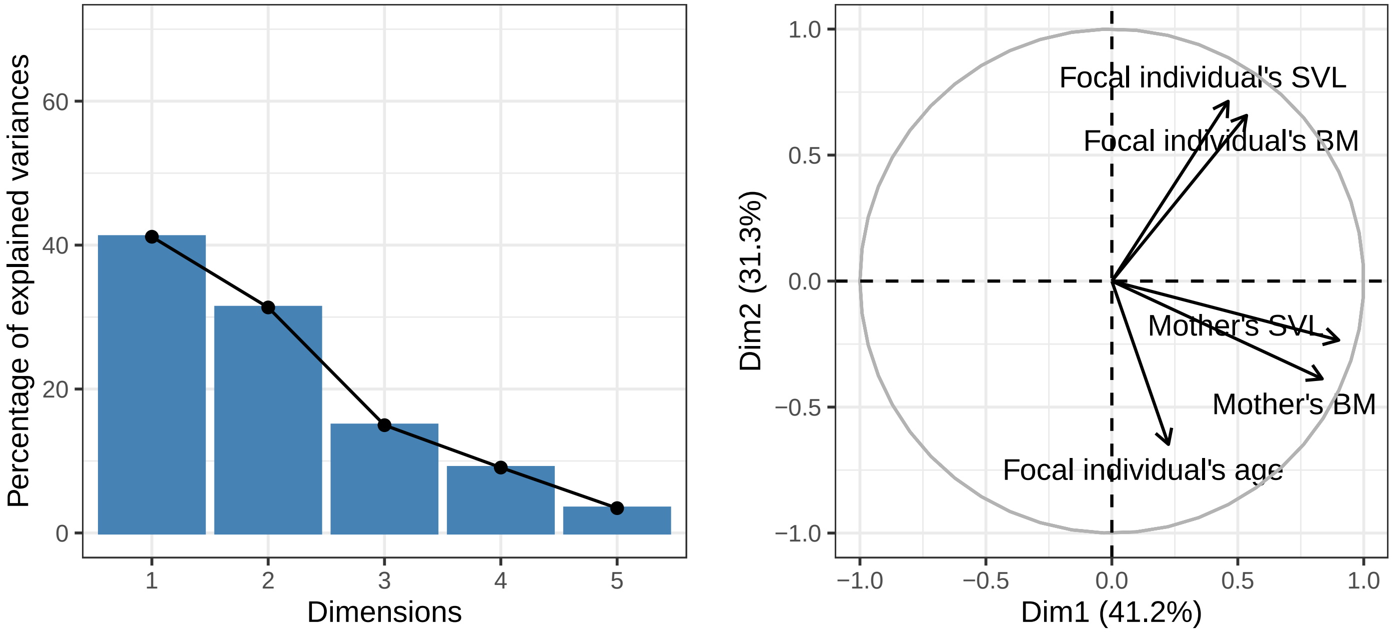
Experimental design is summed up in this scheme. The main four steps are successively presented. Corridors are represented as filled grey rectangles, terrariums as empty rectangles. Accesses closure is represented by the crossed out signs.

Figure S2: Juveniles' behaviors PCA graph of variables.
A- Explained variance of the PCA components.
B- PCA graph of variables (first and second axes).



All used variables are described in Mat&Met, scratching refers to escaping attempts, proximity to non-aggressive proximity, aggression to competitive interactions. Each arrow is associated with a behavior displayed at their extremities. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on the x-axis and y-axis (percentages).

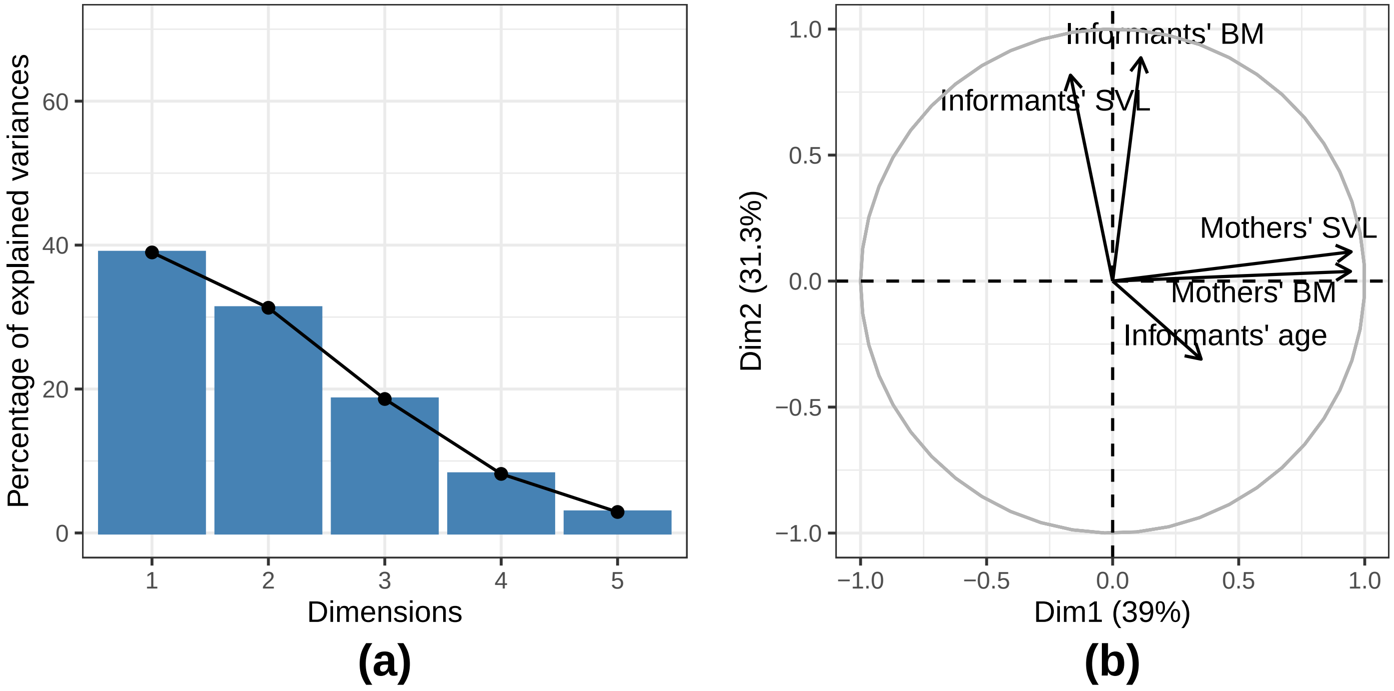
Figure S3: Focal individuals' condition PCA graph of variables.
A- Explained variance of the PCA components.
B- PCA graph of variables (first and second axes).



(a) **(b)**

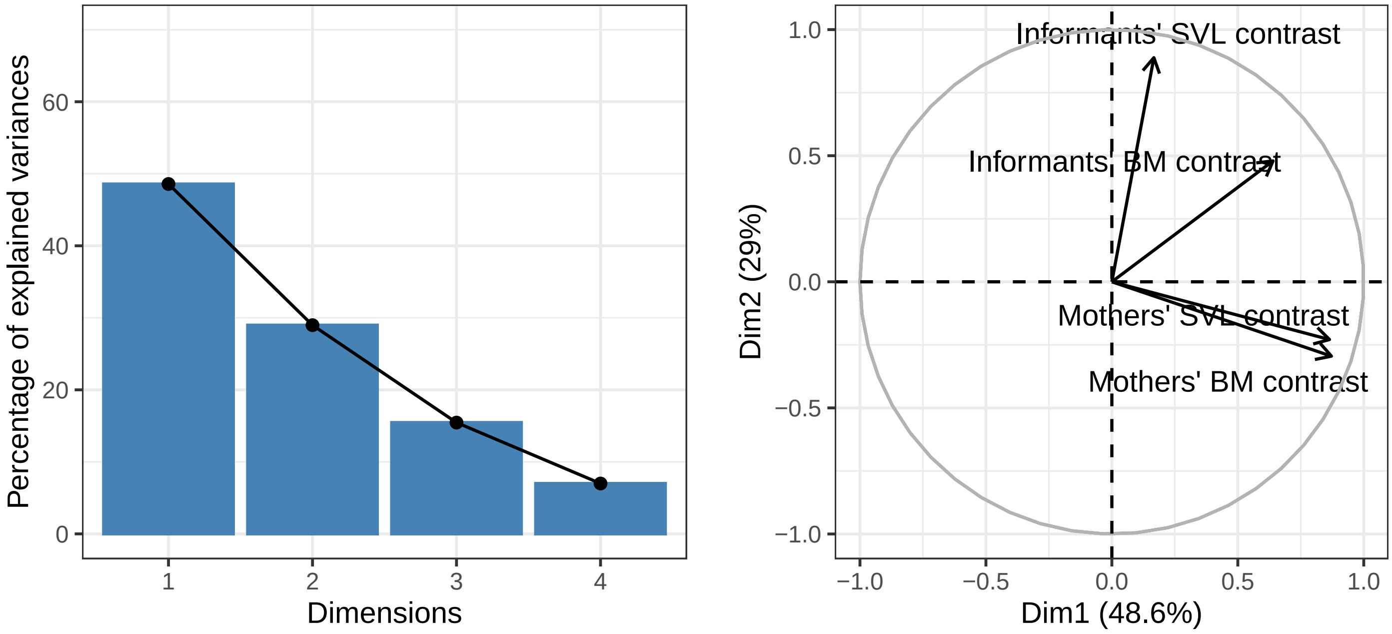
Each arrow is associated with a focal individual trait (body mass, snout-to-vent length, age) or a trait of the focal individual's mother (body mass, snout-to-vent length) displayed at their extremities. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on the x-axis and y-axis (percentages).

Figure S4: Informants’ condition PCA graph of variables.
A- Explained variance of the PCA components.
B- PCA graph of variables (first and second axes).



Each arrow is associated with an average informants’ trait (body mass, snout-to-vent length, age) or an average trait of informants’ mothers (body mass, snout-to-vent length) displayed at their extremities. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on the x-axis and y-axis (percentages).

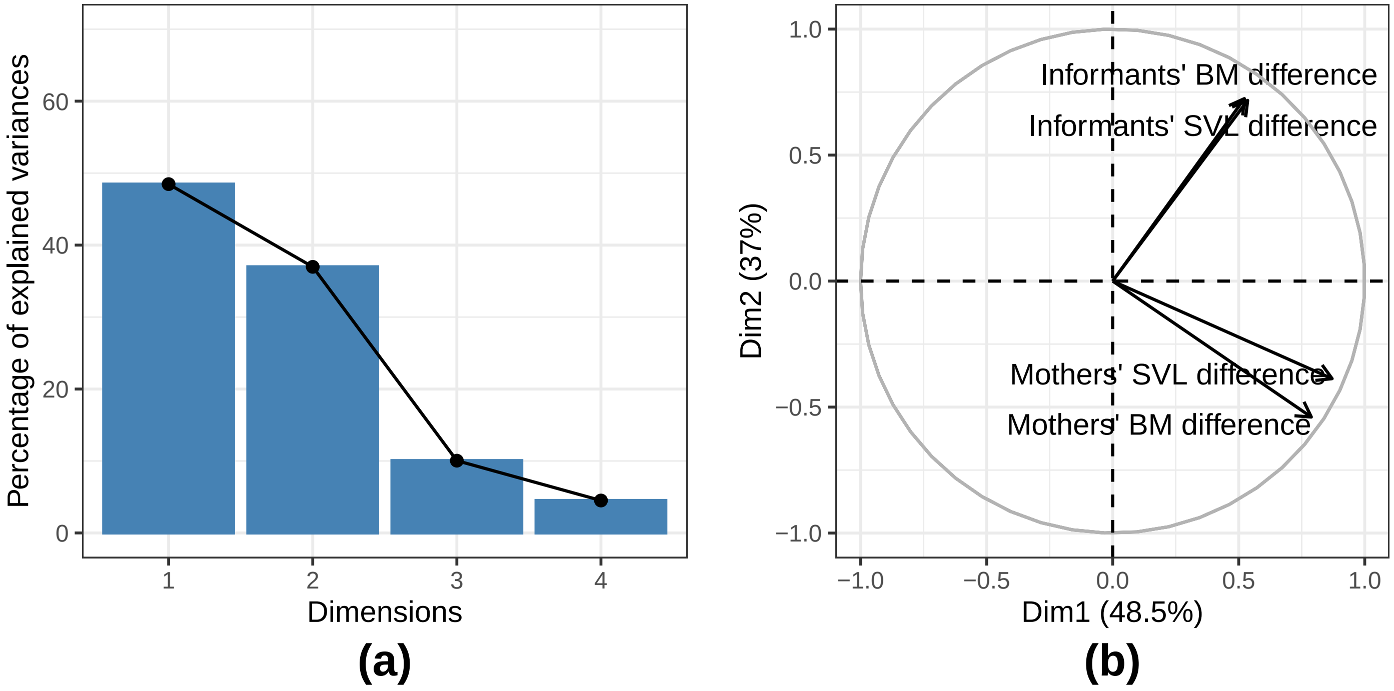
Figure S5: Absolute differences in informants’ condition PCA graph of variables.
A- Explained variance of the PCA components.
B- PCA graph of variables (first and second axes).



(a) **(b)**

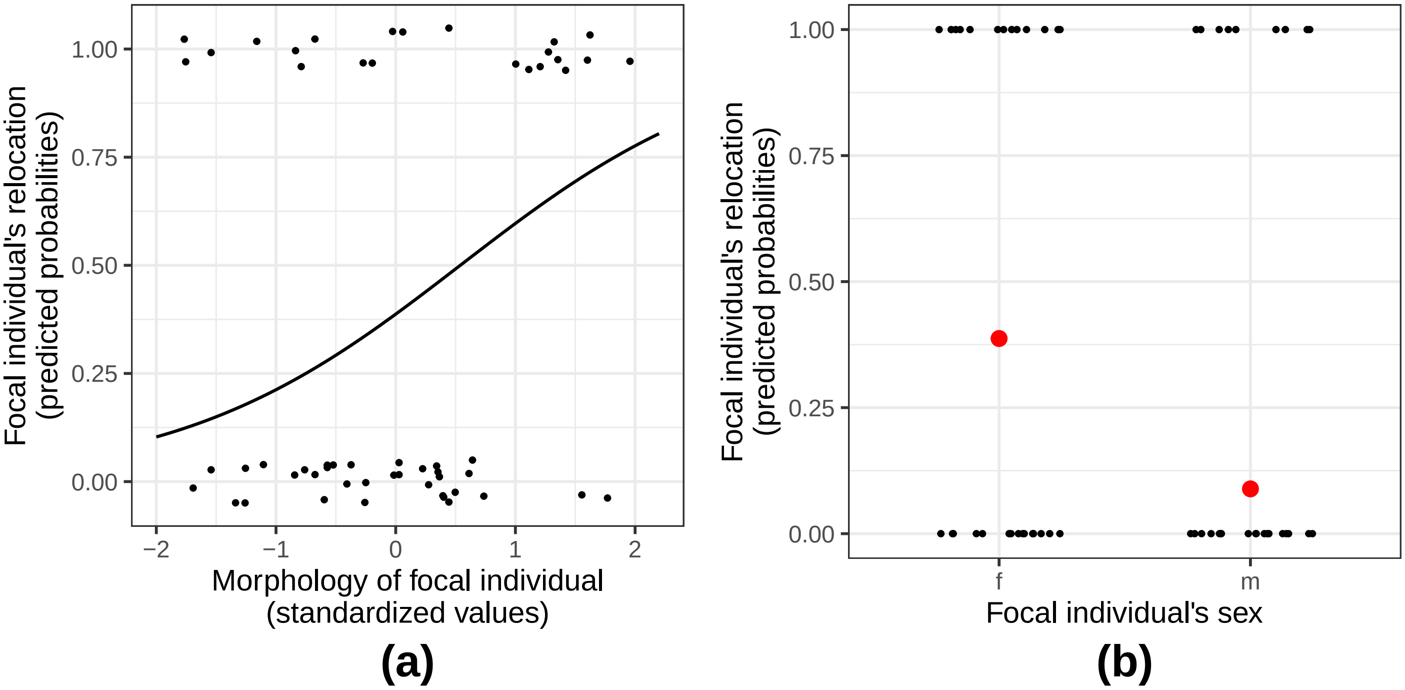
Each arrow is associated to a trait contrast (absolute difference) between informants (body mass, snout-to-vent length) or informants’ mothers (body mass, snout-to-vent length) displayed at their extremities. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on the x-axis and y-axis (percentages).

Figure S6: Relative differences in informants' condition PCA graph of variables.
A- Explained variance of the PCA components.
B- PCA graph of variables (first and second axes).



Each arrow is associated with a trait raw difference between informants (left coming informant minus right coming informant) or informants' mothers (body mass, snout-to-vent length) displayed at their extremities. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on the x-axis and y-axis (percentages).

Figure S7: Focal individuals' traits effects on their relocation probability.
A- Predicted probabilities of focal individuals' relocation as a function of focal individuals' state.
B- Predicted probabilities of focal individuals' relocation as a function of focal individuals' sex.

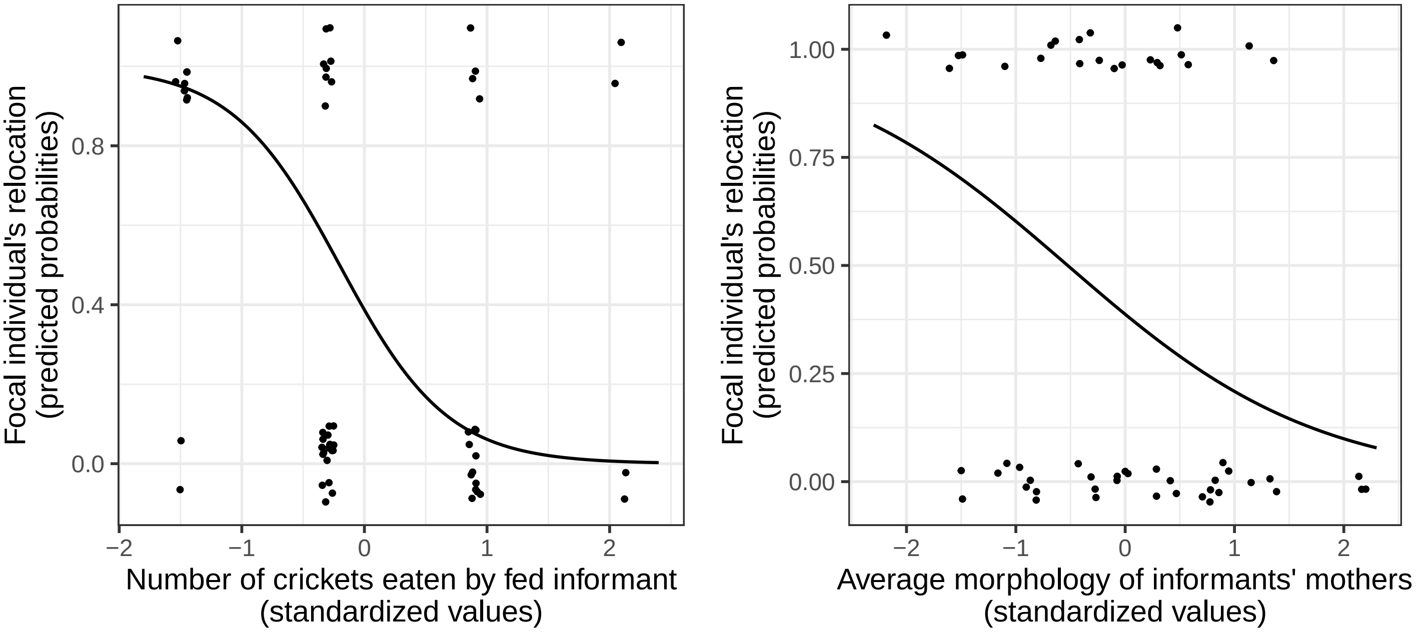


We looked at the distribution of focal individuals' relocation predicted probability as a function of focal individuals' significant traits. Plots were obtained from the Firth's logistic regression results (Table 3) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). Effects degree of significance is displayed in table 3. Black dots display observations from all experimental replicates: a dot around the 0% probability line corresponds to a focal individual who did not leave its terrarium, a dot around the 100% probability line corresponds to a focal individual who left its terrarium. These dots were jittered (vertically for quantitative variables, horizontally for qualitative variables) to gain in readability.

A- The variable is defined in Mat&Met (Table 2).

B- Red dots display the effects at each possible level (female or male). On the x-axis, "f" refers to female individuals and "m" refers to male individuals.

Figure S8: Informants' traits effects on focal individuals' relocation probability.
A- Predicted probabilities of focal individuals' relocation as a function of the fed informant's food intake.
B- Predicted probabilities of focal individuals' relocation as a function of the morphology of informants' mothers.



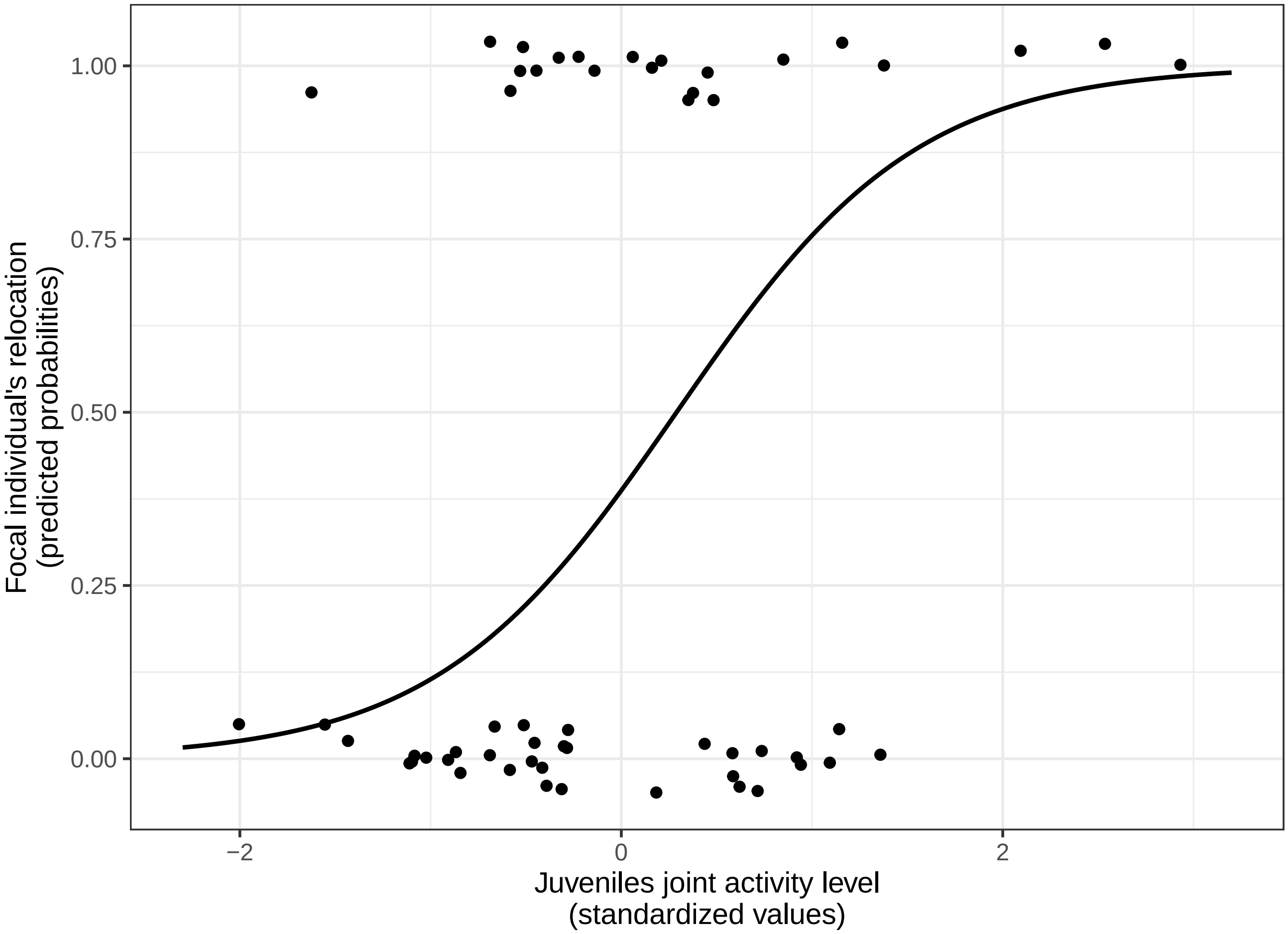
(a) **(b)**

We looked at the distribution of focal individuals' relocation predicted probability as a function of informants' significant traits. Plots were obtained from the Firth's logistic regression results (Table 3) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). Effects degree of significance is displayed in table 3. Black dots display observations from all experimental replicates: a dot around the 0% probability line corresponds to a focal individual who did not leave its terrarium, a dot around the 100% probability line corresponds to a focal individual who left its terrarium. These dots were jittered vertically to gain in readability.

A- The black dots were slightly jittered horizontally to improve readability.

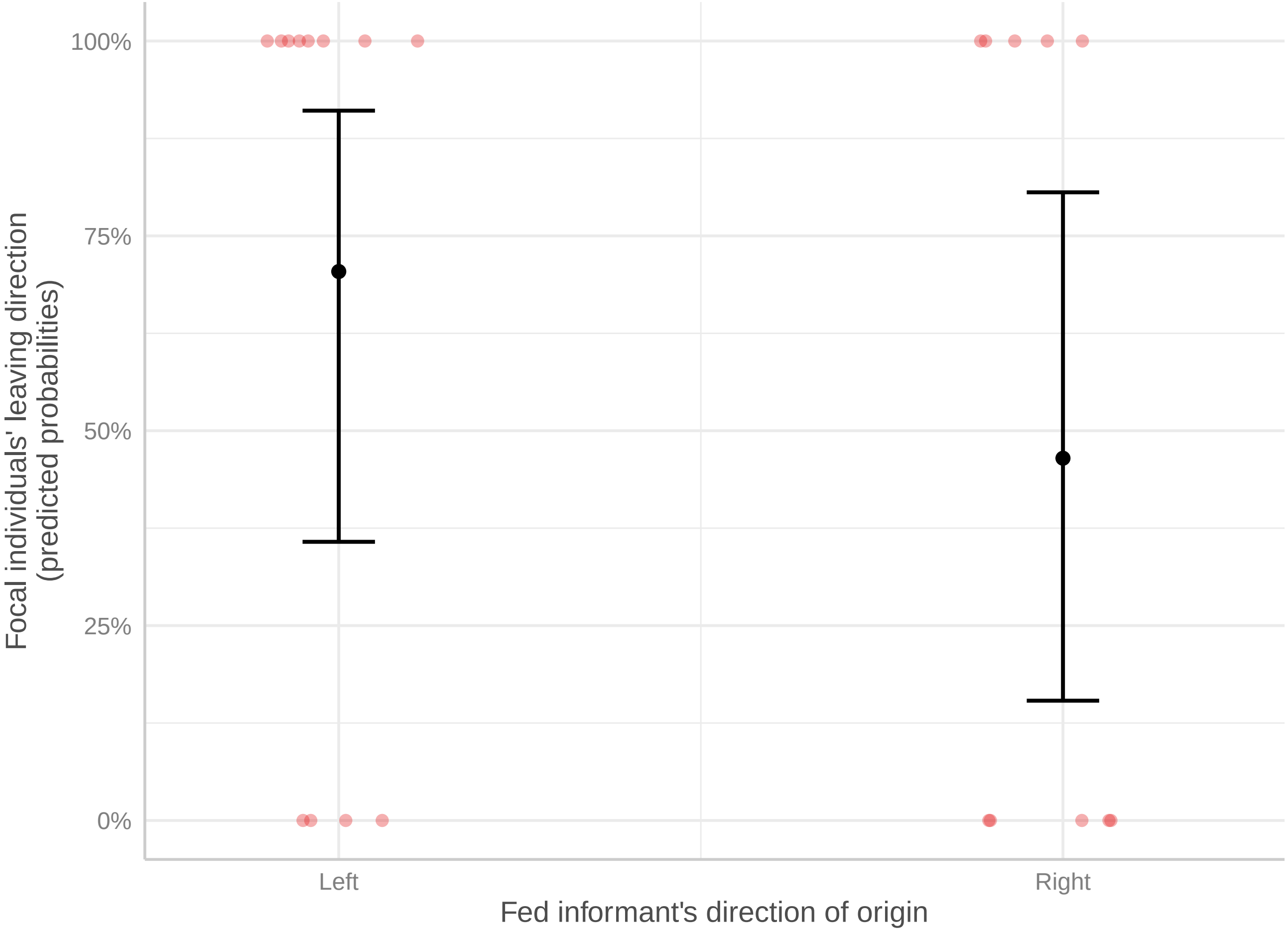
B- The variable is defined in Mat&Met (Table 2).

Figure S9: Predicted probabilities of focal individuals' relocation as a function of juveniles social activity.



We looked at the distribution of focal individuals' relocation predicted probability as a function of juveniles' social activity. The variable is defined in Mat&Met (Tables 1 and 2). The plot was obtained from the Firth's logistic regression results (Table 3) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average or their baseline level as they are standardized). Effects degree of significance is displayed in table 3. Black dots display observations from all experimental replicates: a dot around the 0% probability line corresponds to a focal individual who did not leave its terrarium, a dot around the 100% probability line corresponds to a focal individual who left its terrarium. These dots were jittered vertically to gain in readability.

Figure S10: Feeding treatment absence of effect on orientation.



We looked at the distribution of focal individuals' relocation direction predicted probability as a function of fed informant original direction (through a logistic regression). Effect degree of significance is displayed in table 4. The graph was obtained by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, *i.e.* their average, or were fixed to their mean level for categorical variables), the package "ggeffects" was used to produce the plot. Black bars represent 95% confidence intervals for predicted probabilities. Red dots represent observations from all experimental replicates: a dot on the 0% line corresponds to a focal individual who did not leave its terrarium, a dot on the 100% line corresponds to a focal individual who left its terrarium. These dots were horizontally jittered to gain in readability.

Chapter 3

The use of immigrant-based information for dispersal in nature: importance, information content and interactions with the phenotype and local context

M. Brevet[1,2], S. Jacob[1], M. Massot[3], M. Richard[1], A. Rutschmann[1,4], D. Rozen-Rechels[3], J.F. Le Galliard[3], J. Clobert[1]

[1]Station d'Ecologie Théorique et Expérimentale (SETE), UAR 2029, CNRS, 09200, Moulis, FR

[2]Université Toulouse III Paul Sabatier, 31062, Toulouse, FR

[3]Institut d'Écologie et des Sciences de l'Environnement (IEES) de Paris Sorbonne Université, CNRS-UMR 7618, Paris, FR

[4]School of Biological Sciences, University of Auckland, Auckland, NZ

En preparation pour une soumission dans la revue Ecology Letters

Présentation et résumé du Chapitre

Dans ce troisième chapitre, nous avons exploré l'utilisation des informations basées sur les immigrants dans la nature, afin d'examiner si l'utilisation d'information sociale locale est également accompagnée d'une utilisation de l'information sociale sur des habitats distants. L'objectif était de mieux comprendre comment ces informations basés sur les immigrants étaient précisément utilisées, c'est-à-dire si elles dépendaient du contexte local vécu et/ou du phénotype de l'individu focal, et si leur utilisation dépendaient de la distance, de la variabilité et du nombre de sources d'information. Nous nous attendions à ce que les informations provenant des immigrants soient utilisées en fonction des besoins des individus (définis par leur phénotype et leur contexte), et à ce que les informations ne soient utilisées que lorsqu'elles ne sont pas trop coûteuses (par exemple, accessibles en termes de distance) ou trop incertaines (trop variables ou transmises par trop peu d'immigrants).

Il existe peu de preuves de l'utilisation d'informations basées sur les immigrants pour les décisions de dispersion dans la nature. Nous avons étudié l'existence et l'importance de l'utilisation de telles informations sur des contextes sociaux et non sociaux éloignés. Nous avons également exploré comment cette utilisation dépendait du phénotype, du contexte local et de la nature des informations provenant des immigrants (distance parcourue par les immigrants, nombre et variabilité des sources d'information). Pour ce faire, nous avons utilisé un suivi de 30 ans sur le lézard vivipare, dans un site d'étude naturel, et pendant lequel les déplacements des individus ont été évalués. Nous avons constaté que la dispersion natale dépendait simultanément des contextes locaux et distants (sur lesquels informent les immigrants), principalement en interaction avec le phénotype des nouveau-nés. Les individus ont montré une préférence pour le même contexte vis-à-vis de l'information locale et apportée par les immigrants, ce qui soutient la cohérence des décisions de dispersion. L'utilisation des informations issues de l'immigration dépendait également du phénotype de l'individu et de la nature de l'information : les individus semblaient adapter leur choix d'habitat en fonction de leur phénotype, sauf lorsque l'information était peu fiable ou coûteuse à exploiter (trop grande variabilité, faible répétabilité, longue distance); dans ces cas, nous avons principalement observé une dispersion biaisée vers le contexte natal, ou un évitement des contextes compétitifs. Cette étude a confirmé à la fois la valeur opérationnelle de l'information basée sur les immigrants pour les décisions de dispersion et son utilisation dépendante du phénotype de l'individu et du contexte local. Nos résultats suggèrent aussi qu'un choix d'habitat adapté pourrait se produire avec cette information disponible, mais la prise en compte de sa qualité suggère que l'information potentiellement coûteuse à exploiter est utilisée différemment, probablement pour minimiser les coûts possibles de la dispersion.

Abstract

Dispersal movements may be informed by locally acquired social information, often based on individual phenotype. In contrast, there is little evidence for the use of immigrant information for dispersal decisions in nature. Such information would be advantageous since it potentially indicates the quality of surrounding habitats before departure, but it is also more likely to be unreliable (little information, on potentially difficult to reach and varied habitats). We investigated the existence and significance of the use of such information in distant social and non-social contexts. We also explored how this use was dependent on the phenotype, the local context, and the nature of the immigrant-based information (distance traveled by immigrants; number and variability in information sources). To do so, we conducted a 30-years mark-capture monitoring on the common lizard. We found natal dispersal to be concurrently dependent on both local and distant contexts, mostly in interaction with the focal neonates' phenotype. We observed similar responses in the use of local and immigrant-based information, with symmetrical correlations between natal dispersal and the same environmental parameters locally and at distance (immigrants' habitat of origin), which supports consistency in dispersal decisions. The use of immigrant-based information also depended on the individual's phenotype, the local context, and the nature of information. Individuals appeared to adjust their dispersal decisions depending on their phenotype and the value of information relative to the local context. In contrast, when the information was poorly reliable or costly to exploit (too high variability, little repeatability, long-distance), we mainly observed responses to immigrant-based information about low competitive distant context or context alike the natal one. This study suggests the use of immigrant-based information for dispersal decisions, depending on the individual's phenotype and the local context. Accounting for the cost of using uncertain or difficultly accessible information suggests that information potentially costly to exploit is used differently, probably to minimize the possible costs of dispersal.

Introduction

Dispersal is known to be often context-dependent (Bowler and Benton 2005, Clobert et al. 2009, 2012): an individual adapts its dispersal behavior on information gathered locally or by prospecting other habitats (abiotic characteristics of habitat, conspecific or heterospecific factors). Such dependency is particularly well-known for the departure decision (*e.g.* Clobert et al. 2012, Le Galliard et al. 2012, Scandolara et al. 2014) but occurs also for settlement decisions (*e.g.* Doligez et al. 2002, 2004, Szymkowiak 2013). Acquisition of information on potential habitats for settlement can be acquired by directly interacting with the environment (Bowler and Benton 2005) or by collecting social information on these habitats (*e.g.* Doligez et al. 2002, 2004). Yet, for individuals with low displacement abilities or with high costs associated with exploring unknown environments (Bonte et al. 2012, Delgado et al. 2014), an important fitness gain can be provided if immigrants from distant habitats deliver information on their habitat of origin to individuals of the population they integrate. Such an adaptive use of social information when personal information is more costly, is indeed expected to occur (Kendal et al. 2009, *e.g.* Forsman et al. 2007, Grüter and Leadbeater 2014). Such information transfer had been rarely demonstrated (Cote and Clobert 2007a, Jacob et al. 2015b), and has never been reported under natural conditions nor has its importance been assessed. As for local social information, immigrant-based information should be conditioned on the phenotype and on the local context to balance the cost to disperse (Bowler and Benton 2005). In particular, an individual should disperse when the surrounding habitats appeared to be of better quality than the present one (as predicted by the ideal free distribution: Fretwell and Lucas 1970, Fretwell 1972), or to select a habitat similar to the natal area (natal habitat preference induction: Davis and Stamps 2004, Stamps and Davis 2006, *e.g.* Sanz-perez et al. 2018).

Yet, compared to local social information, immigrant-based information is likely to be associated with a high level of uncertainty. First, such information cannot be confirmed by personal information in particular for species with a restricted capacity for exploration, while such confirmation is central to balance the risk associated with its use (King and Cowlishaw 2007, Kendal et al. 2009, *e.g.* Cronin et al. 2013). Second, even if the social information obtained from immigrants is reliable, there is a potential uncertainty on the attainability of the habitat on which information has been provided (distance, direction, time lag). Responses dependent on the nature of the immigrant-based information (*e.g.* distance of the information source origin, variability between information sources, number of information sources) should also reduce the cost associated with its intrinsic uncertainty (*e.g.* Kern and Radford, 2017). Indeed, the distance of the immigrant's habitat of origin could mediate the use of immigrant-based information. If too close, the immigrant could convey information of low interest because potentially already accessible in the home range of the information receiver, hence information associated with long traveled distance by the immigrant should be favored (Rushing et al. 2015). However, the distance could also be associated with a built-in cost: the further the habitat of origin, the more costly it could be to be reached (Rousset and Gandon 2002, Stamps et al. 2005). At last, when multiple information sources are present the use of the average information (as in Brevet et al. 2022a,b, in prep) could be mediated by the variability and the number of information sources: we could expect information to be more reliable if the information sources are alike (low uncertainty associated with information, *e.g.* Heinen and Stephens 2016) and numerous (reflecting a potential repetition of the information, King and Cowlishaw 2007, or greater accessibility of such distant habitats, Cote and Clobert 2010). Yet, the likelihood of conflicting information sources is also increasing with the number of immigrants and could lead to conflicts over the quality, direction, and distance of the immigrant habitat of origin.

To investigate the use of immigrant-based information in dispersal decisions, we used the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model species. Natal dispersal is particularly well-described in this species, with evidence for a multi-determined context-dependent dispersal (Clobert et al. 2012, Brevet et al. 2022a,b in prep), with particular importance on social information. The use of immigrant-based information has also been experimentally demonstrated (Cote and Clobert 2007a), but only for information on density and with no assessment in a natural context. We used here a thirty-year mark and recapture monitoring (Brevet et al. 2022b in prep) of a natural study site, in which the position and phenotype of all individuals were recorded allowing us to have access to the dispersal status of captured individuals and the social context over all the study site.

Here we specifically aimed to investigate whether immigrant-based information is used for dispersal decisions in natural conditions, by considering a multi-factorial description of both the local context and the ones of the immigrants' origin (referred to as distant context further on). We hypothesized that the environmental parameters locally influencing candidate dispersers' decisions should be also used similarly when information on these parameters is provided by immigrants about their habitat of origin (Figure S1, a.). We also aimed to investigate whether this immigrant-based information use is conditioned by the local context (Figure S1, b.) and/or by the focal individual's phenotype. At last, we examined how the immigrants' traveled distance, the number of immigrants, and the variability among information sources (*i.e.* characteristics of the immigrants' habitats of origin) affected the use of the immigrants' information (Figure S1, c,d.).

Material and Methods

Model species and study site

The common lizard (*Zootoca vivipara*) is an ovoviviparous species of the Lacertidae family. It lives on the ground, mainly in wetlands, and feeds on small invertebrates. It mates in March and April, with parturition occurring in July and August. Dispersal occurred mostly within the ten first days after birth (Massot et al. 1992, Léna et al. 1998a).

We used data from a 30-year mark-recapture monitoring (from 1989 to 2019, Brevet et al. 2022) in a study site located on the Mont-Lozère (44°30'N, 3°45'E, 1420m height), in the Cévennes National Park, France. Individuals were marked by a toe-clipping method (validated by an ethical committee: DAP #5897-2018070615164391 v3). Capture sessions took place mainly in June, before parturition. At each capture, the GPS position was recorded using a Thales GPS ProMark3 device (meter precision). Phenotypic measurements of individuals were also performed: snout to vent length (SVL, mm precision), body mass (BM, half decigrams precision), sex, and age class (subadult: one-year-old, adult: more than one-year-old).

All captured gestating females were brought to a rearing facility. Females were kept in individual terrariums (dimension: 18.5 x 12 x 11 cm) in which they were provided with light and heat (25W light bulb, 6 hours a day), a shelter, and an appropriate substrate (2 cm of sterilized soil). Their terrariums were moistened at least three times a day and they were fed at least once a week. After they gave birth they were separated from their litter and all neonates were measured the day after their birth (SVL, BM and sexed using Lecomte et al., 1992, method). Each female was released with her offspring at the female last capture location, two to four days after parturition.

Dispersal characterization and potential environmental drivers

Based on the existing literature (Massot and Clobert, 2000, Lecomte et al. 1994, Massot 1992, Brevet et al. 2022b), an adult individual's home range is estimated to have a 15m-radius circle. Dispersal was defined according to the literature, as a movement of a neonate beyond a 30m threshold during its first year of life (Massot and Clobert 1995, Clobert et al. 1994: no return rate beyond this threshold), *i.e.* a relocation outside its natal area (such that its new home range have no overlap with its natal area). We did consider only the focal neonates for which at least one immigrant arrived in their home range (N=647).

The used dispersal metric takes into account the emigration of individuals (whether or not they left their natal habitat) but also the mortality differential between dispersers and residents (*i.e.* realized dispersal). Therefore, a low probability of dispersal may reflect here a low emigration rate but also that individuals which dispersed did not survive their first year of life, and thus were not recaptured and considered in the analyses. It should be noted, however, that previous studies on long-term monitoring of this species have found no difference in mortality between dispersers and residents (Le Galliard et al. 2005c), suggesting that the dispersal observed here is mostly related to emigration decisions.

We considered that the perceptual range of a neonate (referred to as the natal area further on) was of the size of an adult home range (Brevet et al. 2022b in prep). Environmental and internal factors that could influence dispersal were chosen according to the literature on the species (Clobert et al. 2012, Cote et al. 2012). We only retained factors that appeared to be significantly or marginally significantly ($p<0.1$) correlated with dispersal when we only considered the local context-dependence (Brevet et al. 2022b in prep): the substrate's characteristics, the density of conspecifics, the sex ratio of neonate conspecifics, and the age, corpulence and sex ratio of adult conspecifics in the natal area (Table S1). This choice was made to avoid over-parameterization while selecting factors that are most likely to be used as information about distant habitats. The parameters that influence choice at the local level are also likely to be those that would be used for a choice of potential arrival habitats (*e.g.* Kim et al. 2009). The environmental context in the natal area was computed as described in Brevet et al. (2022b, in prep): we considered all conspecifics (or substrates) present in the natal area of an individual and we averaged their characteristics. In the particular case of the substrate's characteristic description, we used a principal component analysis, in which we retained only the first axis, which described mainly the openness and temperature of the substrate in the natal area (increase in openness and temperature when the substrate's characteristic index increase). Of note, an increase in the sex ratio corresponds to an increase in the proportion of males.

Immigrant-based information on their environmental context at birth (referred to as distant context further on) was computed by considering the averaged environmental context in the natal area of the immigrant (the same way as for local context estimations, Brevet et al. 2022b for details). We considered only neonate immigrants which were born before the focal neonate to ensure that the immigrants had the potential to be present before the focal individual's departure. Such immigrants are then likely to convey recent information. As most neonates were not recaptured the year of their birth (but in June of the year after), we cannot know the location of immigrant neonates at the time of a focal individual's dispersal decision. We therefore considered that a neonate immigrant was present in a focal neonate's natal area if its ultimate home range (computed from its recapture locations as a subadult or adult, *i.e.* more than one-year-old) overlaps with it. When multiple immigrants were present in the natal area of a focal individual, we averaged the information among immigrants (such averaged information was previously demonstrated to be used for movement decisions: Brevet et al. 2022a in prep). To take into account the encounter probability with an immigrant in a focal natal area, we attributed weight to each immigrant that corresponded to the area common between the focal natal area and the immigrant's ultimate home range.

The distance traveled by an immigrant was computed as the distance between an immigrant's natal location and the barycenter of its recapture locations at subadult or adult age. When multiple immigrants arrived in the same natal area, we averaged their traveled distance (with the same weight accounting for the encounter probability as previously described) and we computed the variability of each element of the distant environmental contexts, through a weighted standard deviation between all immigrants' habitat of origin. The effect of the number of immigrants on information was also tested, it was computed as the sum of weight for each present immigrant in the natal area.

All used variables were scaled before data analyses.

Data analyses

All statistical analyses were performed with R software (R Development Core Team, 2008, version 3.6.3). Graphs were produced using the package "ggplot2" (Wickham 2016).

As focal siblings shared the same local environmental context, the same immigrant-based information, and had non-independent dispersal behaviors (Massot et al. 1994), we choose randomly only one individual per litter when we had available data on the natal dispersal for several siblings (approximately one-third of studied clutches). To measure the sensitivity of our results to the difference in dispersal responses among siblings, we resampled 1,000 times among the siblings for which we had available data and we performed the same analysis as presented subsequently for each resampling. We then compared the distribution of the statistics obtained through resampling with the original model to check for its stability.

We performed two mixed logistic regressions, with the year of capture as a random effect as it was tested to be significant before the implementation of models (analysis of deviance test between null models with and without random effects: $p<0.001$). The first one was used on all neonates and tested for the influences on dispersal of the local context, the information conveyed by immigrants (*i.e.* the distant context), the focal individual's phenotype, and the immigrants' traveled distance (Table S1). We considered the interactions between the local context, the information conveyed by immigrants, and the focal individual's phenotype, as well as the interactions between the local context, the information conveyed by immigrants, and the distance traveled by immigrants (Table S1). We did not consider the interaction terms between the local context and the distance traveled by immigrants, which had no biological meaning. The second one was used only for neonates with multiple immigrants in their natal area (N=493) to test for the influence of multiple immigrant-based information sources, without taking into account the focal individuals' phenotype. We considered the interactions between the local context, the information conveyed by immigrants, and the variability between distant contexts or the number of immigrants (Table S1). We did not consider the interaction terms between the local context and the variability between distant contexts or the number of immigrants, which had no biological meaning.

We used a backward model selection based on the parameters p-values: we sequentially removed the term with the higher p-value, excepting if this term is implied in a higher-order interaction with a lower p-value (in which case we removed it once the higher-order interaction was removed) At each step we computed the Akaike information criterion (AIC). We selected the last model that kept an AIC inferior to the AIC of the previous step model (Table S1).

We used the variance inflation factor to check for multicollinearity ("car" R package, Fox and Weisberg 2018) before implementing our model and performing the model selection. We obtained sufficiently low maximal values in both models to avoid any statistical bias (first model: 1.64, second model: 2). Models fit were estimated by the Nakagawa coefficient of determination (r-squared, Nakagawa and Schielzeth, 2013). The robustness of our models (Royston et al. 2009) was tested through bootstrap resampling on our dataset (1,000 iterations), used to check p-values stability (using "boot" R package, see Canty and Ripley 2020). Models results were analyzed using analyses of deviance (likelihood-ratio tests, "car" R package, Fox and Weisberg 2018). For the first model only, the effect sizes of fixed effects were computed from the odds-ratio of these variables (then converted in Cohen's d, using the « effectsize » package). We then checked if spatial and temporal autocorrelation of environmental variables (computed as in Brevet et al. 2022b in prep) were significantly correlated with their effect sizes (both distant and local context effects size), using a linear regression.

Results

	Parameter	Coefficient	SE	df	χ^2	P-value
First model: all immigrants-informed neonates						
Local context (x Focal individuals' phenotype)	Local adults' sex ratio	-0.711	0.173	1	10.29	0.001**
	Local substrate's characteristics	-0.238	0.131	1	5.07	0.024*
	Local adults' sex ratio x Focal individuals' sex	0.552	0.239	1	5.33	0.020
	Local adults' corpulence x Focal individuals' sex	-1.175	0.299	1	14.22	<0.001***
	Local adults' corpulence x Focal individuals' corpulence x sex	-0.845	0.308	1	7.52	0.006**
(Local x) Distant context x Focal individuals' phenotype	Distant densities x Focal individuals' sex	-0.527	0.259	1	4.12	0.042*
	Distant adults' corpulence x Focal individuals' sex	0.728	0.307	1	4.46	0.034*
	Distant adults' corpulence x Focal individuals' corpulence x sex	1.010	0.349	1	8.38	0.003**
	Distant substrate's characteristics x Focal individuals' corpulence x sex	-0.512	0.235	1	4.75	0.029*
	Local x distant densities x Focal individuals' corpulence	-0.284	0.122	1	5.38	0.020*
(Local x) Distant context x Immigrants' distance	Distant adults' corpulence x Immigrants' distance	-0.365	0.135	1	4.80	0.028*
	Local x distant adults' age x Immigrants' distance	0.248	0.122	1	4.12	0.042*
Second model: all neonates informed by multiple immigrants						
Local context	Local adults' age	-0.291	0.142	1	4.16	0.041*
	Local adults' sex ratio	-0.427	0.156	1	5.97	0.014*
	Local substrate's characteristics	-0.434	0.155	1	7.76	0.005**
(Local x) Distant context x Immigrants number	Distant adults' corpulence x Immigrants' number	0.505	0.176	1	8.17	0.004**
	Distant substrate's characteristics x Immigrants' number	-0.463	0.229	1	4.08	0.043*
	Local x distant adults' sex ratio x Immigrants' number	-0.866	0.259	1	11.10	<0.001***
(Local x) Distant context x Variability	Distant neonates' sex ratio x variability	-0.398	0.137	1	8.35	0.003**
	Distant adults' corpulence x variability	-0.516	0.155	1	11.02	<0.001***
	Local x distant adults' sex ratio x variability	0.350	0.152	1	5.30	0.021*

Table 3.1: Logistic regression on natal dispersal decision according to the local and distant contexts, the focal individuals' phenotype and the distance traveled by immigrants.
Only significant effects are displayed here ($p<0.05$). These results were obtained from an analysis of deviance (likelihood ratio tests) on models retained after backward selection (Materials & Methods for details, Table S1). Variables are distinguished in several categories described in the left column. For each retained variables we displayed the associated coefficient and the standard error (SE) on this coefficient. For each variable the chi-squared statistic and the associated p-values are displayed. Asterisks indicate the degree of significance. $^{\bullet}$: $0.05<p<0.1$, * : $0.01<p<0.05$, ** : $0.001<p<0.01$, *** : $p<0.001$

Marginal and conditional r-squared (*i.e.* coefficient of determination) of our models were respectively of 0.27/0.32 and 0.2/0.29. All subsequently presented significant correlations appeared to be robust as their p-values were all close to the median values obtained after bootstrap resampling (Figures S6 and S8, obtained median values from significant variable always remained significant).

Local context dependence of dispersal

We found a local context dependence of dispersal with significant correlation ($p<0.05$, Tables 1) between dispersal and the adults' age (only in the second model), the adults' sex ratio, and the substrate's characteristics (in both models). We found also significant interactions (in the first model only, Table 1) between the local context and the focal individuals' phenotype, with interactions between the adults' corpulence in the natal area and the focal individuals' sex and corpulence, and between the adults' sex ratio and the focal individual's sex. The triple interaction between the adults' corpulence in the natal area and the focal individuals' sex and corpulence was particularly sensitive to the difference in dispersal responses among siblings (Figure S5: the median of p-values obtained from resampling was superior to 0.1), this relationship will not be discussed afterward.

The direction of the relationships was identical to what had been found in Brevet et al. (2022b in prep): the dispersal probability decreased when the adults' age, the adults' sex ratio, or the temperature and openness of substrate increased (Figure S2-A,B,C), or when the adults' corpulence decreased for males or increased for females (Figure S3-A,B). We also found the adults' sex ratio relationship to be steeper for females compared to males (Figure S3-C,D).

Distant context dependence of dispersal

In addition to the local context, we found a distant context dependence of dispersal (Table 1), *i.e.* a dependence on immigrant-based information, about their original habitats. We first observed significant correlations between the dispersal and the adults' corpulence or the substrate's characteristics in the immigrants' natal areas, in interactions with the focal individuals' sex and corpulence. We also found dispersal to depend on the conspecifics density in immigrants' natal areas, in interaction with the focal individuals' sex. The triple interaction between the adults' corpulence in the natal area, the focal individuals' sex and corpulence, as well as the interaction between the conspecifics density in distant natal areas and the focal individuals' sex, were particularly sensitive to the difference in dispersal responses among siblings (Figure S5: the medians of p-values obtained from resampling were superior to 0.1), these relationships will not be discussed thereafter.

The relationships with the adults' corpulence in the local and distant contexts were symmetric: the dispersal probability of focal individuals increased when the adults' corpulence in immigrants' natal area increased for males and decreased for females (Figure 1-A,B), contrary to what was observed locally (Figure S3-A,B). The dispersal probability of focal males with a low corpulence also increased when the substrate's temperature and openness increased (Figure 1-C,D). This was also observed for females with a high corpulence, but with a less steep relationship. The converse relationship was found for males with a high corpulence (also observed for females of low corpulence, but with a less steep relationship). Finally, we observed a significant interaction between the local density, the density in distant areas, and the focal individuals' corpulence (Table 1): for focal individuals with a high corpulence in a low local density, the dispersal probability increased when the density in distant areas increased (Figure 2-A,B,C).

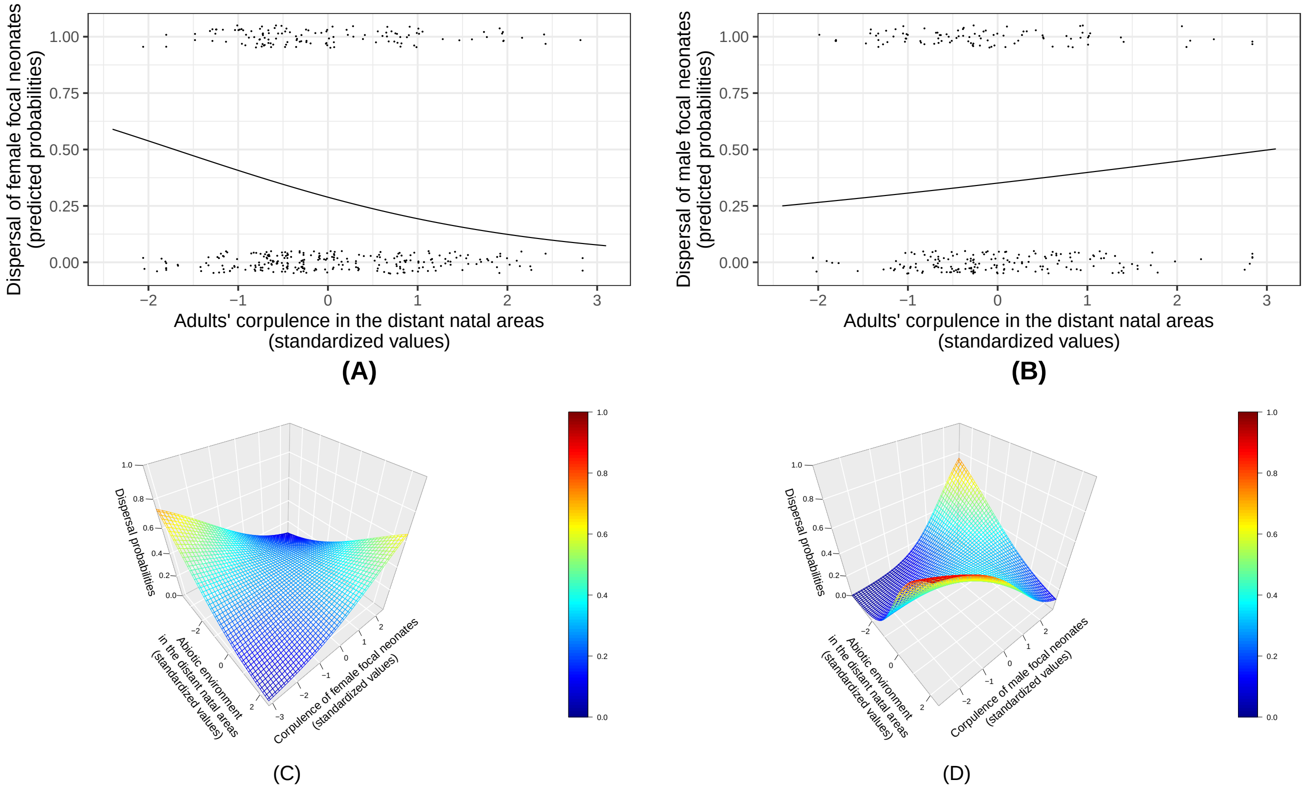


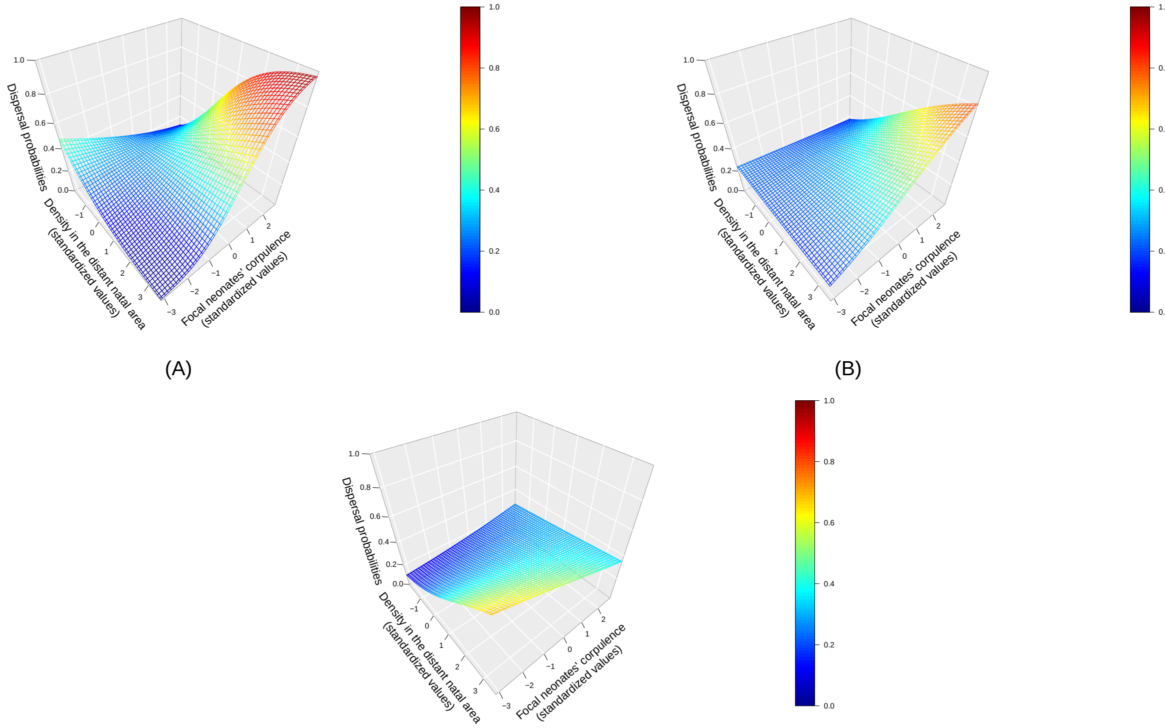
Figure 3.1: Phenotype-dependent use of the information from distant environmental context. These relationships were observed in the first model (with all informed individuals). The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses).

A- Predicted probabilities of the females' dispersal as a function of the adults' corpulence in the distant natal areas. The black dots represent the data set with one dot per individual followed (observations associated with dispersal for dots around the 0% probability line, or with no diserspersal around the 100% probability line). These dots were jittered vertically to gain in readability.

B- Predicted probabilities of the males' dispersal as a function of the adults' corpulence in the distant natal areas. The black dots represent the data set with one dot per individual followed (observations associated with dispersal for dots around the 0% probability line, or with no diserspersal around the 100% probability line). These dots were jittered vertically to gain in readability.

C- Joint effects of the substrate's characteristics in the distant natal areas and the focal individuals' corpulence on dispersal probability of females. An increase in the substrate's characteristics index refer to an increase of openness and temperature of substrates in the natal area. The graph is plotted in the range of observations for the variables considered on the X-axes.

D- Joint effects of the substrate's characteristics in the distant natal areas and the focal individuals' corpulence on dispersal probability of males. An increase in the substrate's characteristics index refer to an increase of openness and temperature of substrates in the natal area. The graph is plotted in the range of observations for the variables considered on the X-axes.



(A)

(B)

(C)

Figure 3.2: Phenotype- and local context-dependence of the information use about the distant density.

These relationships were observed in the first model (with all informed individuals). The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). The graphs are plotted in the range of observations for the variables considered on the X-axes.

A- Effects of the density in the distant natal areas and the focal individual's corpulence on dispersal probability, for a low local density. The local density has been set to the first quartile of its distribution.

B- Effects of the density in the distant natal areas and the focal individual's corpulence on dispersal probability, for a medium local density. The local density has been set to the median of its distribution.

C- Effects of the density in the distant natal areas and the focal individual's corpulence on dispersal probability, for a high local density. The local density has been set to the third quartile of its distribution.

The relative importance between elements of the distant environmental context was closed to what is observed locally (Figure 3, Brevet et al. 2022 in prep) with major importance of the distant adults' corpulence (Cohen's d close to 0.3) and the distant adults' sex ratio (Cohen's d close to 0.2), and relatively high importance of the distant density (Cohen's d>0.1). Interestingly, we observed a symmetry in Cohen's d sign between local and distant context, highlighting opposite direction of effects between distant and local contexts (a context avoided by an individual locally, is also avoided in distant areas). We also observed a significant correlation between the temporal autocorrelation of environmental variable and the variable's effects size (F-value=13, p=0.015): effects' size of variables increased with their temporal autocorrelation (Figure S4).

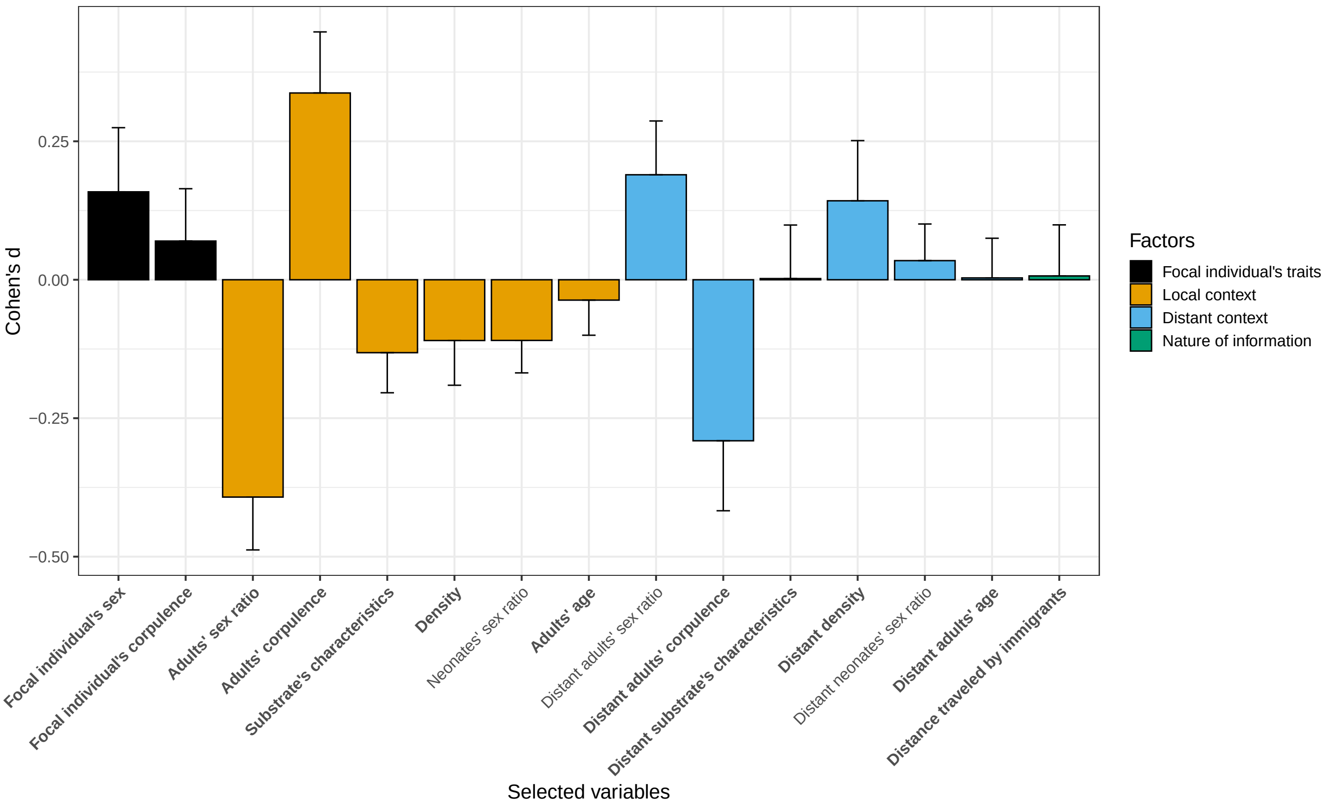


Figure 3.3: Hierarchization of fixed effects for the first model.
The names of significant variables (X-axis) are displayed in bold. The different categories of variables are identified by different colors. The error bars represent the standard deviation of effects size (computed from the standard deviation of coefficients, the same way than effects size).

Influence of the number of immigrants, variability in distant contexts and immigrants' traveled distance on responses to immigrants-based information

Number of immigrants

Correlations between immigrant-based information and dispersal responses were sometimes function of the number of immigrants, occasionally in interaction with the local context (Table 1). The dispersal probability increased when the adults' corpulence in distant areas and number of immigrants increased (Figure 4-A). For high numbers of immigrants (Figure 4-C,D), the dispersal probability increased when the local adults' sex ratio decreased and the distant adults' sex ratio increased (but also, with a less steep slope, when both the local and distant adults' sex ratio increase for a low number of immigrants; Figure 4-B). For low numbers of immigrants (Figure 4-B), the dispersal probability increased when the local and distant adults' sex ratios were both high.

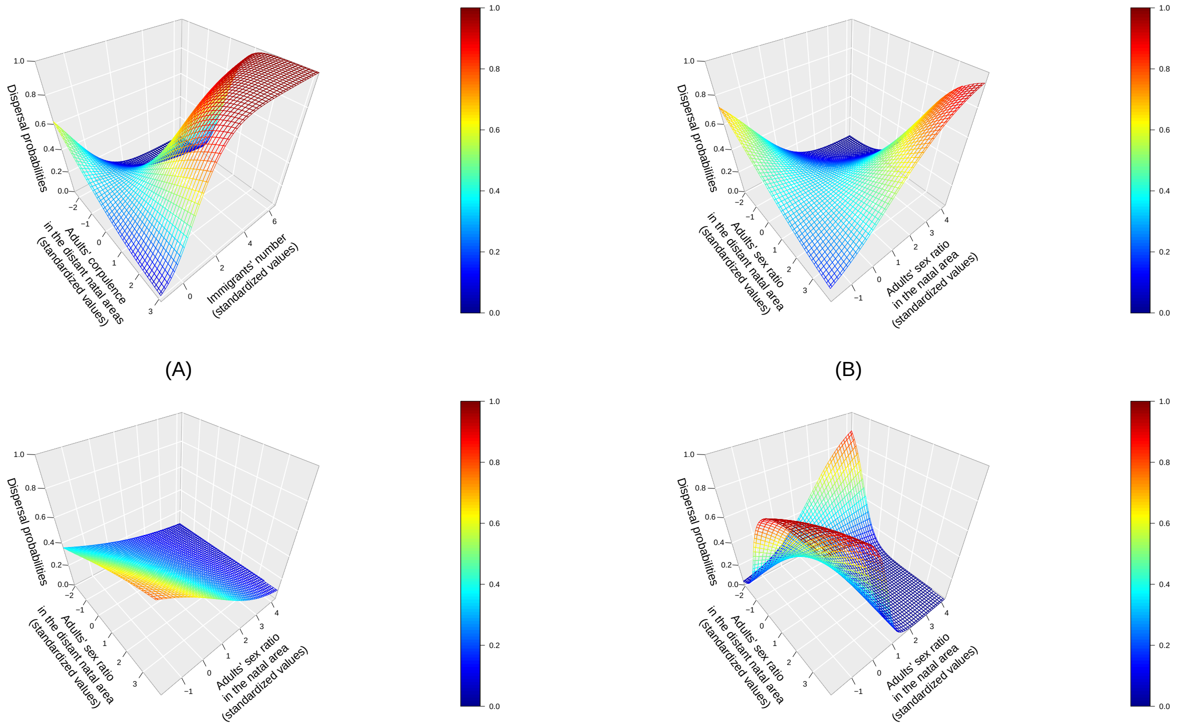
We did not interpret the interaction between the number of immigrant and the substrate's characteristics, because it was particularly sensitive to the difference in dispersal responses among siblings (Figure S6: the median of p-values obtained from resampling was superior to 0.1).

Variability between information sources

Correlations between immigrant-based information and dispersal responses sometimes depended on the variability between the information sources (*i.e.* the variability in the immigrants' natal areas characteristics), occasionally in interaction with the local context (Table 1). For a low variability, we observed an increase of dispersal probability when the distant neonates' sex ratio or the adults' corpulence increased (Figure 5-A,B), or when the local adults' sex ratio decreased and the distant adults' sex ratio increased (Figure 5-C, also valid for the converse situation, but with a less steep relationship). When the variability among information sources increased, the dispersal probability increased when the distant neonates' sex ratio or the adults' corpulence decreased (Figure 5-A,B) and the previously described interaction between the distant and the local adults' sex ratio fade out (Figure-C,D,E).

Immigrants' traveled distance

Correlations between immigrant-based information and dispersal responses depended in some cases on the distance traveled by immigrants, occasionally in interaction with the local context (Table 1). The dispersal probability increased when the adults' corpulence in distant areas decreased and the intensity of the relationship increased as the distance traveled by immigrants increased (Figure 6-A). We also found the dispersal probability of focal individuals increasing when the adults' age in local and distant areas were both low or both high and when the distance traveled by immigrants increased (Figure 6-B,C,D).



(A) (B)

(C) (D)

Figure 3.4: Influence of immigrants' number on immigrant-based information use.
These relationships were observed in the second model (with multiply-informed individuals only). The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). The graphs are plotted in the range of observations for the variables considered on the X-axes.

A- Predicted probabilities of the individuals' dispersal as a function of the adults' corpulence in the distant areas and the number of immigrants.

B- Effects of the adults' sex ratio in the local and distant natal areas, for a low number of immigrants. The number of immigrants has been set to the first quartile of its distribution.

C- Effects of the adults' sex ratio in the local and distant natal areas, for an intermediate number of immigrants. The number of immigrants has been set to the median of its distribution.

D- Effects of the adults' sex ratio in the local and distant natal areas, for a high number of immigrants. The number of immigrants has been set to the third quartile of its distribution.

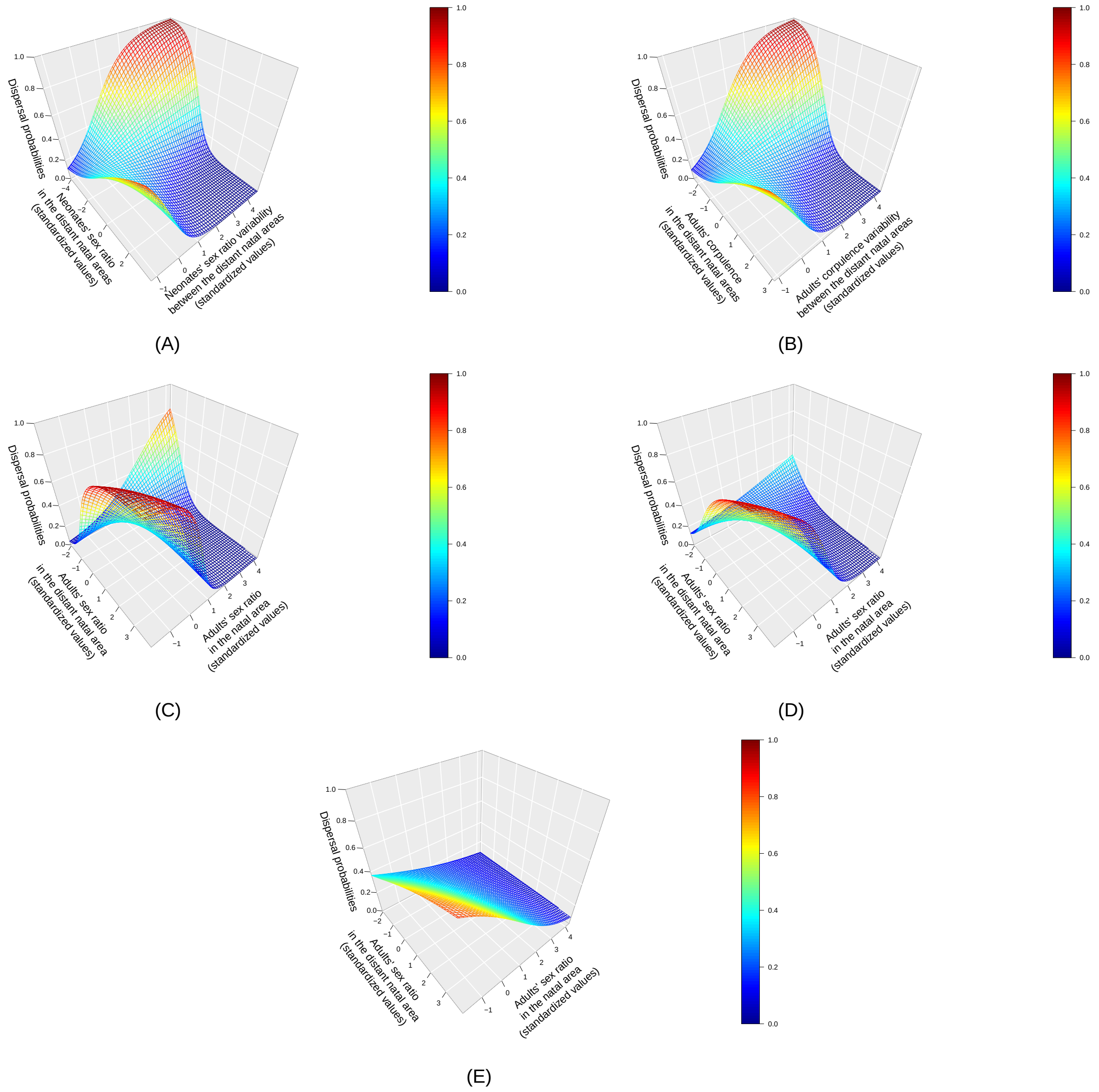


Figure 3.5: Dependence of information use about distant context on the variability between information sources and the local context.

These relationships were observed in the second model (with multiply-informed individuals only). The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). The graphs are plotted in the range of observations for the variables considered on the X-axes.

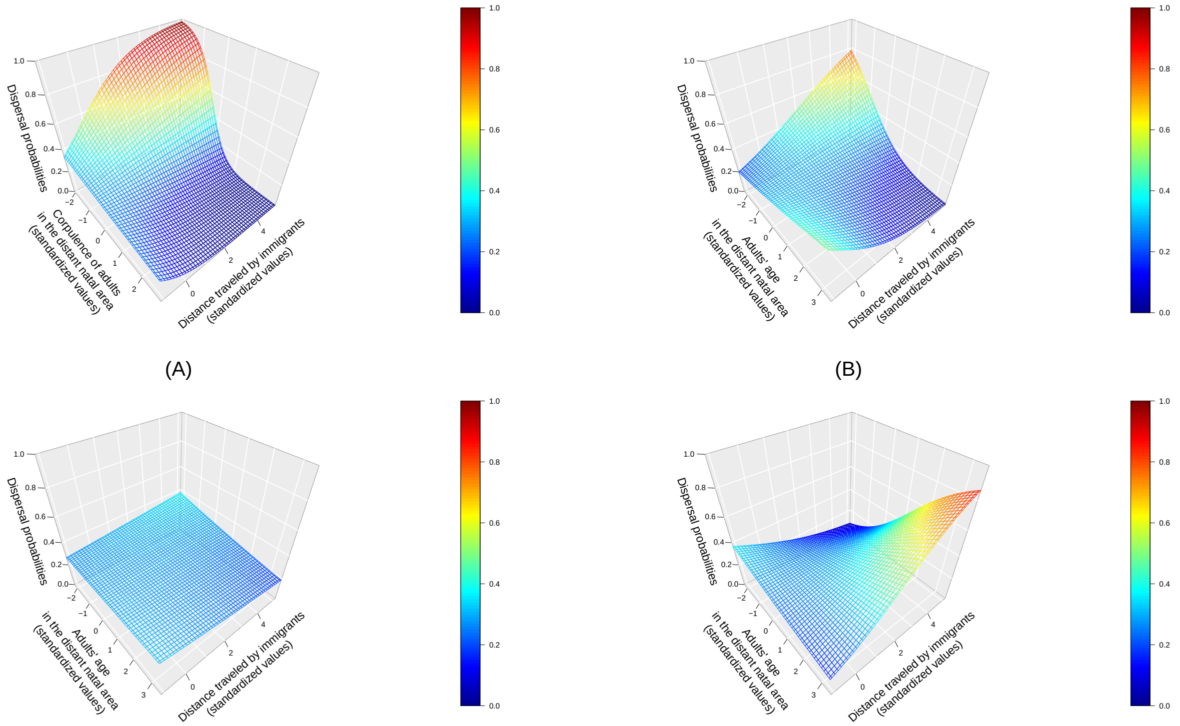
A- Predicted probabilities of the individuals' dispersal as a function of the neonates' sex ratio in the distant areas and its variability.

B- Predicted probabilities of the individuals' dispersal as a function of the adults' corpulence in the distant areas and its variability.

C- Effects of the adults' sex ratio in the local and distant natal areas, for low variability in distant adults' sex ratio. The local adults' sex ratio has been set to the first quartile of its distribution.

D- Effects of the adults' sex ratio in the local and distant natal areas, for an intermediate variability in distant adults' sex ratio. The local adults' sex ratio has been set to the median of its distribution.

E- Effects of the adults' sex ratio in the local and distant natal areas, for high variability in distant adults' sex ratio. The local adults' sex ratio has been set to the third quartile of its distribution.



(A) (B) (C) (D)

Figure 3.6: Influence of immigrants' traveled distance on immigrant-based information use. These relationships were observed in the first model (with all informed individuals). The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). The graphs are plotted in the range of observations for the variables considered on the X-axes.

A- Joint effects of the adults' corpulence in the distant natal areas and immigrants' traveled distance on dispersal probability.

B- Joint effects of the adults' age in the distant natal areas and immigrants' traveled distance on dispersal probability, for a low local adults' age. The local adults' age has been set to the first quartile of its distribution.

C- Joint effects of the adults' age in the distant natal areas and immigrants' traveled distance on dispersal probability, for a medium local adults' age. The local adults' age has been set to the median of its distribution.

D- Joint effects of the adults' age in the distant natal areas and immigrants' traveled distance on dispersal probability, for a high local adults' age. The local adults' age has been set to the third quartile of its distribution.

Discussion

We investigated the influence of immigrant-based information on realized dispersal in nature. We also test for its dependence on the focal individual's phenotype, the local context, and several aspects of the information (number of immigrants, variability in information sources, distance traveled by immigrants). We found evidence for a use of immigrant-based information for dispersal decisions, consistently to the dependence on local context: focal individuals appeared to respond similarly to the local habitat and immigrants' original habitat (symmetry in the relationships). This immigrant-based information use depended on the individual's condition and the local context (for the immigrant-based information about density). Finally, the use of immigrant-based information appeared to depend on the information nature, with a previously described dispersal response to immigrant-based information observed mainly when having a low variability among information sources and a high number of immigrants. In contrast, we found dispersal responses to immigrant-based information about low competitive habitat or natal habitat-biased dispersal when there is high variability in information sources, a low number of immigrants, or particularly distant information origin.

A phenotype- and context-dependent dispersal, integrating local and distant information

Distant context-dependence: use of immigrant-based information

Our results further highlighted the multi-deterministic aspect of dispersal: not only did an individual use several elements of the environmental context to disperse (multi-determinism of dispersal: Clobert et al. 2012 in our species, but also Galliard et al. 2012, Morales-Gonzales et al. 2021 in other species) but also used these elements at different spatial scales, with the use of both local and distant information, conveyed by immigrants. Interestingly, the relative importance of immigrant-based information was comparable to the relative importance of the local context (Figure 3), even if slightly lower. We also observed a more than two-fold increase in our model r-squared when comparing it to the model we performed on the same monitoring but by considering only local dispersal factors (Brevet et al. 2022b, in prep). This highlights the likely use of such information in dispersal decisions, as already observed experimentally (Cote and Clobert 2007a, Jacob et al. 2015b). Such use may participate in a better knowledge of the distant habitats by the information receiver and should make it possible to converge towards the ideal free distribution (Fretwell and Lucas 1970, Fretwell 1972; as suggested in Cote and Clobert 2007a, Clobert et al. 2009) through more informed spatial decisions. Indeed, it could allow an individual to estimate the cost of staying or not in its initial habitat and the potential benefit it could obtain after the settlement at the same time (Bonte et al. 2012), without necessitating prior exploration phases. The slightly lower relative importance of distant factors could be explained by the local information being more reliable than the distant one (Sepännen et al. 2007): such information indeed necessitates finding the origin of the information, a potentially costly process particularly if orientation (as particularly evidenced in fragmented landscapes, Cote et al. 2017) or locomotor abilities are limited (Bonte et al. 2012).

Dispersal responses to immigrant-based information are difficult to interpret. When individuals that survived their first year of life appeared to disperse more in the presence of information about a distant habitat (from which one or more originated), it could indicate that individuals leave their natal area in response to the possible presence of such a habitat nearby. This could then reflect a preference for such habitats, with individuals seeking to reach them. However, we cannot be sure here that such a habitat is selected after the individual leaves. This would require testing whether the habitat ultimately selected by the individual is indeed closer to the original habitat of the immigrant than the average habitats present nearby. An alternative explanation would be that the information provided by the immigrants is in fact representative of the habitats in the vicinity. The observed response would then be the result of the suitability of the surrounding habitats, with a mortality of the dispersers more or less high depending on the quality of these habitats. However, this latter hypothesis is quite unlikely given the interaction effects observed between the information provided by the immigrants and the nature of this information (distance of origin, number of sources, variability among sources), suggesting a more sophisticated use of the information.

The relative ranking of environmental factors is alike locally and in distant contexts (Figure 3). Only the effect size of substrate characteristics differed locally and at distance. The greater importance of this factor locally could suggest that this factor mainly drives the choice to emigrate from unsuitable abiotic conditions while information about distant habitats could be associated with more diverse strategies. Such hypothesis is well-supported by the observations we made here: the dispersal response to the distant substrate's characteristics depended on the focal individual's sex and corpulence, whereas closed local habitats were avoided (Figure S1-C, Brevet et al. 2022b in prep), probably because forest cover could be related with a diminished availability of resources and thermoregulation accessibility (Lecomte et al. 1993). The increase in dispersal probability when immigrants originated from distant closed habitats was observed for corpulent neonate males and neonate females with low corpulence (Figure 1-C,D), and might result from alternative strategies. Perhaps, corpulent males might prefer these habitats because having sufficiently high corpulence to endure the associated costs (Meylan et al. 2002, Le Galliard et al. 2004, 2010, 2013), and/or avoid male-male competitive interactions (Fitze et al. 2005), and/or exploit an available free niche with low competition (as in Bolnick et al. 2001). This potential preference is confirmed by personal observations since corpulent males were mainly observed in the study site margins which are woodier. For corpulent females, the possible preference for open habitats (both locally and at distance) is perhaps due to their better competitive abilities which enables them to stay or colonize rich good-quality habitats (Clobert et al. 1994, Léna et al. 1998a), whereas

low corpulent ones might find less competitive conditions in more closed environments trading survival over growth (habitat selection driven by intra-specific competition, Alley 1982, *e.g.* Sol et al. 2000, Davey et al. 2005), with less prey availability being compensated by their low body condition requiring less food intake (González-Suárez et al. 2011).
An alternative explanation for the difference in the relative importance of the substrate's characteristics locally and at distance could be due to the way information is transmitted by immigrants. There could be a possibility that the substrate's openness and temperature less influence the immigrants' traits and that less precise cues were perceived on this factor by the local neonates, contrary to elements of the social context. This argument is well-supported by the fact that the social context has been often demonstrated to influence the traits of individuals experiencing it in this species: as for density, with a modification of behavior and morphology (Lecomte et al. 1994, Meylan et al. 2007, San-jose et al. 2016), or sex ratio, with males aggression biting marks and modification on body coloration (Fitze et al. 2005, Le Galliard et al. 2005a,b, Cote et al. 2008c).

More broadly, we focused here on the use of immigrant-based information, but we did not explore how an individual had access to this information. The natal habitat of immigrants could probably impact their traits such as their morphology, their behavior, and their odors, through maternal effects or phenotypic plasticity (*e.g.* Mugabo et al. 2010, Bestion et al. 2014, but also Martín and López 2006). It had already been proved for density, with a modification of behavior and morphology (Lecomte et al. 1994, Meylan et al. 2007, San-jose et al. 2016) that could be used as cues for space use decisions (Cote et al. 2008a). For other factors, this remains to be explored: for example, we could suggest cues such as activity patterns, and thermoregulation behavior for abiotic characteristics of the habitat such as the humidity or water accessibility (Lorenzon et al. 1999, Rozen-Rechels et al. 2018, 2021).

Consistency in the use of local and immigrant-based information

Both locally and at distance, we observed the major relative importance of the adults' sex ratio (as observed in Brevet et al. 2022b in prep) and the average adults' corpulence (Figure 3). Interestingly, for these factors, we observed symmetrical correlations when comparing local and distant contexts (Figure S1, a.): focal neonates appeared to respond similarly to the same conditions locally and at distance (Figure S3-A,B compared to Figure 1-A,B, and Figure S2-B compared to Figures 4-B,C,D, 5-C,D,E). As more precisely explained in the previous section, this might results from the same preferences for emigration and immigration, even if such a hypothesis needed to be properly tested. These two factors are likely to reflect the habitats competition level for neonates, as competitive abilities of adults probably increase with their corpulence (as suggested in Mugabo et al. 2010, 2011) and a probable competition with adult females occurs for resources (Lecomte et al. 1994, observed in subadults). Alternatively, these factors could reflect the habitat quality, as adults' corpulence could be a cue for resources availability (Mugabo et al. 2010, 2011, Galliard et al. 2005d) and high males proportion could reflect better chances of survival (as males have lower survival rates than females, Galliard et al. 2010) or a good habitat quality through the persistence of males despite agonistic interactions (Aragon et al. 2006, interpreted from Kennedy and Gray 1994). Thus, both locally and at distance, the potential preference for environments with low-body corpulence adults in neonate females, and corpulent adults in neonate males, could be due to a trade-off between the focal individual's competitive abilities, females being probable poorer competitors than males (Lecomte et al. 1994, Pilorge et al. 1987), and the availability of resources. The potential preference for a low sex ratio, could in turn reflect the avoidance of competitive interactions with adult females or attraction toward a habitat with better male survival rates. We also observed a significant interaction between the local adults' sex ratio and the focal individual's sex (Figure S3-C,D): the avoidance of a locally high proportion of females appeared to be much more pronounced in females. This difference could be due to the higher sensitivity of neonate females to the competition, and to potential competition with other females for mate access later in life.

The mentioned symmetry of effects between the local and distant contexts (Figure S1, a.) could be generalized to almost all variables, as it can be observed when looking at the overall direction of fixed effects (*e.g.* signs of the effects sizes in Figure 3). This consistency in the use of local and distant context information suggested that the local and immigrant-based cues vehiculate similar information. Such complimentary use of local and distant information is theoretically expected to improve population persistence (Chaine et al. 2013).

The consistency in the use of local and distant information was also highlighted with the interaction between local and distant densities (Figure 2). We found a positive relationship between the probability of dispersal and the corpulence of the focal individual at low local and high distant densities, showing a potential preference for dense habitats. These results are an exact replication of the experimental result in Cote and Clobert (2007a). The attraction towards densely populated habitats was also observed locally in other experimental studies (Lena et al. 1998a, Galliard et al. 2003a, Meylan et al. 2007), with high densities reflecting competitive but also good habitat quality. In this particular case, the use of immigrant-based information appeared to be conditioned by a sufficient contrast between the local and distant contexts (Figure S1, b.) which might then balance the cost of dispersal (Bonte et al. 2012). The increase of dispersal with the focal individual's corpulence could be related to the individual's ability to compete in a potentially dense arrival habitat, or to its energetic reserves that could support the cost to disperse (Bonte et al. 2012). Indeed, the neonate's body condition can be related to an increase in survival rate (Le Galliard et al. 2010, 2013) or performances (Le Galliard et al. 2004, Meylan and Clobert 2004) that may display high competitiveness (Garland et al. 1990), and is also related to more important energetic reserves (Olsson et al. 2002).

As previously observed (Bowler and Benton 2005, Baines et al. 2019, Brevet et al. 2022b in prep) and expected theoretically (Kisdi et al. in Clobert et al. 2012) the use of both local and immigrant-based social information about the environmental contexts mostly appeared to depend on the individual's phenotype (Figure, 1,2, S3), and more precisely on its ability to compete or endure potential dispersal costs. The match between the individual's phenotype and its potential habitat preferences might suggest a potential matching habitat choice (Eldelaar et al. 2017, *e.g.* Jacob et al. 2018), that remains to be tested properly. Such informed habitat choice could stabilize the metapopulation dynamics (Mortier et al. 2018).

A cost-dependent immigrant-based information use

Not only similar variables were used both locally at a distance, but the number of immigrants, the variability between distant information sources, and the distance traveled by the immigrants also modulated the way the immigrant-based information was used.

Dependence on the number of immigrants

The number of immigrants positively influenced the previously described relationships between dispersal and the context in distant areas (Figure S1, c.). When a high number of immigrants settled in the surroundings of the natal area, dispersal probability increased with the adults' corpulence in the distant habitat (Figure 4-A). It could be interpreted as a potential preference for a habitat considered of good quality as corpulence might reflect high resource availability (for which we observed local and distant attraction for neonate males), despite an also high competition level in the presence of corpulent adults. We also observed, in presence of a high number of immigrants, an increase in the dispersal probability when the local and distant adults' sex ratios were opposed (Figure 4-C), and more particularly when the local proportion of females was high (potentially considered as a disadvantageous context, previous sections for details). The interpretation would be here that an individual would endure the cost associated with a change in habitat context (Morris 1992), or more broadly use information potentially costly to use (*e.g.* competition costs at settlement), only when the information sources are sufficiently numerous. Such dependence on the repeatability of information was expected when individuals do not have prior knowledge of the environment (Pike and Laland 2010, Rieucau and Giraldeau 2011). Another possibility is that the number of immigrants gives information on the habitats connectivity (Cote and Clobert 2010). Thus, a high number of immigrants could be associated with good habitat connectivity, in which case individuals could be more inclined to initiate dispersal toward distinct habitats potentially difficult to precisely localize. However, this result is somehow in contradiction with both the theory (Chaine et al. 2013) and experimental results (Cote and Clobert 2007a, Jacob et al. 2015b), where the number of immigrants was not found to influence the dispersal rate. The latest results were found in simple environments where the information brought by an immigrant was simple and not multi-dimensional. Therefore, it is possible that by increasing complexity, more information is needed to reach some level of reliability.

However, a low immigrants' number was also observed to influence positively dispersal when the local and distant adults' sex ratios were alike (Figure 4-A), and more particularly when the local proportion of females was low (considered an advantageous context). In the case where dispersers are actually seeking to reach the immigrant's habitat (first section of discussion for more details about this hypothesis), such a relationship might reflect a natal habitat-biased dispersal. Such potential preference for a habitat like the natal one could reflect an individual attempt to decrease the risk associated with potentially uncertain information (Rieucau and Giraldeau 2011), by avoiding important changes in the environmental context and costs that could be associated with plastic changes when arriving in a distinct habitat (Davis 2008).

Dependence on the variability between information sources

As expected (Figure S1, d.), a low variability between the information sources was associated with an immigrant-based information use consistent with the local context-dependence we observed (Figure 5: avoidance of high neonates' sex ratio, as in Brevet et al. 2022b in prep, high adults' sex ratio, high adults' corpulence, as observed for neonate males only), suggesting that the information is consistently used when sufficiently reliable (Rieucau and Giraldeau 2011, Bocedi et al. 2012, *e.g.* Heinen and Stephens 2016). In the case of the adults' sex ratio, we observed more broadly an increase of dispersal when the local and distant contexts were opposite (especially for a low local sex ratio, a situation considered disadvantageous, previous sections for details), which might suggest that the risks of changing of contexts can be only afforded when the information is reliable (Piper 2011). Thus, this relationship vanished in presence of high variability, *i.e.* high unreliability of information, as expected (Koops 2004). Conversely, high variability between information sources is correlated with an increase in dispersal in response to low neonates' sex ratio and low adult corpulence in distant habitats. Such response could be interpreted as an avoidance of potential competition costs with corpulent adults and with neonate females that could be important competitors for focal neonates (Brevet et al. 2022b in prep). Thus, when the reliability of the information decrease, dispersers might reduce the risk of choosing a too competitive context (Bonte et al. 2012).

Dependence on the distance traveled by immigrants

We found a significant interaction between the dispersal probability, the distant adults' corpulence, and the distance traveled by immigrants: dispersal decreased with an increase in the distant adults' corpulence (Figure 6-A), with a relationship steeper while the original habitat of immigrants was further away. It potentially reflects a preference for low competitive contexts, particularly when the original habitats of the immigrants are far away. Such particularly distant habitats could be costly to reach: by increasing the distance to travel, there is an increasing potential risk of predation, risk of mismatch compared to the initial habitat condition, and costs related to the exploration in unknown habitats (Stamps et al. 2005, Bonte et al. 2012). The attainability of such distant habitats should also be more difficult, in particular in the case of low information on orientation: for that reason, distance should erode the value of information (Seppännen et al. 2007). Thus, this potential avoidance of competitive context could be interpreted as a reduction in costs when seeking distant habitats, potentially already associated with important costs.

The dispersal probability also increased when the local and distant habitats were similar in terms of adults' age (both high or low) and the distance traveled by immigrants was high (Figure 6-B,C,D). The potential conservation of habitat by preferring the same local and distant contexts could also reflect a minimization of the cost by keeping the same environmental condition (natal habitat preference induction, Davis and Stamps, 2004, *e.g.* Sanz-perez et al. 2018), for distant habitats that could be difficult to reach because quite far away (Rousset and Gandon 2002, Stamps et al. 2005). We have to be cautious with the interpretation of this correlation as the distribution of immigrants' traveled distance is far to be symmetric (long distribution tail) and, as a result, it relies on relatively few observations on the most important immigrants' traveled distances.

Interpreting the real value/content of the information carried by long distant dispersers is difficult. Is the distance per se or is it some information about the immigrant's habitat of origin, likely to be particularly distinct through distance, remains open to question. In the same way, how this information will affect dispersal distance and settlement of the receiver is largely unknown.

All these results supported a consistent use of immigrant-based information relative to the responses to the local context only when the information was sufficiently reliable. When the information appeared to be potentially costly to use (too uncertain or associated with distant habitats) we observed a potential minimization of costs by potentially favoring natal habitat-biased dispersal or seeking low-competitive habitats. Such context-dependence in the natal habitat preference induction was already observed in another study (Lhomme et al. 2018), with a preference induction only when fitness benefits are high.

These interpretations were reinforced by what we observed at the margins of the distribution of some described correlations. We avoided considering extreme values while interpreting triple interactions because those extremes were less well-supported by our data. Yet, interesting patterns appeared when considering extreme values (minimal and maximal observed values of the local density, the variability in the distant adults' sex ratios, or the local adults' age, implied in the interactions respectively displayed in Figures 2, 5-C,D,E, 6-B,C,D). We observed in all these cases additional relationships (Figure S9) with an increase in dispersal probability when the local and distant habitats were alike (for low corpulent individuals in the densities interaction, or particularly high variability in the distant adults' sex ratios), or opposite (for low immigrant's traveled distance in the adults' age interaction). It could reflect a need to decrease the cost of dispersal in extremes situation (Bonte et al. 2012): by keeping a habitat match for low corpulent individuals who could not endure the costs of an important change of context (Figure

S9-A,B), keeping a similar habitat when high variability is present to potentially avoid to arrive in a too different habitat compared to the natal one with high cost for settlement (Figure S9-C), or escaping a too disadvantageous habitat cued by the local adults' age (too high mortality for a low averaged age, or too competitive for an important averaged age: Massot et al. 2011, higher size and corpulence of neonates from aged mothers) by seeking the opposite only when short distance are at stake, to minimize the risks of mismatch (Figure S9-D,E).

We probably also missed some phenotype dependencies here, since we did not test for the interactions between distant context, phenotype, and nature of information (not sufficient statistical power to test this). In particular, we could hypothesize that the observed relationships between adults' corpulence and distance traveled by immigrants or the number of immigrants would be only valid for females and males respectively, so the relationships would be consistent with observations on local context-dependence. Such complex dependencies need to be tested to understand more precisely the way these different factors interact.

Conclusion

This study suggested that there is a use of immigrant-based information about the distant environmental context for dispersal decisions, with relative importance for this information type similar to information about the local environmental context. In most cases, we found consistent patterns between the use of information about local and distant contexts, with symmetry between the relationships observed locally and at distance, potentially suggesting that an individual would have the same habitat preference locally and at distance (Bowler and Benton 2005, Clobert et al. 2009). Only the distant and local substrate's characteristics deviated from such observations, with different use locally and at distance: information about the distant substrate appeared to be used with alternative strategies according to the individuals' competitive abilities. Phenotype-dependence was also more broadly observed for most of the studied environmental factors locally and/or at distance and suggests a probable match between habitat preference and the individual's ability to compete or endure dispersal costs (Bowler and Benton 2005). We also found a context-dependent use of immigrant-based information: distant information generates the departure mostly when the local context is disadvantageous (except for the interaction between local and distant adults' age), suggesting that the information brought by immigrants might help to balance the cost-benefits of dispersal decision-making (*e.g.* context- and cost-dependent use of social information Tibetts 2008, Wray et al. 2012, Wurtz et al. 2021). These phenotype- and context-dependent information use also militate for the multidimensionality of the information conveyed by immigrants, as already experimentally demonstrated in a ciliate (Jacob et al. 2015b) where such information use depended on the receivers' genotype, or as frequently demonstrated when looking at individual variation in social information use (Rosa et al. 2012, Lindstedt and Hamilton 2013, Leris and Reader 2016, Smolla et al. 2019).

We further observed the use of immigrant-based information to be mediated by the variability between information sources and their number, in a way that could be understood as an estimation of information reliability (variability and repeatability of information). A possible hypothesis would be that individuals use this potential reliability of information to minimize the costs of dispersal when the information was uncertain (too much variability or an insufficient number of information sources) by keeping the same 'familiar' habitat context, favoring low competitive habitat, or preventing dispersal. The same was observed when considering the cost related to the distance to travel for particularly distant habitats. It should further represent for these individuals a potentially important fitness gain if they could reach efficiently the distant habitats on which they were informed (Delgado et al. 2014). An immigrant-based orientation could therefore be central for individuals and should be tested in natural conditions, even if the first experimental results did not find such an orientation capacity in appearance (Brevet et al. 2022a, in prep) In the same perspective, a central concern would be to test whether focal individuals informed by immigrants and having dispersed eventually selected a habitat close to the immigrants' ones.

Author contribution

MB, SJ and JC defined the research questions. JC and MM designed the field monitoring. JC and MM mostly collected the data, all the other authors participated substantially but to a lesser extent to the field monitoring. MR, MB, AR and DRR prepare the dataset for analyses. MB performed all the statistical analyses. MB, SJ and JC conducted the writing and all the other authors significantly helped revising it.

Funding

This work was supported by the Agence Nationale de la Recherche (ANR-17-CE02-0013) and TULIP (Laboratory of Excellence Grant ANR-10 LABX-41).

Acknowledgements

We gratefully thank all interns who contributed to the field monitoring work over the thirty years and for their precious help to manage the rearing facility. We thank the Parc National des Cévennes for allowing us to use the study site. This work beneficiated from the scientific environment of the Laboratoire d'Excellence entitled TULIP (ANR-10-LABX-41). SJ benefitted from financial support by the Agence Nationale de la Recherche for the project CHOOSE (ANR-19-CE02-0016). The 'Office Nationale des Forêts', the 'Parc National des Cévennes', and the regions Auvergne, Rhône Alpes and Languedoc Roussillon delivered permits to capture and handle lizards (last permits: 81-17 2013-05;

2013274-0002, 2013/DREAL/259). The used monitoring method was validated by an ethical committee (DAP #5897-2018070615164391 v3). No conflict of interest has to be declared.

Supplementary Materials

Focal individual's phenotype (1)	**Sex** (1)
	Corpulence (1)
	Corpulence x Sex (1)
Local context (1)(2)	***Local density*** (1)(2)
	Local adults' age (1)(2)
	Local neonates' sex ratio (1)(2)
	Local adults' sex ratio (1)(2)
	Local adults' corpulence (1)(2)
	Local substrate's characteristics (1)(2)
Distant context (Immigrant-based information) (1)(2)	***Distant densities*** (1)(2)
	Distant adults' age (1)(2)
	Distant neonates' sex ratio (1)(2)
	Distant adults' sex ratio (1)(2)
	Distant adults' corpulence (1)(2)
	Distant substrate's characteristics (1)(2)
Immigrant-based information components (1)(2)	*Number of immigrants* (2)
	Distant densities variability (2)
	Distant adults' age variability (2)
	Distant neonates' sex ratio variability (2)
	Distant adults' sex ratio variability (2)
	Distant adults' corpulence variability (2)
	Distant substrate's characteristics variability (2)
	Immigrants' traveled distance (1)

Local context x Focal individuals' phenotype (1)	**Local density x Focal individuals' corpulence** (1)
	Local adults' sex ratio x Focal individuals' sex (1)
	Local adults' corpulence x Focal individuals' corpulence (1)
	Local adults' corpulence x Focal individuals' sex (1)
	Local adults' corpulence x Focal individuals' corpulence x sex (1)
	Local substrate's characteristics x Focal individuals' corpulence (1)
Distant context x Focal individuals' phenotype (1)	**Distant densities x Focal individuals' corpulence** (1)
	Distant densities x Focal individuals' sex (1)
	Distant adults' age x Focal individuals' corpulence (1)
	Distant adults' sex ratio x Focal individuals' corpulence (1)
	Distant adults' sex ratio x Focal individuals' sex (1)
	Distant adults' sex ratio x Focal individuals' corpulence x sex (1)
	Distant adults' corpulence x Focal individuals' corpulence (1)
	Distant adults' corpulence x Focal individuals' sex (1)
	Distant adults' corpulence x Focal individuals' corpulence x sex (1)
	Distant substrate's characteristics x Focal individuals' corpulence (1)
	Distant substrate's characteristics x Focal individuals' sex (1)
	Distant substrate's characteristics x Focal individuals' corpulence x sex (1)
Local x Distant context (x Focal individuals' phenotype) (1)(2)	**Local x distant densities** (1)(2)
	Local x distant adults' age (1)(2)
	Local x distant adults' sex ratio (1)(2)
	Local x distant adults' corpulence (1)(2)
	Local x distant substrate's characteristics (1)(2)
	Local x distant densities x Focal individuals' corpulence (1)
	Local x distant adults' corpulence x Focal individuals' corpulence (1)
	Local x distant substrate's characteristics x Focal individuals' corpulence (1)
(Local x) Distant context x Immigrants number (2)	*Distant densities x Immigrants' number* (2)
	Distant adults' sex ratio x Immigrants' number (2)
	Distant adults' corpulence x Immigrants' number (2)
	Distant substrate's characteristics x Immigrants' number (2)
	Local x distant adults' sex ratio x Immigrants' number (2)
(Local x) Distant context x Variability (2)	*Distant neonates' sex ratio x variability* (2)
	Distant adults' sex ratio x variability (2)
	Distant adults' corpulence x variability (2)
	Local x distant adults' sex ratio x variability (2)
(Local x) Distant context x Immigrants' distance (1)	**Distant adults' corpulence x Immigrants' distance** (1)
	Distant adults' age x Immigrants' distance (1)
	Distant adults' sex ratio x Immigrants' distance (1)
	Local x distant adults' corpulence x Immigrants' distance (1)
	Local x distant adults' age x Immigrants' distance (1)
	Local x distant adults' sex ratio x Immigrants' distance (1)

Table S1: Studied dispersal factors and variables retained after model selection.
The left table displays all studied factors (focal individuals' phenotype, local and distant context, information nature: number of immigrants, variability in information sources, immigrants' traveled distance). The right table displays some of the studied interactions between the previously mentioned fixed factors: only the interactions retained in at least one model after backward selection (Mat&Met for details), but all possible interactions in each categories were included in the initial models. In both tables the presence of variables (before model selection) in the first model (all neonates informed by at least one immigrant) and the second model (all multiply-informed neonates) were denoted by the respective symbols (1) or (2). All variables retained in the first model after backward selection are in bold, all those retained in the second model after backward model selection are in italic.

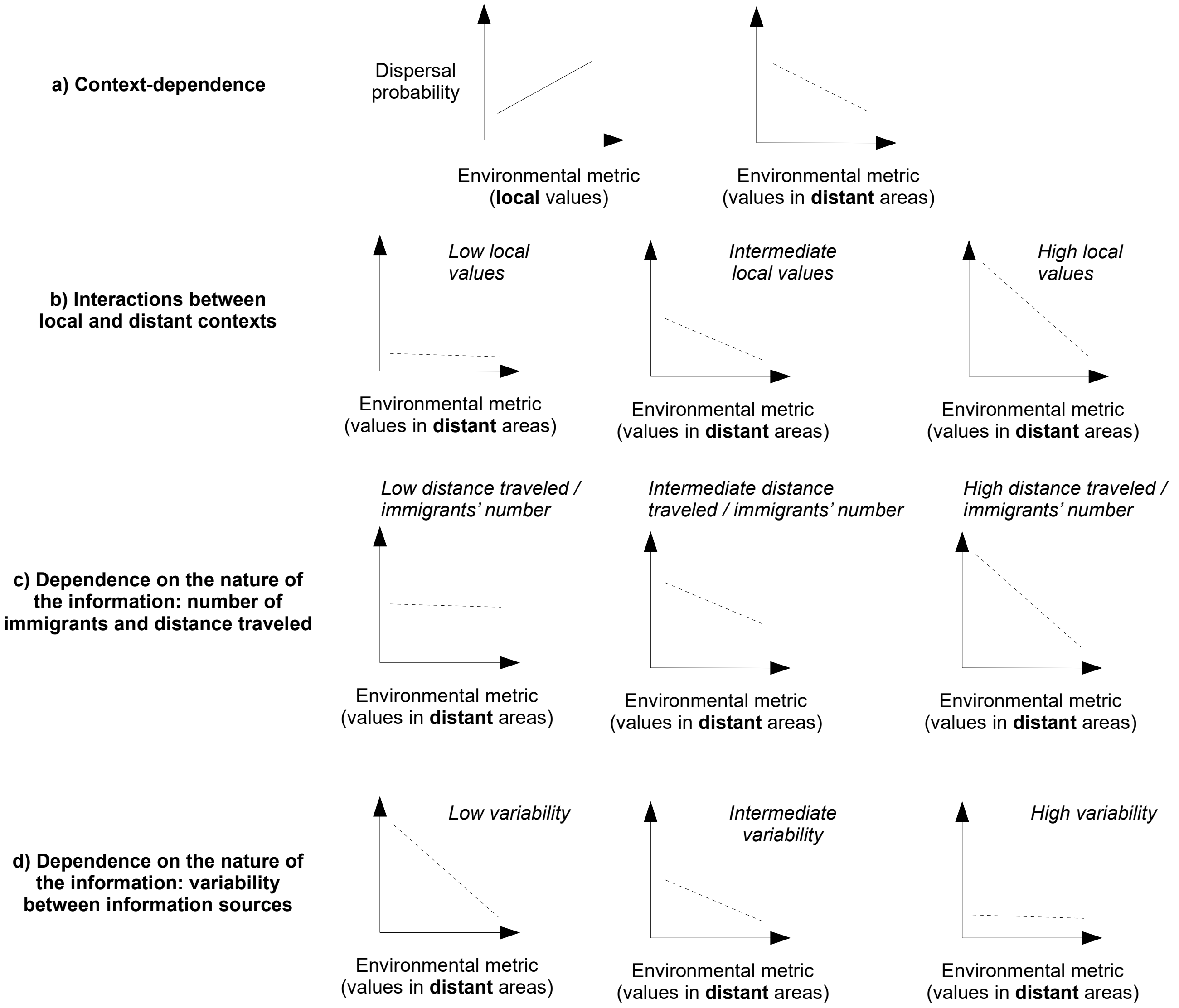
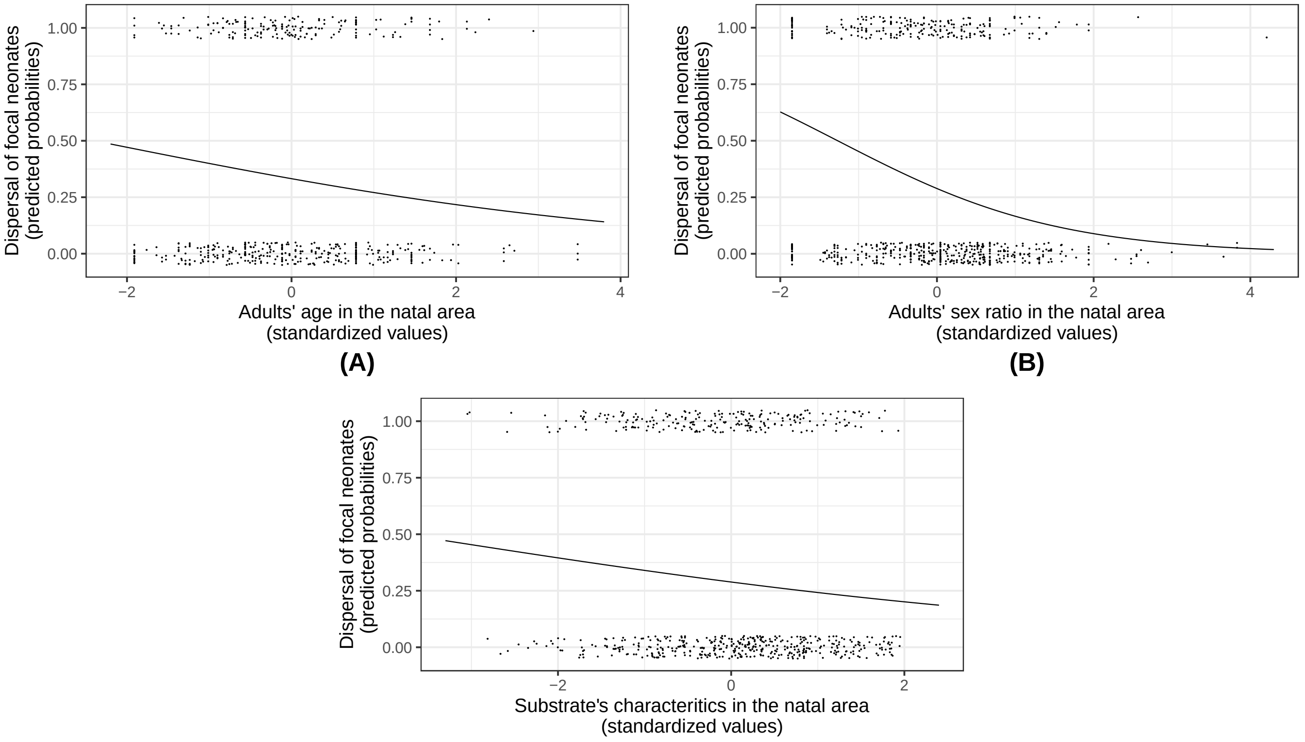


Figure S1: Use of immigrant-based information, relatively to the local context and the nature of information (distance traveled by immigrants, number of immigrants and variability in information sources).

This figure illustrates the expectations we had for the use of immigrant-based information (Introduction for details). For a given environmental metric, for which a local use was found (a. context-dependence), we expect the dispersal probability to depend on the environmental metric in distant areas, from which immigrants are coming, in a way opposite to the local dependence (*i.e.*, the same contexts repel or attract an individual locally and at distance). When considering the interaction between the local and distant contexts (graphs b.), we expect the relationship between the distant environmental context and the dispersal probability to increase in intensity when the local context decrease in quality (*i.e.* for a local context for which the dispersal probability increased). The use of immigrant-based information could also depend on the nature of information (graphs c. and d.): we expect the relationship between the distant environmental context and the dispersal probability to increase in intensity when information about high-distance habitat is given and when the information is repeated (increase in immigrants' number) and constant (decrease in information sources variability). Yet, predictions on graphs c. could also be reverted as alternative hypotheses implying the cost of reaching far habitats and blurring the information by the arrival of numerous immigrants could also be at stake (Introduction for details).



(A)

(B)

(C)

Figure S2: Local context-dependence of dispersal.
These relationships were observed for both the first and the second model, with the exception of the correlation with the averaged adults' age (only found in the second model). The graphs were computed from the coefficient of the studied variable and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). Black dot represents all observed data (associated to an individual that dispersed when being placed around the 0% probability line, or not in the other case). These dots were jittered vertically to gain in readability.

A- Predicted probabilities of the individuals' dispersal as a function of the adults' age in the natal area.

B- Predicted probabilities of the individuals' dispersal as a function of the adults' sex ratio in the natal area. Computed from the first model coefficients.

C- Predicted probabilities of the individuals' dispersal as a function of the substrate's characteristics in the natal area. Computed from the first model coefficients. An increase in the substrate's characteristics index refer to an increase of openness and temperature of substrates in the natal area.

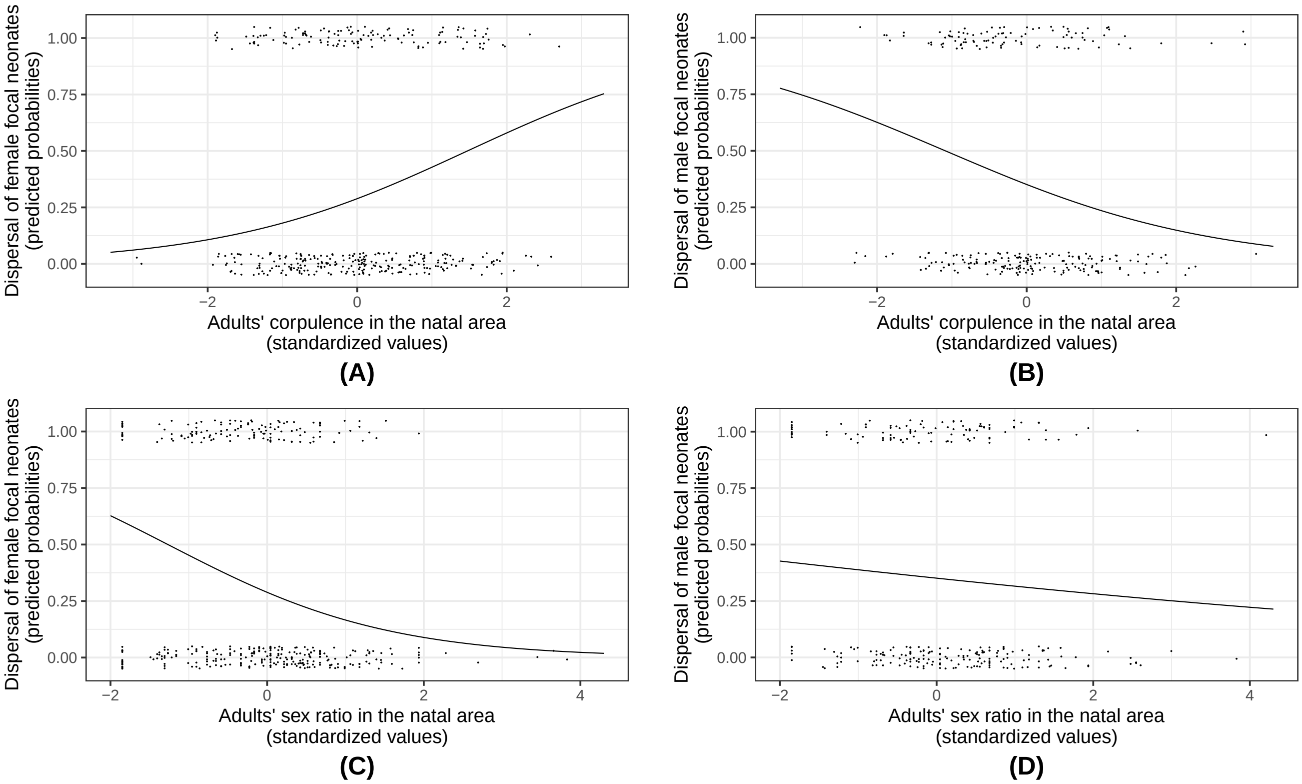


Figure S3: Phenotype-dependence of the use of local social information.
These relationships were observed in the first model (with all informed individuals). The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). Black dot represents all observed data (associated to an individual that dispersed when being placed around the 0% probability line, or not in the other case). These dots were jittered vertically to gain in readability.
A- Predicted probabilities of the females' dispersal as a function of the adults' corpulence in the natal area.
B- Predicted probabilities of the males' dispersal as a function of the adults' corpulence in the natal area. The graph is plotted in the range of observations for the variables considered.
C- Predicted probabilities of the males' dispersal as a function of the adults' sex ratio in the natal area. The graph is plotted in the range of observations for the variables considered.

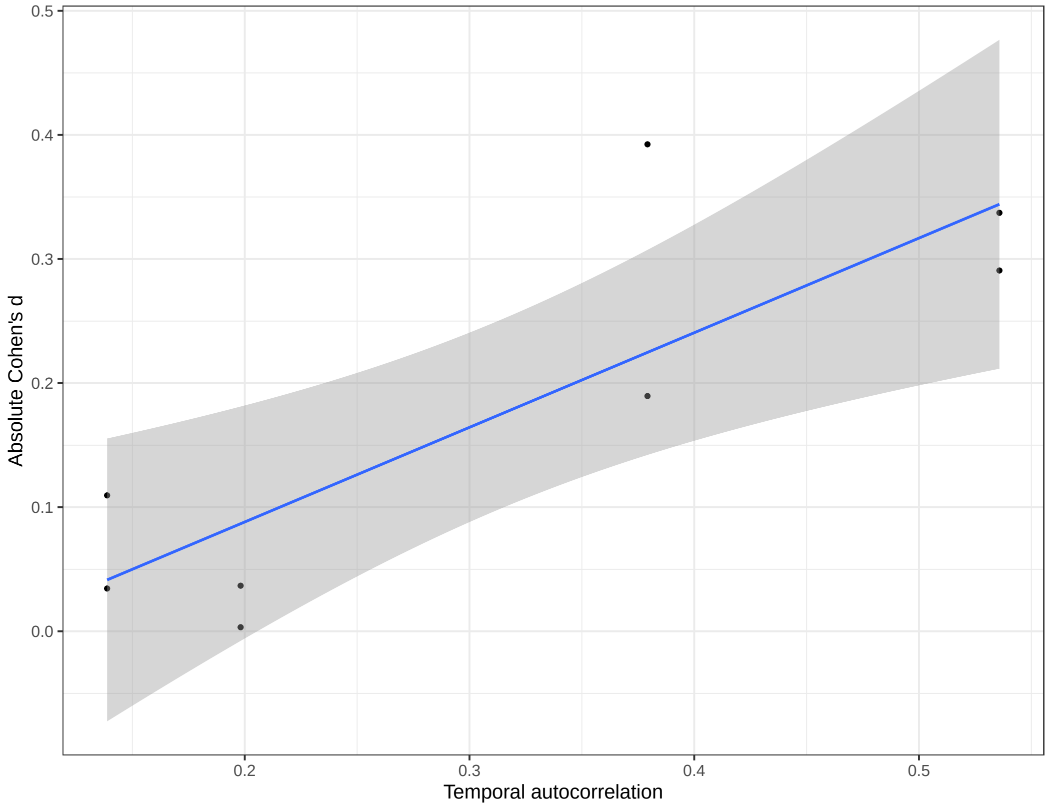


Figure S4: Correlation between effects size of distant and local environmental variable and their temporal autocorrelation.
The regression analysis was led for the first model (testing for phenotype and distance dependencies). The blue line displays the linear regression between the two variables. Black dots are associated with the observations. For a same variable, distant and local values shared the same temporal autocorrelation (dots in the same vertical line).

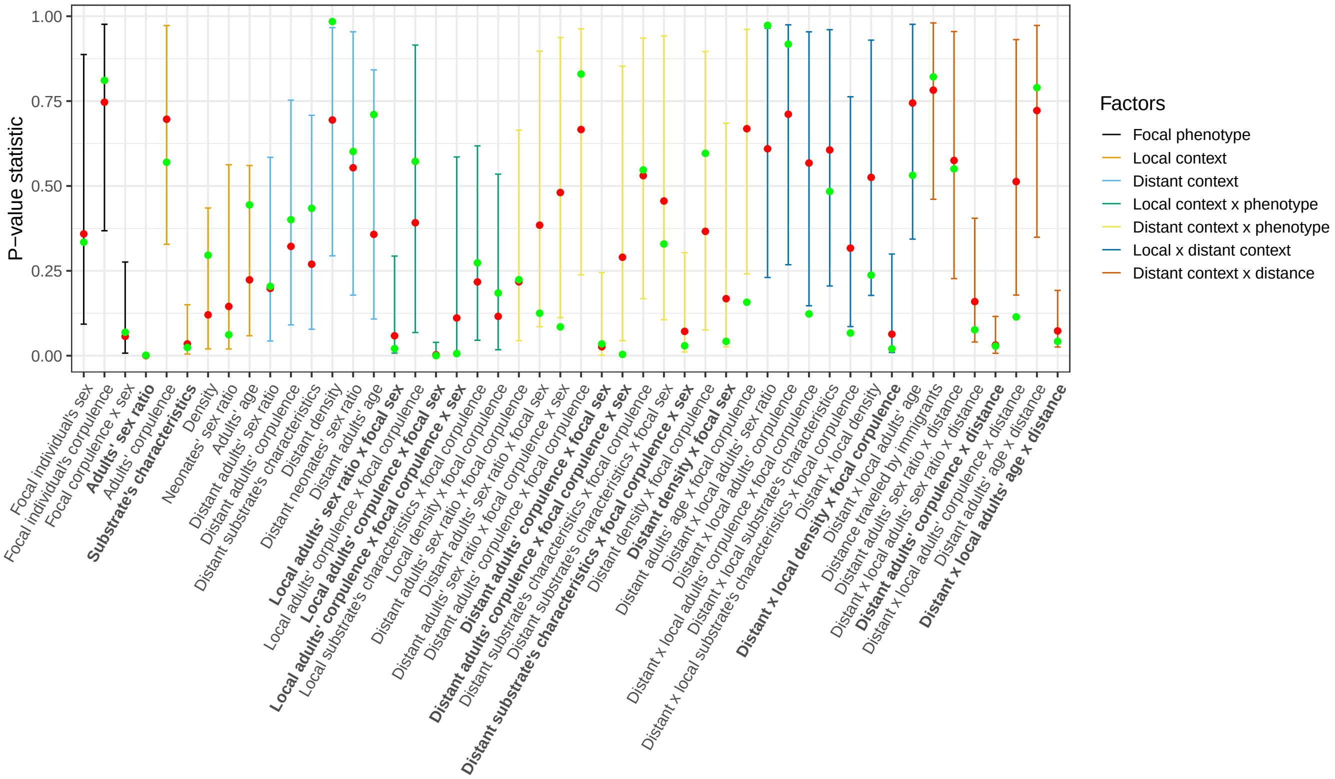


Figure S5: Sensitivity to differences in dispersal response among siblings (First model: all immigrants-informed neonates).

Original p-values of each variable from the first model are represented by green dots. Median of the p-values obtained through resampling among siblings (1,000 times) are displayed by red dots. Errors bars represented the 95% distribution of resampled p-values (percentiles). The different group of factors used in our model are indicated by different error bars' colours. Names of variables found significant in the original model, are in bold. Error bars of the "Adults' sex ratio" variable are not visible because too close to the median p-values.

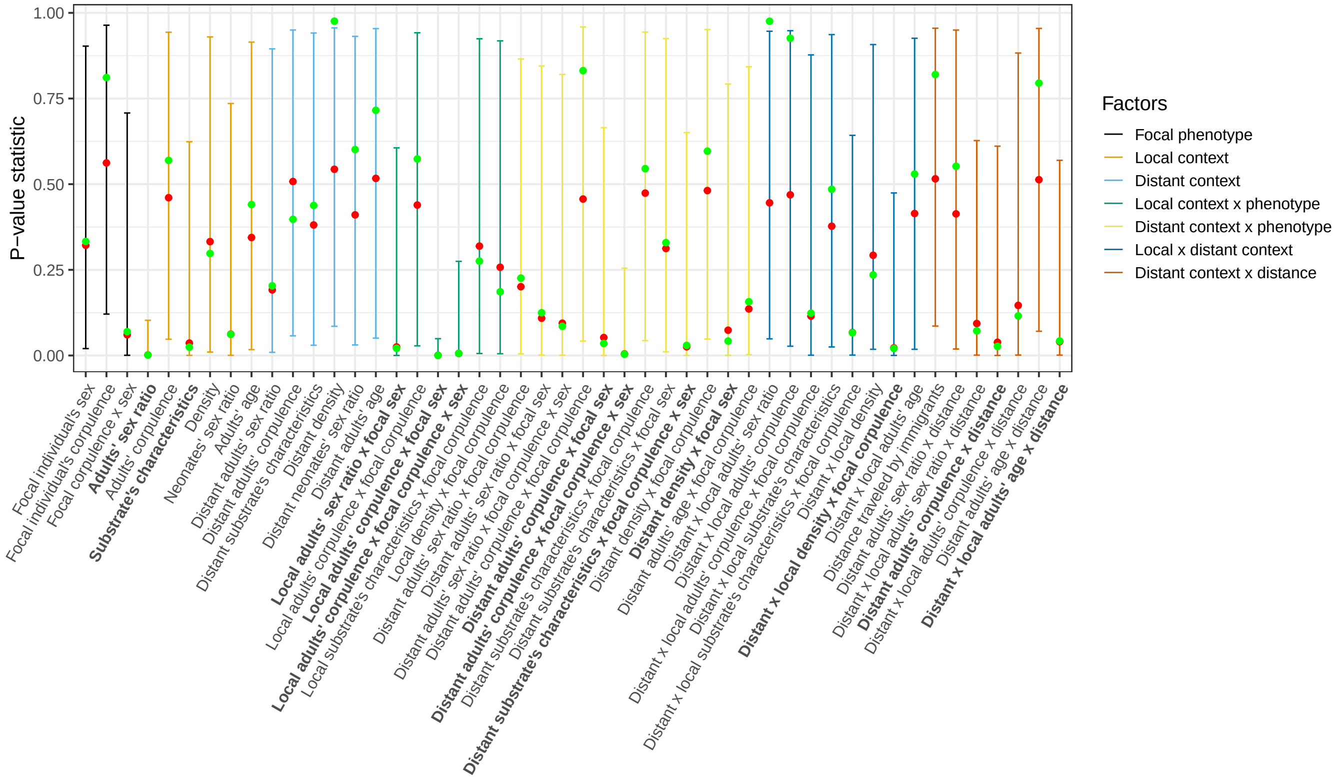


Figure S6: Robustness analysis by bootstrap resampling (First model: all immigrants-informed neonates)

Original p-values of each variable from the first model are represented by green dots. Median of the p-values obtained through bootstrap resampling (1,000 times) are displayed by red dots. Errors bars represented the 95% distribution of resampled p-values (percentiles). The different group of factors used in our model are indicated by different error bars' colours. Names of variables found significant in the original model, are in bold.

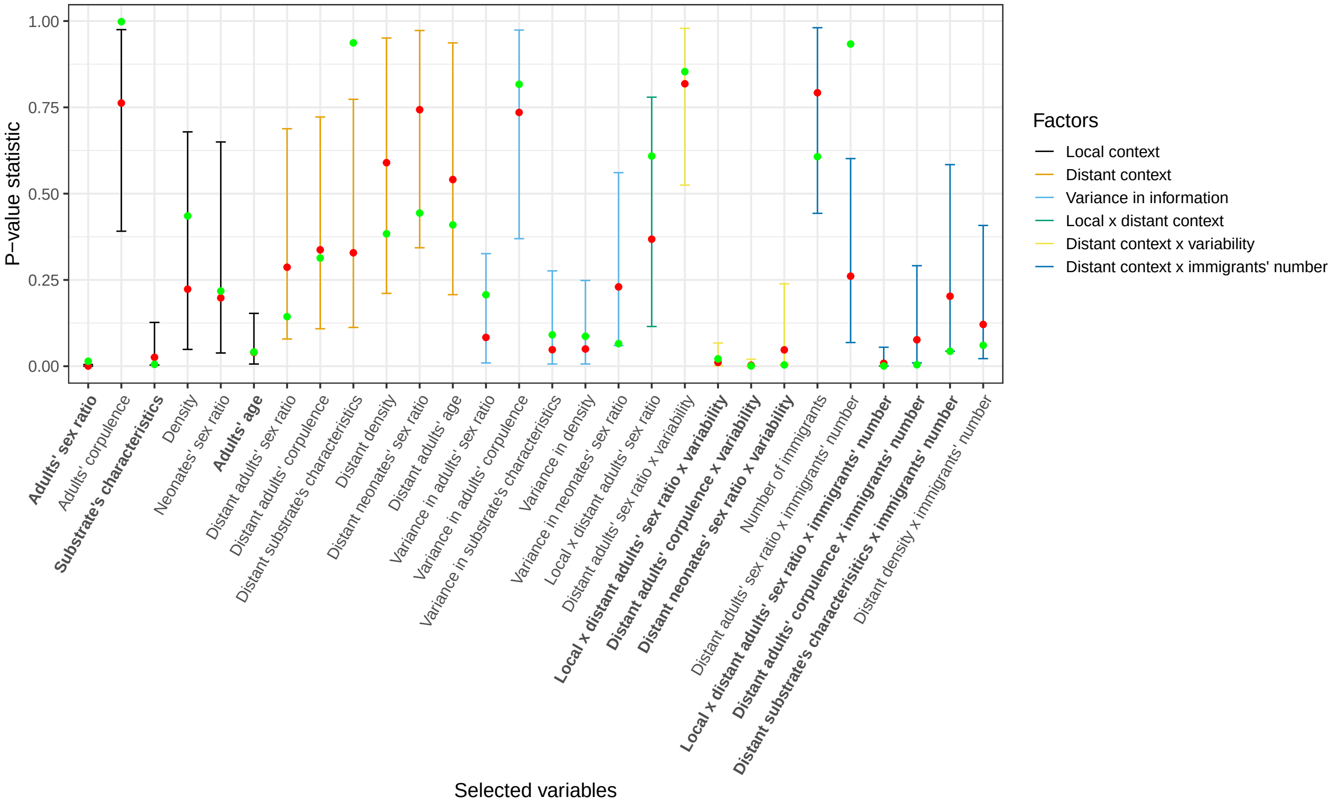


Figure S7: Sensitivity to differences in dispersal response among siblings (Second model: all neonates informed by multiple immigrants)

Original p-values of each variable from the second model are represented by green dots. Median of the p-values obtained through resampling among siblings (1,000 times) are displayed by red dots. Errors bars represented the 95% distribution of resampled p-values (percentiles). The different group of factors used in our model are indicated by different error bars' colours. Names of variables found significant in the original model, are in bold.

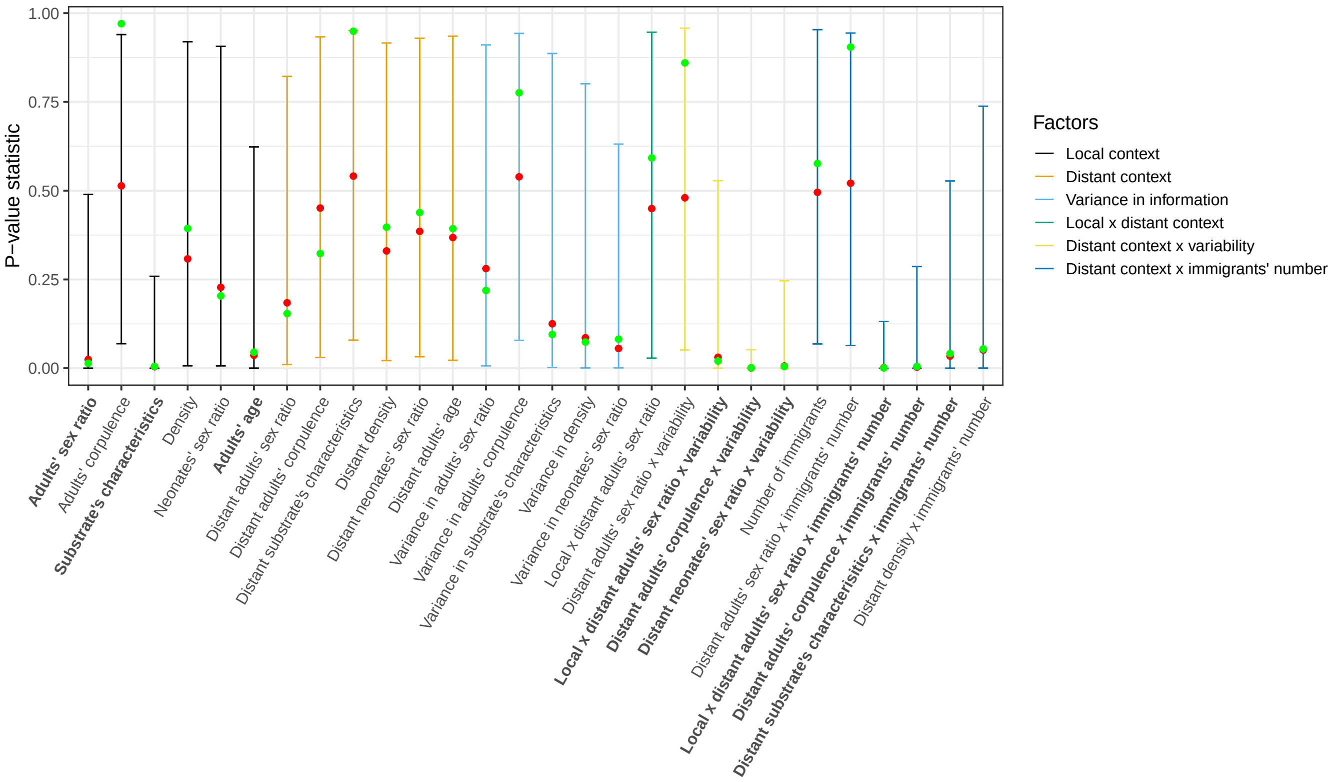
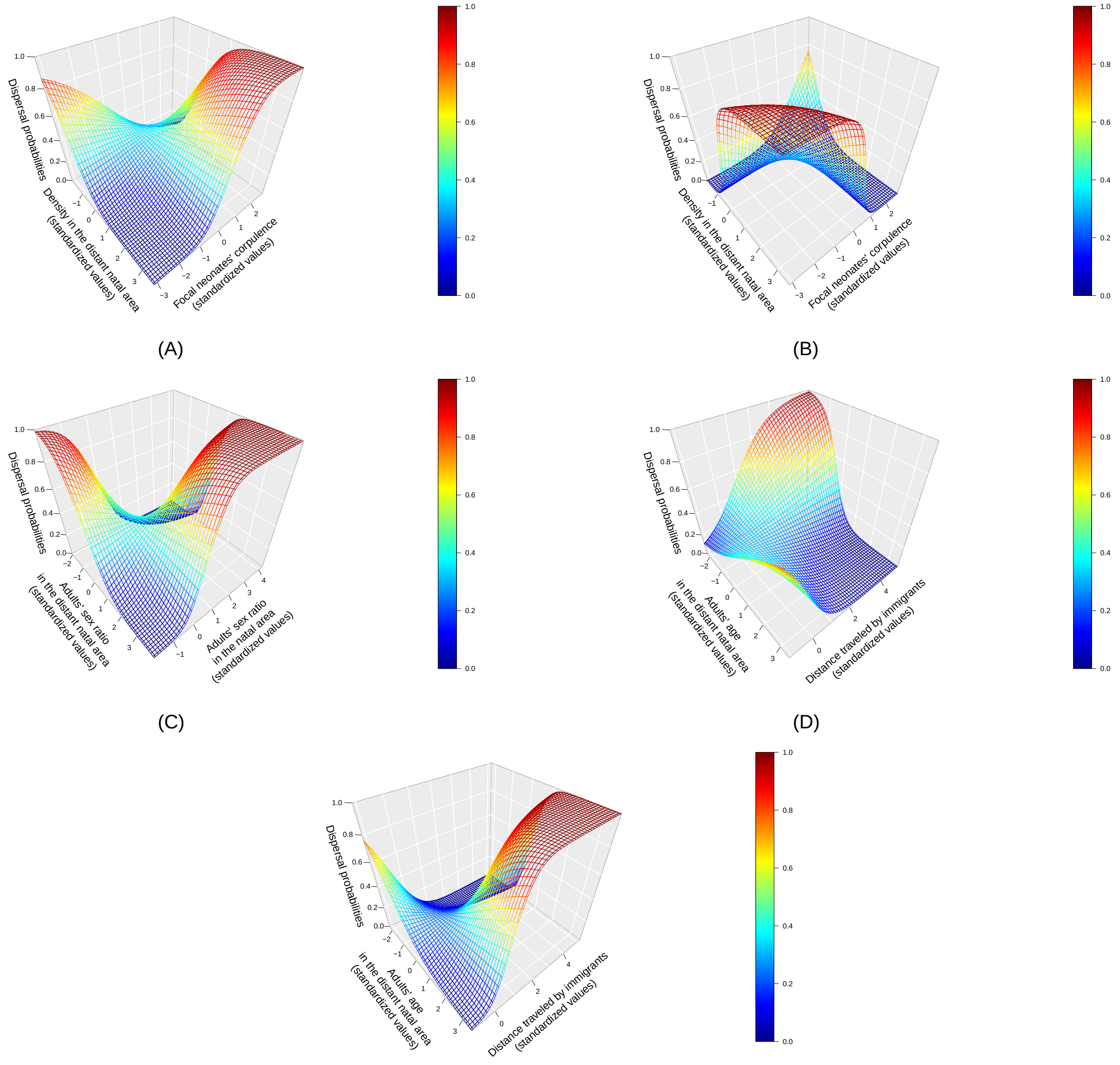


Figure S8: Robustness analysis by bootstrap resampling (Second model: all neonates informed by multiple immigrants).
Original p-values of each variable from the second model are represented by green dots. Median of the p-values obtained through bootstrap resampling (1,000 times) are displayed by red dots. Errors bars represented the 95% distribution of resampled p-values (percentiles). The different group of factors used in our model are indicated by different error bars' colours. Names of variables found significant in the original model, are in bold.



(A) (B) (C) (D) (E)

Figure S9: Relationships at the margin of significant triple interactions.

The graphs were computed from the coefficient of the studied variables and the intercept obtained in our model (all other coefficients were set to their mean, *i.e.* 0 as they were scaled prior analyses). The graphs are plotted in the range of observations for the variables considered on the X-axes.

A- Predicted probabilities of the individuals' dispersal as a function of the density in the distant areas and the focal individuals' corpulence, for a very low local density. This relationship was observed in the first model (with all immigrant-informed neonates). The local density has been set to the minimum of its distribution.

B- Predicted probabilities of the individuals' dispersal as a function of the density in the distant areas and the focal individuals' corpulence, for a very high local density. This relationship was observed in the first model (with all immigrant-informed neonates). The local density has been set to the maximum of its distribution.

C- Predicted probabilities of the individuals' dispersal as a function of the local and distant adults' sex ratios, for a very high variability in the distant adults' sex ratio. This relationship was observed in the second model (with multiply-informed individuals only). The variability in distant adults' sex ratio has been set to the maximum of its distribution.

D- Predicted probabilities of the individuals' dispersal as a function of the adults' age in the distant areas and the immigrants' traveled distance, for a very low local adults' age. This relationship was observed in the first model (with all immigrant-informed neonates). The local adults' age has been set to the minimum of its distribution.

E- Predicted probabilities of the individuals' dispersal as a function of the adults' age in the distant areas and the immigrants' traveled distance, for a very high local adults' age. This relationship was observed in the first model (with all immigrant-informed neonates). The local adults' age has been set to the maximum of its distribution.

Contribution of the present thesis

Multi-determinism of dispersal

This thesis particularly highlighted the multi-deterministic nature of movements, specifically dispersal. Indeed, I found the dispersal to depend on multiple factors, as expected from the literature (Introduction for details, *e.g.* Clobert et al. 2012, Le Galliard et al. 2012, Scandolara et al. 2014, Suh et al. 2020, Cayuela et al. 2020, Behr et al. 2020). We observed concomitant effects of the focal individual's phenotype (mainly its sex and body condition), potentially reflecting its ability to compete for resources and mates, or endure dispersal cost (Bowler and Benton 2005, Gyllenberg et al. 2008, 2011, Li and Kokko 2019), the social context (which directly informs a habitat's competitiveness or indirectly its quality, Bowler and Benton 2005, Clobert et al. 2009, Wey et al. 2015), and the non-social environmental context (defining the suitability of habitat, Bowler and Benton 2005). Therefore, we confirmed in natural conditions the dependencies observed through experiments, mostly separately (Clobert et al. 2012, Cote and Clobert 2012), and that they simultaneously impact dispersal.

Surprisingly, we did not find any effects of the kin competition when tested, while kin competition is known to be a major determinant of dispersal (Gandon 1999, Lambin et al. 2001, Taylor and Buckling 2010, Matthysen 2012), with significant evidence in common lizards (Léna et al. 1998a, Ronce et al. 1998, Cote et al. 2007, Cote and Clobert 2010). However, we did not comprehensively test for its influence, nor for inbreeding avoidance (another potentially major dispersal determinant: Pusey 1987, Bollinger et al. 1993, Perrin and Mazalov 1999, Szulkin and Sheldon 2008). Indeed, some of the most important factors describing kin competition or inbreeding avoidance were not available for our analyses, such as the mothers' age (Ronce et al. 2000), presence (Le Galliard et al. 2003a), or stress level (Meylan et al. 2002, Mestre and Bonte 2005, Bestion et al. 2014). In addition, kin competition and inbreeding might have more influence on other dispersal parameters than emigration decisions, such as the dispersal distance: individuals avoiding kin competition or inbreeding are indeed expected to disperse over particularly long distances (Rousset and Gandon 2002, *e.g.* Long et al. 2008, Bitume et al. 2013 Hardouin et al. 2015, Aguillon and Duckworth 2015). In support of such expectations, we found the size of mothers to be a major factor influencing dispersal distances, with a significant increase in dispersal distances when the size of mothers was of intermediate value (Brevet et al. in prep, Appendix 5 for details).

Our observed ranking of movement correlates highlighted the importance of focal individual sex (Chapters 1-3), adults' body condition and sex ratio, substrate's characteristics (Chapters 1 and 3), or conspecifics' food intake (Chapter 2).

As detailed in these chapters (to consult for references), adults' corpulence and sex ratio may reflect the competitiveness of a habitat (avoidance of corpulent adults and adult females potentially competing for resources), but also the environmental quality (high corpulence being associated with important resources availability, and better males survival being potentially associated with high habitat quality). In the same way, information on conspecifics' food intake (Chapter 2) appeared to be particularly used in movement decisions.

The substrate's characteristics may reflect the suitability of the habitat with attraction toward open and warm habitats, probably providing more thermoregulation opportunities and also greater availability of prey.

Finally, the importance of sex should both result from the way this species reproduces and competes (polygynous species with males competing for mates and females for resources, Greenwood et al. 1980), leading to sex-biased movements. It may also be of primary importance as an indicator of an individual ability to compete (*i.e.* social dominance), leading to alternative responses to the environmental context (as for the adults' corpulence or the substrate's characteristics, Chapters 1 and 3) to trade off the habitat quality and the ability to compete in such habitat.

However, these results may vary depending on the studied context, individual conditions, and species. First, dispersal factors ranking should depend on the environmental context: for example, we can expect factors related to particularly high spatiotemporal variability to be less used in movement decisions (Riotte-Lambert 2019, Doligez et al. 2003). Such environmental predictability varies among sites and populations, with potentially important consequences on demographic parameters (*e.g.* Masó et al. 2020, in common lizards). A dependence of dispersal factors' importance on their predictability was potentially observed here (Chapter 3: correlation between the temporal autocorrelation of environmental variables and their effect sizes) but remains to be properly tested. Other elements of the context, such as the competition, the predation pressure, or the availability of resources, could be involved in determining dispersal factors' importance. For example, higher importance of intraspecific competition or predation was observed for dispersal when resource availability decreased (Morosinotto et al. 2014, Szymkowiak and Thomson 2018, Yip et al. 2019). Therefore, it appears central to further test potential interactions between the different elements of the environmental context to better understand the way they are precisely used (*e.g.* Baines et al. 2014).

Second, the ranking between these factors should depend on the individual traits. As all individuals do not have the same sensitivity to competition or more broadly to environmental variations, one might expect different strategies to emerge in response to the environmental context (*e.g.* Endriss et al. 2018, Baines et al. 2019). Our studies suggest such condition-dependence, as we observed varying responses to the social context depending on the individuals' sex or corpulence (Chapters 1-3). How these individual preferences in the use of various dispersal factors may vary across dispersal syndromes should be of particular interest to explore (Raffard et al. 2022).

Finally, the ranking of dispersal determinants should vary with the species' biology. For example, we might expect more importance of social context elements depending on a species' social competence, *i.e.* the ability of an individual to make appropriate social decisions relative to the available social information (Taborski and Oliveira 2012, Duboscq et al. 2016). We might also expect the importance of the social context to depend on the level of sociality (Lefebvre and Giraldeau 1996, Templeton et al. 1999, Chouinard-Thuly and Reader 2019), even if a majority of studies do not report such relationships (Reader and Lefebvre 2001, Webster and Laland 2017). More broadly, dispersal factors' importance should vary with the ability to perceive the surrounding environment, depending on existing sensory abilities (*e.g.* Lohman et al. 2010: perception of magnetic fields, allowing individuals to orientate in space). For instance, kin recognition abilities could significantly reduce the importance of inbreeding avoidance and kin competition by allowing an individual to identify and avoid kins (*e.g.* Blaustein et al. 1988, Riehl and Stern 2015). How the determinants of dispersal evolve with these abilities and lifestyle patterns (main habitats, sociality) remains to be explored, as does the phylogenetic inertia of these preferences.

Highlighting the use of multiple social information sources in movements decisions

As originally expected (Clobert et al. 2009, 2012), we found the use of social information to be central in movement decisions. In all chapters, individuals appeared to use the social context for emigration decisions. The consistently high relative importance of social information in our studies highlights that such information is central for informing about the local and distant environments, at least in our model species. This social information was either directly about the social context or consisted of cues on other environmental factors, such as resource availability (Chapter 2 in particular).

We also consistently observed significant interactions between the focal individual's phenotype and the social context. It appeared that the influence of social context might depend on an individual's ability to endure competition costs or other energetic costs (Chapters 1-3 for details). That potentially reflects diverse life-history strategies with dispersal decisions that may depend on an individual's abilities to compete or colonize new habitats (Clobert et al. 2009).

Interestingly, the use of social information for movement decisions appeared to be complex, with the simultaneous use of various social cues, potentially provided by several individuals. For instance, focal individuals were influenced by both the conspecifics' food intake and the condition of their mothers in Chapter 2, and concurrently by the conspecifics' age, sex ratio, corpulence, and density in Chapters 1 and 3. This information was provided by two conspecific intruders in Chapter 2, and potentially by all conspecifics in the natal area in Chapters 1 and 3 (including recent immigrants in Chapter 3). The focal individuals' movement response was, in all Chapters, influenced by the average information among conspecifics it had encountered (Chapter 2) or was likely to encounter (Chapters 1 and 3: averaged traits of conspecifics at direct proximity). Yet, it appeared that individuals were not able to use the contrast between information sources to orientate (Chapter 2).

A major finding was the concurrent use of both local and immigrant-based information in nature, with symmetrical responses and similar relative importance between the two types of information (Chapter 3). These results suggest that individuals similarly use local and immigrant-based information: for example, female neonates dispersed more when the local adults' corpulence was high and when the adults' corpulence in the original habitat of immigrants (*i.e.* neighboring habitats) was low. Such consistent use of local and immigrant-based information could then reflect the same habitat preferences at emigration and immigration, if individuals that emigrate following some information about distant habitats, do indeed leave seeking to reach the habitats about which they have been informed, which remains to be properly tested.

A relationship between the information quality and its use?

In our studies, the use of social information appeared to depend on its value (as expected in Koops 2004), a function of the individual's phenotype and the local context. Therefore, information on competition should be used differently depending on the individual's ability to compete (*e.g.* corpulence and sex interactions with the social context: Chapters 1 and 3). One may also expect the use of information about resource availability to depend on the energetic reserves and needs of an individual (Chapter 2, but also 1 and 3). In the same way, the value of distant (*i.e.* immigrant-based) information for movement should depend on the local context: an individual should disperse only when the potential benefit of settling in a novel environment exceeds the benefit of staying in its current one (Bonte et al. 2012, as observed for the density preference in Chapter 3).

Second, in the case of immigrant-based information (Chapter 3), the use of social information depended on the nature of the information itself: the number of information carriers (*i.e.* the number of immigrants), the variability among information sources (*i.e.* the variability among distant habitats on which immigrants informed), and the accessibility of the origin of information (*i.e.* the distance traveled by immigrants). The previously described use of social information occurred only when the information appeared to be reliable, with sufficiently low variation among sources, and sufficient information carrier number. Conversely, we may consider that high variability among sources, few immigrants number, and high distance to travel, constitute unreliable information, with a significant risk of not accessing the information as it is perceived. In such cases, we observed no responses, or emigration toward similar or low competition habitats, which are potential cost-limiting strategies (as expected in Koops et al. 2004).

Yet, the present thesis is not intended to be comprehensive and many other questions are raised from such results. First, we did not explore the way social information was precisely used, since it is quite difficult to know which cues are used and what precise information is transmitted. Second, we mainly focused on the emigration response but other movement phases should be impacted by social information use, such as settlement or transience. Finally, the evolution of socially acquired information during movements and its impact on demography and evolution remained largely overlooked. I will now discuss these perspectives and future study prospects.

Perspectives on the use of social information in movements

How is precisely used social information?

Which information, which cues?

A first issue related to the use of social information during movements is to understand what information is precisely used (an issue also identified in Samplonius and Both 2017) and with which cues. During this thesis, we correlated the movement initiation responses with parameters of the social context (average traits of conspecifics) but we did not control for the information that was precisely used (excepting for the food intake of conspecifics in Chapter 2, and for the microcosm experiment using *Tetrahymena thermophila*: Appendix 3, for which we obtained no conclusive results on this point). It results that we do not know for sure the ultimate information used behind these traits (in particular for the information finally provided by the immigrants in Appendix 3).

They could first represent direct information: for example, the average conspecifics' age potentially informing on the survival rate in a given area (Chapters 1 and 3). Second, traits could also correlate with other parameters of the habitat and therefore be a cue for these parameters (*e.g.* Parejo et al. 2008, Samplonius and Both 2017): for example, conspecifics' corpulence could correlate with the resource availability in an area, or with conspecifics' abilities to compete (Chapter 1 for details). Such a trait might also be associated with more complex information, by conveying multiple messages at the same time, which could be combined to assess several elements of the environmental context (Dore et al. 2018). It could be the case for body coloration (Martín and Lopez 2009), or heterospecific/conspecific density, potentially related to both the competition and the habitat quality (Forsman et al. 2008, Baude et al. 2011). Such a multiple-message cue may be used differently according to the receiver's needs or abilities (*e.g.* Morinay et al. 2020b: song quality used as information on habitat quality or level of competition based on individual competitiveness). Then, by conveying multiple messages at once, conspecifics' traits can be both information on themselves and a social cue. adult age potentially represents direct information about conspecific survival rates but also about their competitive abilities, which may decrease with senescence (Massot et al. 2011).

Knowing which cue is associated with information can also be an issue: we often expected social information to be used without knowing precisely which social cues or signals were associated with it (*e.g.*, the social cues about environmental context experienced by immigrants in Chapter 3). Information about intraspecific competition might be an example of such an issue (Appendix 7, section 1, for a detailed example in the common lizard), being either related to density (numerical counts of conspecifics, directly by presence or cues such as odors and sounds), behavior, or coloration. Information can also result from a combination of several of these cues (multi-compound cues, as often observed for chemical cues: Ben-Shaul et al. 2015).
Specific experiments are needed to disentangle the association between social information and cues. Experimental conditions can allow for fine control of environmental parameters to isolate their effects (what we attempted to do with microcosm experiments: Appendix 3), to study which traits vary with the environmental parameters of interest and whether these traits individually drive the same movement responses as the initial parameter alone. We have attempted to perform such an experiment during this thesis on experimental microcosms (Appendix 3, proposal for further possible studies on our model species: Appendix 7, section 1).

We should also consider the multiplicity of messages when multiple social cues are present simultaneously (Bro-Jørgensen et al. 2010, *e.g.* Ward and Mehner 2010). These multiple cues can be complementary and clarify the information conveyed (Bro-Jørgensen et al. 2010, Dore et al. 2018). They may also interact, with the use of some cues depending on the presence or absence of other cues (*e.g.* Yossen et al. 2021), or with a modulation of the use of one social cue depending on the variation of another cue (*e.g.* Fletcher 2007: use of social cues on conspecific or heterospecific presence depending on overall population density). These interactions were not tested here, but it seems very likely that they could occur in our model species (*e.g.*, Lena et al. 1998a: opposite effect of density on dispersal depending on conspecific sex, effect of female adults' corpulence only when familiar females). Thus, we would need further study of these interactions between social cues in the context of movement-related decision making.

Another possible problem is the distinction between cues and signals (as defined in Danchin et al. 2004, Dall et al. 2005). Indeed, it is expected that certain traits are selected in response to certain environmental constraints (*e.g.*, greater corpulence or aggressive displays for social dominance, Summers and Andrews 1996, Carrascal et al. 1998, Gosler and Carruthers 1999). These traits benefit individuals through direct effects on their success (better access to mate and resources due to traits associated with social dominance), but also through indirect effects by influencing the decisions of other conspecifics (*e.g.*, avoidance by other conspecifics of an individual exhibiting traits associated with social dominance, Summers and Andrews 1996, Jonart et al. 2007). In this case, these traits are considered social cues but because they are likely under selection (Moore et al. 2002 for social dominance traits), it is unclear whether they should be designated as signals. Because the primary benefits of these traits may or may not be direct, or both indirect and direct, the distinction between cues or signals for these traits might then require a signal to be specifically associated only with benefits gained through social information transmission (*i.e.*, active information exchange or communication, Dall et al. 2005). In cases where doubt remains, it could be tested by attempting to decouple potential direct and indirect benefits (*e.g.*, by studying the impact of the trait on fitness under social and non-social conditions). In the context of the present thesis, it is clear that the main traits that can convey information (corpulence, age, sex) are most likely to cue because they primarily impact survival or reproduction (Le Galliard et al. 2004, Massot et al. 2011).

Considering larger timescales and heterospecifics for social information use in movements

During this thesis, we did not consider social information use implying heterospecifics and long-term processes (Sepannen et al. 2007). Social information conveyed by heterospecifics may have a prominent role in movement decisions (Goodale et al. 2010), either by more efficiently informing on habitats quality during movements (Mönkkönen et al. 1999, particularly well-evidenced in birds, for habitat selection: Szymkowiak 2013, Szymkowiak et al. 2017), or by giving reliable cues on environmental factors that could be central for distribution dynamics as predation pressure (*e.g.* Mönkkönen et al. 2009, Parejo et al. 2012, Forsman et al. 2013), heterospecific competition level (*e.g.* Forsman et al. 2008, Cayuela et al. 2018), or prey availability (*e.g.* Hromada et al. 2008). In the model species used during this thesis, the movements were already found to depend on the presence, or cues on the presence, of heterospecific competitors (Fronhofer et al. 2015a, Williams et al. 2020) and predators (Bestion et al. 2014, Winandy et al. 2021, Hauzy et al. 2007). Further integration of these factors in the determinism of movement, and particularly dispersal, should be performed to supplement the presented results in Chapters 1 and 3. It would be interesting to quantify the density of prey, predators, and heterospecific competitors in the natal area before dispersal, and more especially in immigrants' habitats since immigrant-based information on heterospecifics presence was never tested before to my knowledge.

We also did not consider potential temporal effects for the use of immigrant-based social information. As theorized in Seppanen et al. (2007), we could expect the value of information to decrease with spatial and temporal distance (*e.g.* Van Bergen et al. 2004, Fletcher and Miller 2008, Thomson et al. 2013). However, temporally distant information could be valuable in some cases when no immediate information is available to anticipate future conditions (*e.g.* Doligez et al. 1999, 2002, 2004). If we already explored the importance of spatial distance for the use of social information in movements (Chapters 3), the importance of temporal and spatial distance remains to be more properly tested (Appendix 7, section

2 for experiment proposals). In particular, we could hypothesize about the probable importance of the immigrants' timing of arrival on the use of social information with a preference for the most recently arrived immigrants. Another unexplored aspect is the role of former immigrants in natal dispersal decisions, having dispersed the previous seasons, at least a year before the focal neonates' birth. It is indeed possible that their natal habitat imprints their phenotype as grown-up individuals (Grafen 1988, Monaghan 2008) which may then influence the decisions of the focal neonates. Yet, such influence should be particularly difficult to test as it is tricky to disentangle the direct effect of the immigrants' traits on the focal neonates with the extent to which these traits reflect information about the immigrant's original habitat in the field (particularly because such individuals are likely to settle in an environment matching their condition: Stamps et al. 2006, Benard and McCauley 2008, but see Appendix 7, section 2 for study proposals).

Lastly, there is also a possibility that diffusion of social information occurred (chain of information through different conspecifics: Seppanen et al. 2007). The existence of social information diffusion is already well-established through social learning examples mainly (Duboscq et al. 2016, Toth et al. 2020, *e.g.* Battesti et al. 2012, Atton et al. 2012), but remains to be tested for social information use in movement decisions, other than for foraging movements (Atton et al. 2014, Tóth et al. 2017, Jones et al. 2017). It could have major importance for immigrant-based information, with initial information being potentially transmitted to long distances through the sequential transmission by several conspecifics. Such transmission of "rumors" and their impact on movement decisions have already been tested by De Fraipont and Pous (unpublished results) some years ago, and preliminary results appeared to attest to sequentially transmitted use of the initial information (through avoidance of specific areas the first individual was confronted to), even if more formal tests remain to be led (Appendix 7, section 2 for study proposals).

Phenotype and context-dependence in the use of social information

As we evidenced during this thesis, the use of social information in movement decisions is widely phenotype- and context-dependent (Chapters 1-3). A first aspect, that has been quite overlooked during this thesis, is the potential existence of variations in the propensity to use social information among individuals or contexts (*e.g.* Grüter and Leadbeater 2014, Mesoudi et al. 2016). As well-theorized by Riotte-Lambert et al. (2019), social information is expected to be used under certain regimes of environmental predictability (both temporal and spatial). The environment should be sufficiently variable for the information to be valuable (cannot be anticipated by present personal information, *e.g.* Boyd et al. 2016) but sufficiently predictable to be usable (to avoid the use of obsolete information, *e.g.* Galef and Whiskin 2004). The importance of predictability was partially evidenced during this thesis with the correlation between social information effects size and their temporal autocorrelation (Chapter 3, social information appears to be more used when predictable). It however needs to be properly tested, with experiments on social information use under different regimes of environmental predictability (*e.g.* Campana et al. in prep in *Tetrahymena thermophila*, under different regimes of temporal autocorrelation).

The propensity of social information use could also depend on the individual phenotype, with different strategies in the use or not of information that might coexist (Mesoudi et al. 2016, *e.g.* Rosa et al. 2012, Tait and Naug 2022). A good example of that could be pace-of-life syndromes (Réale et al. 2010), with varying levels of sociality and propensity to move among individuals that could lead to different sensitivity to social information for movement decisions ("slow" individuals with high personal prospecting and low movement activity associated to low sensitivity to social information, *e.g.* Marchetti and Drent 2000, Nomakuchi et al. 2009). Co-existence of such strategies may potentially lead to producer-scrounger dynamics ("slow" individuals as indicators of habitat quality, informing "fast" individuals during their movements: Rieucau and Giraldeau 2011). There is also a possibility that the propensity to use social information may more broadly vary with the variation in sociability traits (*e.g.* cooperation level, Jacob et al. 2015b), or with the level of aggressiveness and boldness (Kurvers et al. 2010, Trompf and Brown 2014, Morinay et al. 2020b). Such variations in the propensity to use social information should be more properly tested. For instance, we may consider individuals with such different life-history strategies and investigate their movement responses in the presence or absence of social information, to determine their sensitivity to it.

Beyond the propensity to use social information, there are also variations in social information use for movement decisions. Social information is not expected to be used the same way depending on the local context (as observed in Chapter 3, for the use of immigrant-based information), with social information use depending on the competition level (Lee et al. 2016, *e.g.* Baude et al. 2011, Brown et al. 2022), the level of predation risk (Bairos-Novak et al. 2017, Brown et al. 2022), or the level of resources (Szymkowiak and Thomson 2019, Brown et al. 2022). Indeed, we may expect a social information value to depend on the potential benefits of using it (Rieucau and Giraldeau 2011), *i.e.*, here the benefit of moving or not, a function of the present environment, since it defines the benefits/costs of movement (Bonte et al. 2012). The weight attributed to the present context should also vary with the individual's experience of this context (Galef et al. 2008, Leadbeater and Chittka 2009, Sasaki and Pratt 2013, Leris and reader 2016, Crane and Ferrari 2017), and therefore its age (Parejo et al. 2007, Loukola et al. 2012, Noble et al. 2014, Morinay et al. 2018, 2020a), or with maternal effects potentially informing on it (Boogert et al. 2013, Winandy et al. 2021).

Variability in using social information also depends on the individual phenotype (as evidenced in Chapters 1-3), it appeared that there are alternative strategies in social information use in movements according to the individual phenotype as its competition level or more broadly physiological state (see also Lindstedt and Hamilton 2013, Smolla et al. 2019). As theorized by Clobert et al. (2009), the use of social information could for example be driven by sociability strategies, with the potential co-existence of “joiners” (social individuals, good competitors, poor colonizers) and “colonizers” (asocial individuals, bad competitors, good colonizers) strategies. Such phenotype-based strategies could have a major impact on individuals distribution, in particular for colonization or rescue of habitat patch for colonizer-joiners dynamics, or distribution of individuals depending on their competitive abilities, with potential segregation of traits in space (as personality traits, e.g Croft et al. 2009, Carter et al. 2015). Using our long-term monitoring, we observed that the distribution of dispersers may be dependent on social constraints: dispersers originate primarily from the margin of the study site and appear to settle near the resident distribution core without being exactly distributed in the densest resident areas (Appendix 4). Better studying settling strategies of dispersers would be necessary to understand the way they precisely distribute, and whether specific strategies in using the social information co-exist.

Resolving conflicts between social information sources

This thesis highlighted the potential multiplicity in information sources, with the confrontation with multiple conspecifics before movement decision, originating from local and distant (*i.e.* immigrant-based information) habitats. Such multiplicity in information sources should lead to potential conflicts between sources (Kendal et al. 2009, Stienessen and Parrish 2013). If information conflicts were widely studied when looking at the conflict between personal and social information (Kendal et al. 2009), very little is known about the conflict among social information sources. The importance of such conflicts was partially investigated during this thesis through the study of variability among social information sources (Chapter 3) highlighting that information appeared to be less used and used in a way minimizing costs when uncertain (as expected in Koops 2004). More precise experiments on social information conflict between two sources in controlled conditions were also led on *Tetrahymena thermophila* but did not lead to conclusive results on this point (Appendix 3). We need more experiments to precisely understand the outcome of such conflicts (Appendix 7, section 3 for study proposal). Using the framework developed by Kendal et al. (2009), we can expect sources to be favored compared to others in case of conflict, with the so-called “Who” and “When” strategies. Thus, we might first expect the social information to be used differently depending on the information conveyer traits (“who” strategies), by according more value to information conveyed by successful individuals (Duffy et al. 2009, Pike et al. 2010, Pasqualone and Davis 2011, Mesoudi et al. 2016), more experienced individuals (Kern and Radford 2017, Rauber and Manser 2018), or familiar individuals (Trapp and Bell 2017, Bairos-Novak 2019a,b). Values of social information could also vary between conspecifics or heterospecifics (potentially depending on the level of competition and niche overlap, defining the cost of using the information and its relevance, Kivelä et al. 2014, Jaakkonen et al. 2015, Romero-González et al. 2020).

Second, the information value should depend on the context and the nature of information (“when” strategies), with a preference for more reliable cues (more directly informing on a parameter of interest: O’Mara et al. 2014), on signals over cues (*e.g.* Vilella-Pacheco et al. 2021), particularly honest signals (Smith 1994, Biernaskie et al. 2018), or more predictable cues (Smolla et al. 2016). Cues with previous personal experience should also be more valuable (Mesoudi et al. 2016), especially when related to their own success (Parejo et al. 2007, Sánchez et al. 2008, Leris and Reader 2016). Value of conforms, repeated, cues should also be greater, even if it could depend on information value (Sumpter 2008, Rieucau and Giraldeau 2009, Pike and Laland 2010, Stienessen and Parrish 2013). We may also expect a higher value of cues being more recent or with more close origins (Van Bergen et al. 2004, Fletcher and Miller 2008, Thomson et al. 2013), and more broadly when information is less costly to obtain or use than another (*e.g.* using social information depending on the associated predation risk: Webster and Laland 2008, Bairos-Novak et al. 2017, Feyten et al. 2020, Barnes and Beale 2021).

Enlarging the use of social information during movements

During this thesis, I mainly focused on the effect of multiple social information sources on the emigration behavior, but social information should impact other phases of the movement, with information transfer evidenced during the transience or the settlement, and with potential influences on the motion characteristics such as the traveled distance, individual's orientation, linearity of movements, and more broadly its space use.

Influences on traveled distances: how social information can shape transience and settlement

Social information may influence the individual's traveled distance during movements. First, the traveled distance could depend on the initially gathered information before movement initiation (Figure 1): indeed individuals may avoid specific social context and may therefore vary in the distance they disperse from it (*e.g.* Matthysen 2005, Aguillon and Duckworth 2015). Such results were found during this thesis (Brevet et al. in prep., Appendix 5), with a particular influence of traits potentially associated with kin competition (mother's body size). The traveled distance could also depend on immigrant-based information (Figure 1): if an individual could estimate the distance traveled by an immigrant that informed him on distant potential habitats, we might expect this individual to travel a distance proportional to the immigrant's distance. This hypothesis could be easily tested with the common lizard long-term monitoring (Brevet et al., analyses in progress), even if preliminary exploration of data does not suggest such a relationship (no significant correlation between distance traveled by immigrants and dispersal distance of focal neonates, Pearson correlation test: p=0.81). The way information on distance is conveyed remains to be explored in our model species, it could be associated with physiological or behavioral changes in traits directly related to the investment in traveling (Bonte et al. 2012), through specific traits associated with long-distance dispersers (Goossens et al. 2020, *e.g.* Lowe and McPeek 2012) or by dissimilarity in the phenotype compared to the focal individual with cues indicating that the immigrants are coming from a contrasted environmental context. More generally, it could also be informed via specific behavior (*e.g.* waggle dance in bees, De Marco and Menzel 2005) or sound cues (*e.g.* Naguib and Wiley 2001).

The initial habitat could also impact settlement dynamics: in case of a natal habitat preference induction (Stamps 2001, Davis and Stamps 2004, Stamps and Davis 2006, Piper 2011), an individual could prefer social cues reflecting a habitat close to its natal one during dispersal (Stamps et al. 2009a,b, *e.g.* Miller et al. 2012, Merrick and Koprowski 2016). Yet, if an individual does not find such a habitat, there is a possibility that it settles in less close habitat to avoid a too important cost of dispersal (*e.g.* Sanz-Perez et a. 2018). In such a case, we might expect habitat dissimilarity to increase with traveled distance during dispersal. Conversely, if an individual that disperses tries to increase its fitness compared to its initial habitat we could expect that it would settle in a habitat different than the natal one (*e.g.* Kim et al. 2009), sometimes as a function of its phenotype (matching habitat choice: Edelaar et al. 2008, *e.g.* Camacho et al. 2015, Jacob et al. 2018), but if such habitat is not found, individuals should avoid too long dispersal associated with high costs (Bonte et al. 2012) and may then favor familiar habitat, easy to detect and with possible prior imprinting (Stamps and Davis 2006). In this case, we might expect similarity in habitat to increase with traveled distance. Such observation could also be related to the primary cause of dispersal: if an individual disperses to avoid kin competition or inbreeding, the emigration does not necessarily mean that the current habitat is not suitable or that other suitable habitats are available remotely (*e.g.* Cote and Clobert 2010). In such a case, it could actively seek a habitat with characteristics close to its initial habitat, as it would be easier to detect, and potentially accommodate (Stamps and Davis 2006). As the dispersers avoiding kin competition or inbreeding are known to travel particularly long distances during dispersal (Rousset and Gandon 2002), it could also increase habitat similarity with traveled distance. Such expectations on habitat similarity could be tested using the common lizard long-term monitoring (Brevet et al., analyses in progress, Appendix 7, section 4 for details). We should also explore in which way immigrant-based information is used, by investigating if dispersers informed by immigrants select habitats close to the ones the immigrants were coming from and if this similarity also correlates with dispersal distance (Brevet et al., analyses in progress, Appendix 7, section 4 for study proposals).

Second, traveled distance could depend on social information gathered during the transience phase. We may expect the social landscape to inform the individual on the cost of maintaining the movement (social resistance and landscape of fear hypotheses, Gallagher et al. 2017, Armansin et al. 2020; Figure 1), with also possible social information on the energetic landscape (Williams and Safi 2021). Social cues during transience can be diverse and inform on competition level, resource scarcity (*e.g.* Cozzi et al. 2018), predation (*e.g.* Huang et al. 2012), and could lead an individual to stop its movement to avoid supplementary costs (Baker and Rao 2004). The social context between the initial habitat and the habitat of settlement might thus predict the dispersal traveled distance if social resistance in the landscape prevails for movements (Brevet et al., analyses in progress).

Third, social information acquired during the settlement phase is crucial: by estimating habitat quality during its transience an individual could choose to settle in it (Oro et al. 2021; Figure 1). The quality of these candidate habitats should determine dispersal distance, often relative to the initial habitat (*e.g.* Serrano et al. 2003, Kim et al. 2009) and the individual's phenotype (matching habitat choice, *e.g.* Camacho et al. 2015), but also possibly relatively to immigrant-based information, even if it remains to be tested. Testing for social information use in the arrival habitat should therefore be central (Appendix 7, section 4 for further experiments proposal on our model species), many have been already performed, in particular when studying conspecific or heterospecific attraction (Szymkowiak 2013, Buxton et al. 2020) or reproductive success cues (*e.g.* Doligez et al. 1999, 2002, 2004), but relatively few on more complex social context components (Wey et al. 2015, but see Vercken et al. 2012, Endriss et al. 2018, Morinay et al. 2020a).

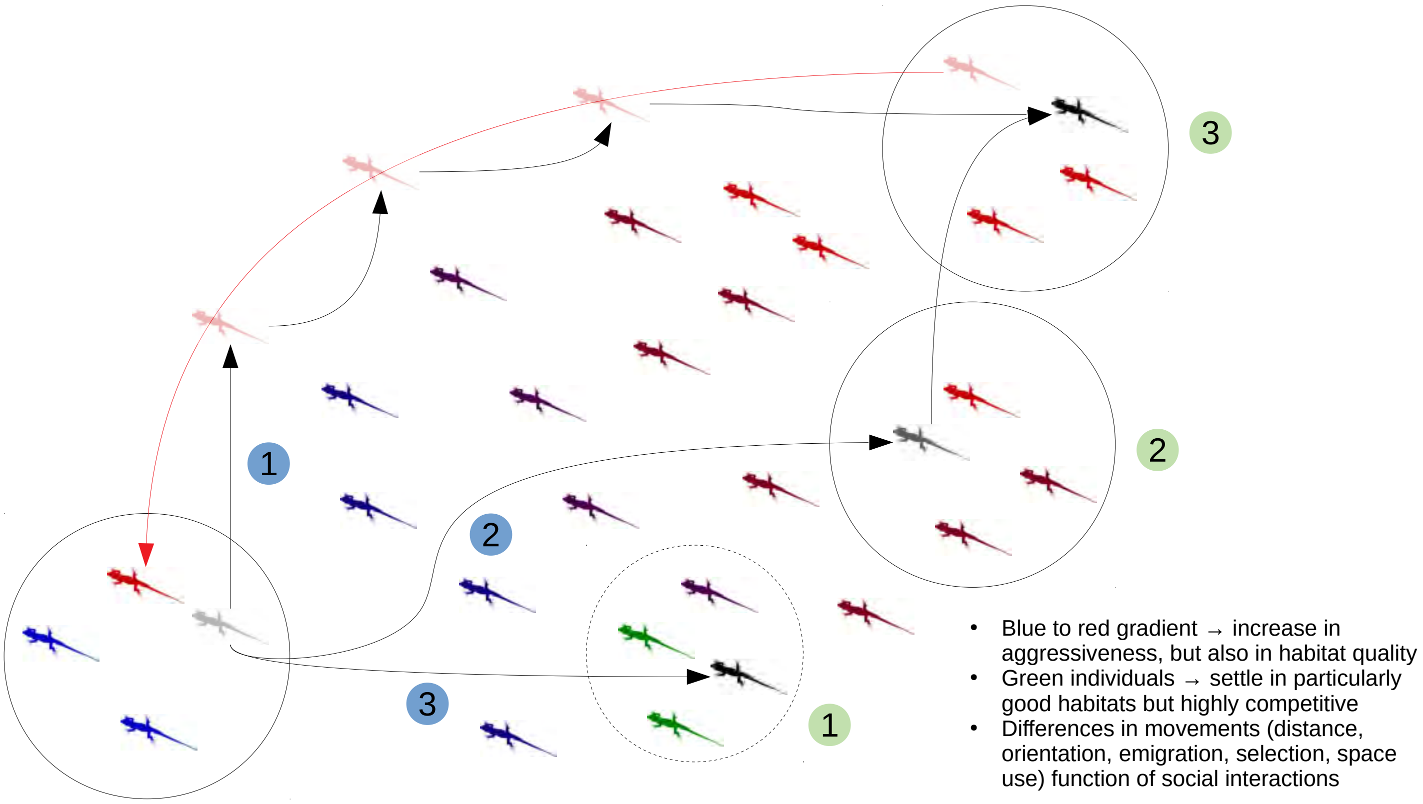
Influences on motion and navigation processes?

Social information could also change the motion characteristics, *i.e.* the navigation in space. First social information could be associated with the orientation of movements (Figure 1): movement could be directly oriented by visual cues associated with the information conveyer (*i.e.* its corporal and behaviors orientation, *e.g.* Kaminsky et al. 2005, Neff 2008, Potrich et al. 2019), but also with indirect cues let by the informant, creating a potential "tracks" as it the case for scents (*e.g.* pheromone trails in ant, Farkas and Shorey 1972, Morgan 2009). During this thesis, we tested for such socially informed orientation on common lizards without obtaining conclusive results (Chapter 2). We should, however, continue to explore such eventuality in natural conditions where potential cues could be more complex, and with perhaps more time for scents deposit (*e.g.* possible uses of present feces, as in Moreira et al. 2008). To do so, we may specifically test whether the arrival of an immigrant, followed by an emigration decision, leads to an orientation of the movement toward the original habitat of the immigrant (Brevet et al., analyses in progress). Microcosm experiments using *Tetrahymena thermophila* should also be particularly useful to test for such ability to orientate, but also to explore which cues could be used for such orientation (as detailed in Appendix 7, section 1). In particular, the use of 2D systems (Appendix 7, section 3 for details) could allow following the way each cell precisely navigates during movement, with potential tracking of its orientation ability along chemical tracks or during previously informed movements.

The social information could also impact movement linearity, which reflects the level of environmental exploration and prospecting, and movement kinetics (*i.e.* movement latency, velocity during movements). Indeed, these parameters could reflect the speed of movement (Wilson et al. 2015), an element expected to vary with movement motivations, in particular with the pressing necessity of leaving an environment (*e.g.* avoidance of predation risk, Howland 1974), or by seeking objective necessitating rapid reaction (resource acquisition, *e.g.* Soto and McHenry 2020, particularly in a competitive environment, Anholt et al. 2000). Conversely, slow and more erratic movements may reflect a need to explore, to gather as much personal information as possible before making a decision (Reader 2015), which is particularly useful for information that would need to be confirmed because potentially costly in case of error. Reduced movement activity is also a cost-minimization strategy in risky environments to gain vigilance and reduce the probability of encounters with predators (Anholt et al. 2000, Vásquez et al. 2002, Lopez and Martin 2013, Farnworth et al. 2019). Delayed dispersal could also represent the interest of an individual for its present habitat (*e.g.* for habitat quality: Ausprey and Rodewald 2013), by benefiting from good habitat conditions before initiating dispersal (Mayer et al. 2017). For instance, delayed dispersal can be advantageous for cooperative breeders (Kingma 2018, Nelson-Flower et al. 2018) or group-living species (*e.g.* Thorlacius et al. 2015), that change their dispersal timing depending on group size, sociability, and social dominance in their natal area. Once again, 2D microcosms systems with organisms such as *Tetrahymena thermophila* should be ideal to test such movement responses when confronted with various types of information more or less pressing to use because involving a high potential risk.

Influences on space use in living areas?

Social information use is common for micro-habitat selection in the living area of an individual, associated with specific behaviors, such as avoiding predation (Crane and Ferrari 2013), reproducing (Candolin 2003), or foraging (*e.g.* Reader et al. 2003, Webster and Hart 2006, Martin et al. 2010, Hanna and Eason 2013). Yet, few things are known about how social information could modulate the overall size of a living area (refs; Figure 1). Social information about the competition level should impact home range size, with individuals restraining their living areas to avoid competitive interactions (*e.g.* Trombulack 1985, Bond and Wolff 1999, Schradin et al. 2010, Le Roex et al. 2022) or shifting home range in the case of interspecific interference competition (Tannerfeldt et al. 2002), or enlarging it to maximize the chance to encounter mate or resources in particularly competitive habitats (Forsman et al. 2014). Such relationships potentially depend on the individual's competitive abilities (Civantos 2011, Sih et al. 2018). Finally, home-range size should depend on social information on the availability of resources, with a necessity to adjust the living area to the amount of resource (*e.g.* Le Roex et al. 2022, Saïd et al. 2009, Schradin et al. 2010). The role of the social context on the size of living areas in common lizard was investigated during this thesis by considering either the average social context during the whole life or the natal social context (Brevet, Renoirt et al., in prep., Appendix 6 for some preliminary results).



- Blue to red gradient → increase in aggressiveness, but also in habitat quality
- Green individuals → settle in particularly good habitats but highly competitive
- Differences in movements (distance, orientation, emigration, selection, space use) function of social interactions

Figure 1: Hypothetical influences of social information on movements.
If we consider a focal individual (in grey and black) in its initial environment (circle at the bottom left), this individual's emigration can first be influenced by its initial social context, with local phenotypes reflecting low habitat quality and the arrival of an immigrant with a phenotype reflecting good habitat quality. When dispersing the focal individual's orientation could then be oriented, through the immigrant's social cues forming a path the focal individual can follow (1. blue circle), or by navigating along a phenotypical gradient during transience (2. blue circle). In the case of random orientation (3. blue circle), movement is prominently led by exploration. Thus, the focal individual will settle as soon as it finds a more suitable habitat, with the encounter of social information on good habitat quality (1. green circle), including social information reflecting the information it had access to through immigrants (3. green circle). Yet, depending on the social context during transience an individual could stop its movement to avoid too important costs such as the ones due to conspecifics' aggressiveness (2. green circle). Finally, once settled the focal individual could adapt its movement in its living area depending on the intra-specific competition level for example (1. vs. 2.,3. green circles).

The evolution and demographic consequences of social information use during movements

An evolution perspective of social information used during movements

Social information use during movement may allow an individual to plastically respond to an environmental change (Edelaar et al. 2017), with probable gain for the individual (Rieucau and Giraldeau 2011, Grüter and Leadbeater 2014, Gil et al. 2017) that could by this way rapidly accommodate in changing environments (Dore et al. 2018). As in Morinay et al. (2018) and Tolvanen et al. (2020), phenotypic plasticity might prevail over genetic determinism for social information use: as this behavior is especially advantageous under changing conditions (Schmidt and Massol 2019), gains in fitness are more likely if it is performed by adjusting to the present condition. Such a mechanism should allow rapid evolution of social information use (Cliff et al. 2022), in which plasticity levels might depend on global environmental change levels (Ferrari et al. 2019, Brown et al. 2020). Yet, the precise fitness gained from using social information during movements has been rarely investigated (but see Forsman et al. 2007, Shermann and Visscher 2002), if at all in the case of immigrant-based information (but see Appendix 7, section 5 for study proposal).

Heritability of the use of social information remains yet to be explored in most parts (but see Morinay et al. 2018, Tolvanen et al. 2020), with interesting discussions on what is under selection (social information use per se or ability to "learn" through the acquisition of social information: Leadbeater 2015). There are promising possibilities to study such heritability using the common lizard long-term monitoring: as micro-satellites analyses were led for all captured individuals, the pedigree of all individuals is theoretically accessible (Richard et al., analyses in progress). Coupling this pedigree with experiments aiming at determining how consistently is used social information by the same individual (as a personality trait), could allow testing the heritability of such traits. More broadly, it could be interesting to determine which genes and traits are responsible for the determinism of such behavior (Leadbeater 2015). Good candidates should be associated with traits necessary to perceive and use such information, and should be related to sensory abilities, metabolic pathways for social information use in non-neural species (*e.g.* Gortz et al. 1999, Vogel and Dussautour 2016), cognition (Insel and Fernald 2004, Fernald and Maruska 2009, Varela et al. 2019, *e.g.* Morinay et al. 2020a) or traits related with sociality (Foucaud et al. 2013, Meylan et al. 2017, McCune et al. 2022). Some experiments already evidenced major roles of pathways implied in the determinism of social behavior, such as the serotonergic pathway, in the social learning of birds (Attaran et al. 2021), arginine vasotocin in lizards (Campos and Belkasim 2021), or oxytocin and arginine–vasopressin in mammals (Choleris et al. 2009). Production of cues is in turn probably due to genes determining traits related to success, the performance of the individual, also perceptible by other individuals, or to pleiotropic genes, determining success, performance, but also traits perceptible by conspecifics (Andrade et al. 2019). Cues could specifically evolve toward signals by losing their primary function related to performance and keeping only the informative aspect (as suggested in Tinbergen 1952, Lotem et al. 1999, Biernaskie et al. 2018). The exact evolutive mechanism for a trait to become a cue remain to be explored. In particular, it remains to understand how such a particular trait is perceived and treated by individuals: is there an unconditioned treatment of traits benefiting the individual? Or is there learning of its value by considering its own success or observing the success of others? This discussion about the use of cues through social learning (Hoppitt and Laland 2008) or not, appears to lean toward the hypothesis for associative learning in the majority of the literature (Leadbeater 2015), even if unconditioned responses appear to exist (*e.g.* innate responses to parental alarm calls: Davies et al. 2004, Platzen and Magrath 2004, Suzuki 2011) implying possible genetic or developmental determinism (Noguera and Velando 2019, Winandy et al. 2021, Crane et al. 2021, Rivera-Hernández et al. 2022), with potential alternative evolutive pathways depending on the cognitive abilities of the individuals and the advantage to produce a rapid response without preliminary learning (Reader 2014).

Finally, understanding if such social information use is phylogenetically widespread among motile species remains also to be more extensively explored, even if the current study provides evidence for a wide range of species using such information during their movements (Buxton et al. 2020). The drivers and modalities of such behaviors could be highly diversified, even in the same taxon (*e.g.* Johnson et al. 2019 in lizards), potentially evidencing evolutive convergence toward such social information use. It could also be interesting to investigate what drives inter-specific differences in social information use, with potential major importance of the position in the trophic network (with the existence of competitors, predators, amount of resources: *e.g.* Coolen et al. 2003), the environmental predictability in the ecological niche of the species (Brandl et al. 2018) or the level of sociality (probability of social encounter, the level of antagonism, cooperation, *e.g.* Voelkl and Huber 2007).

Demographic and evolutive consequences of social information use during movements

The use of social information during movement strongly affects population and meta-population dynamics (Gil et al. 2018). Social information use appeared to be particularly central in range expansion dynamics (Fronhofer et al. 2017a, Gruber et al. 2017), with different social information use at range margins and core, with a potential benefit in performing informed movements in less dense (*i.e.* poorly competitive) habitats (trade-off between competition and social information use: Lee et al. 2016, *e.g.* Szymkowiak et al. 2016). More broadly, social information use in movement should have high importance in population distribution by better informing on the suitability of habitats. Social information use has also been theoretically demonstrated to improve the stability of population (Schmidt and Massol

2019, Gil et al. 2019), metapopulation (Clobert et al. 2009, Chaine et al. 2013), and metacommunities (Fronhofer et al. 2015a, Gil et al. 2018, 2019), even if information Allee-effect (attractivity toward dense and competitive habitat) may also drive to population decline (Delgado et al. 2011, Schmidt et al. 2015, Gil et al. 2018). As initiated by Fronhofer et al. (2015a,b, 2017a,b) experiments on *Tetrahymena thermophila* can be particularly useful to test theoretical predictions on the use of social information during movements. It should be specifically interesting to use different strains with different propensities to use social information in fluctuating meta-population systems. By associating fluctuations with social information just before variations (or not) we could test how the use of social information would impact demographic parameters, and how it could evolve under different regimes of predictability (Bocedi et al. 2012 for theoretical expectations).

Social information use during movements should be of primary importance in evolutive dynamics. For example segregation of traits in space through phenotype-dependent use of information can occur, and might lead to colonization of close or peripheral niche by a particular phenotype, or specific niche in the population area (Clobert et al. 2009). Such niche segregation by individual traits could then lead to possible genetic isolation by non-random gene flow, divergence, and even speciation (Edelaar and Bolnick 2012). The use of social information in movements could also drive the evolution of other traits such as social learning (Leadbeater 2015), sociality (*e.g.* Guttal and Couzin 2010, Gil et al. 2016, Gager 2018, Borg and Channon 2021), and even cooperation (Erovenko 2019a,b, Jacob et al. 2016b).

APPENDIXES

Appendix 1: Behavioral traits measurement

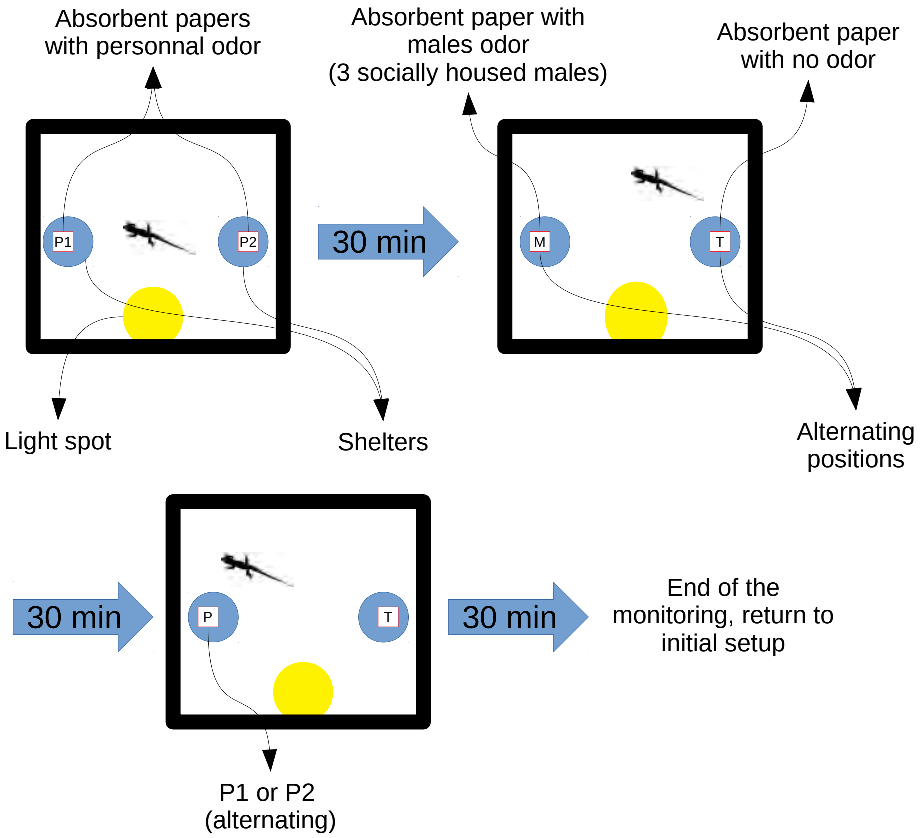


Figure 1: Experimental design of the behavioral monitoring.
In 2019 and 2020 each captured individual was submitted for behavioral measurements. We filmed individuals for 90 minutes inside their home terrariums. During the first phase, we recorded the time they spent moving, sheltering, basking on a shelter (a behavior that could be interpreted as a marker of boldness, Cote et al. 2008b), and attempting to escape (by scratching the walls), as well as the number of tongue-flicking (olfactory cues acquisition). We then measured their social tolerance by comparing the time spent in the shelter without odor with the time spent in the shelter with males odors (phase 2), and their preference for personal cues by comparing the time spent in the shelter with their odor with the time spent in the shelter with no odor (phase 3).

Appendix 2: Sampling common lizards' secreted/excreted chemical compounds

This project aims to better understand how chemical compounds secreted or excreted by individuals would influence the dispersal movements of other individuals in contact with them (as already partially proven by Moreira et al. 2008 in another lizard, or by Lopez et al. 1998, Martin and Lopez 2007, Martin et al. 2007 for the importance of such compounds in social interactions in lizards). To do this, we left two layers of absorbent papers at the bottom of terrariums in which individuals of interest (adult males or females captured on a natural monitoring site) were kept for 48 h. We collected for each individual a square of absorbent paper (5x5 cm, avoiding as much as possible to sample the parts of the absorbent paper presenting urine or feces) in the center of the terrarium and we stored them in hermetic vials (1.5 mL, with membrane for automatic sampling) stored at -20°C. We performed approximately 400 samplings overall.

We want to perform an extraction of the lipophilic compounds that would have been deposited on these absorbent papers, the idea would be to perform a cold extraction in an n-hexane solution for each sample (in the manner of Van Moorleghem et al. 2020 on snake skin samples) and then perform a GC-MS to identify all the different components present in each sample (by the family of compounds or more precisely if it is possible) and quantify them (using "the percent of the total ion current: TIC"). This type of analysis has already been performed in our model species (Gabirot et al. 2008) or other related species (*e.g.* Van Moorleghem et al. 2020, Escobar et al. 2001, 2003).

Here is a quote from Gabirot et al. (2008), detailing the protocol previously used for the same species that we want to follow for GC-MS:

"We analyzed lipophilic compounds in samples by using a Finnigan-ThermoQuest Trace 2000 gas chromatograph (GC) fitted with a poly (5% diphenyl/95% dimethylsiloxane) column (Supelco, Equity-5, 30 m length x 0.25 mm ID, 0.25-mm film thickness) and a Finnigan-ThermoQuest Trace mass spectrometer (MS) as detector. Sample injections (2 μL of each sample dissolved in n-hexane) were performed in splitless mode using helium as the carrier gas, with injector and detector temperatures at 270 °C and 250 °C, respectively. The oven temperature program was as follows: 50 °C isothermal for 10 min, then increased to 280 °C at a rate of 5 °C/min, and then isothermal (280 °C) for 30 min. Mass spectral fragments below m/z = 39 were not recorded. Impurities identified in the solvent and/or the control vial samples are not reported. Initial temptative identification of secretion components was done by comparison of mass spectra in the NIST/EPA/NIH 1998 computerized mass spectral library. Identifications were confirmed by comparison of spectra and retention times with those of authentic standards from Sigma-Aldrich Chemical Co. For unidentified or unconfirmed compounds we report here their characteristic ions, which we used together with retention times and characteristic m/z ratios to confirm whether these compounds were present in a given individual."

Then two types of analysis are possible, firstly to compare the lipid patterns without any formal identification (in the manner of Winandy et al. 2021), simply to be able to identify if patterns are associated with particular responses/phenotype, secondly to identify compounds either by family (*e.g.* Campos et al. 2020) to at least specify the major classes of molecules that appear to play a role, or exhaustively (Gabirot et al. 2008, using a NIST library) to precisely identify molecules that provide a potential signal, or by targeting molecules (using standards) already identified as having a role (Martin and Lopez 2015 for a review, or also Romero-Diaz et al. 2021) based on the already existing literature. In particular, here is a list of elements that I think are central to identify and quantify relatively in view of the literature: cholesterol, hexadecanoic and octadecanoic acid, campesterol, sitosterol and ergosta-5,8-dien-3-ol, corticosterone, eicosanoic acids, oleic acid, α-tocopherol, ergosterol, cholesta-5,7-dien-3-ol, testosterone, hexacosanol and tetracosanol. All these molecules are related to important physiological or social traits in phylogenetically related lizard species (Martin and Lopez 2015), this list of components is almost identical to the one found in Gabirot et al. (2008), showing the feasibility of these analyses in our model species. An interesting point is that we have a few replicates of measurements between the two years, and even a few others within the same year, allowing us to check the stability of individual profiles.

These individual profiles can then be used to test how they correlate with dispersal responses, how an individual responds to the average profile in its natal range, and how these profiles correlate with other environmental metrics that have a strong influence on dispersal. Finally, they could be used to explore how correlations are set up between dispersal responses, average lipid profiles, and average environmental contexts through path analyses.

Appendix 3: Use of conflicting social information for dispersal decisions in experimental microcosms

Introduction

Social information acquisition in natural conditions often comes from multiple sources (*e.g.* Coolen et al. 2003, Drullion and Dubois 2008, Pilon 2020, Jaakkonen et al. 2015, Romero-Gonzalez et al. 2020). We can distinguish between (Dall et al. 2005, Schmidt et al. 2010) social sources of information acquired through the perception of other individuals' traits, and personal information acquired directly through interaction with the surrounding habitat. The study of information conflict has been particularly well-studied when social and personal sources are involved (Kendal et al. 2009). However, relatively few studies have focused on conflicts between different social information sources (but see Pike and Laland 2010), and to my knowledge, none have focused on spatialized information from different sources that may influence movement decisions.

Using an experimental setup to track dispersal movements in microcosms, we test how social information from two distinct and potentially conflicting sources might be used, and how this use might vary according to the local context. To do so, we used *Tetrahymena thermophila* as a model species, with the same clonal strain used in all our experiments (D13, Doerder and Brunk 2012). The use of immigrant-based social information was previously evidenced in this species (Jacob et al. 2015b). We used an experimental setting (Figure 2) where the dispersal rate, and traits of dispersers and residents, were measured at the end of the dispersal of focal cells. Here, we defined dispersal syndromes as the difference in traits between dispersers and residents. We replicated dispersal experiments (Table 1) under different local temperature conditions (20, 25, and 30°C) and different information treatments (5 treatments: no social information, two consistent sources of immigrants, having dispersed both at 20, 25, or 30°C, or two conflicting sources, one having dispersed at 20°C and the other at 30°C).

This species' growth rate, dispersal, and phenotype are sensitive to temperature (Jacob et al. 2017, 2018, Melo et al. 2020). Even if it has never been tested previously, we thus expected such social information on temperature to be used by focal cells: the dispersal rate and syndromes should differ from a situation without social information (Figure 1A). Cells' growth rate was found to increase along the temperature gradient we chose (Jacob et al. 2018, Figure S1) and the strain we used performed habitat selection at emigration (Jacob et al. 2018). As a consequence, we expected the dispersal rate to increase when local temperature decreased or when the temperature in the original habitat of immigrants increased (as it should represent the potential arrival habitat). The use of social information is also likely to depend on the local context (Dall et al. 2005, the value of information depending on its prior experience; Figure 1B). Therefore, we could expect the relationship between social information and the dispersal rate to be steeper in local temperature considered disadvantageous (lower temperature). Such effect could also affect dispersal syndromes, with possible plastic changes of dispersers traits depending on the received immigrant-based information (potentially to anticipate arrival habitats). We could also expect temperature treatments to affect the immigrant traits (Melo et al. 2020), therefore we can explore if the physiological traits of immigrants correlated with the temperature treatment and dispersal, highlighting the presence of potential cues associated with these traits. Finally, our experimental treatment allowed us to explore if conflicting social information sources were used and how they were used. We can formulate different hypotheses about this use. First, the conflict between sources could make the information too uncertain, in which case its use should not differ from a situation without information (Figure 1C). Second, only one component of the information could be used, in which case the dispersal response should not differ from information alone at 20°C or alone at 30°C (Figure 1D). Third, the information could be used in an average way, in which case the dispersal response should not differ from information alone at 25°C (Figure 1E). The use of information from conflicting sources may also differ depending on the local context: for example, it may be advantageous to use only the most advantageous component of the information when the local context is particularly disadvantageous.

Materials and Methods

We studied the dispersal rate and dispersal syndromes variations of focal cells according to the local temperature (dispersal condition: 20, 25, or 30°C) and immigrants' temperature of dispersal (*i.e.* social information: no information, two sources both being at 20, 25 or 30°C, or each one being respectively at 20 and 30°C). Immigrant cells dispersed before the focal cells and were added to the focal dispersal system just before their dispersal (Figure 2). One clonal laboratory strain has been used here, this strain came from Doerder sampling (Doerder and Brunk 2012, annotated D13). In this species, dispersal is associated with traits modifications, with a tendency for dispersers to be more elongated and smaller, with a higher velocity and linearity in movements (Nelsen 1978; Fjerdingstad et al. 2007; Schtickzelle et al. 2009; Pennekamp et al. 2014a; Jacob et al. 2016a). Such traits have been measured here to test if the information and temperature treatments could impact the way these traits vary for dispersers and residents of focal populations and if the variability in immigrants' could mediate the social information use. Variability in focal cells' traits has been studied in the shape of dispersal syndromes, defined as the

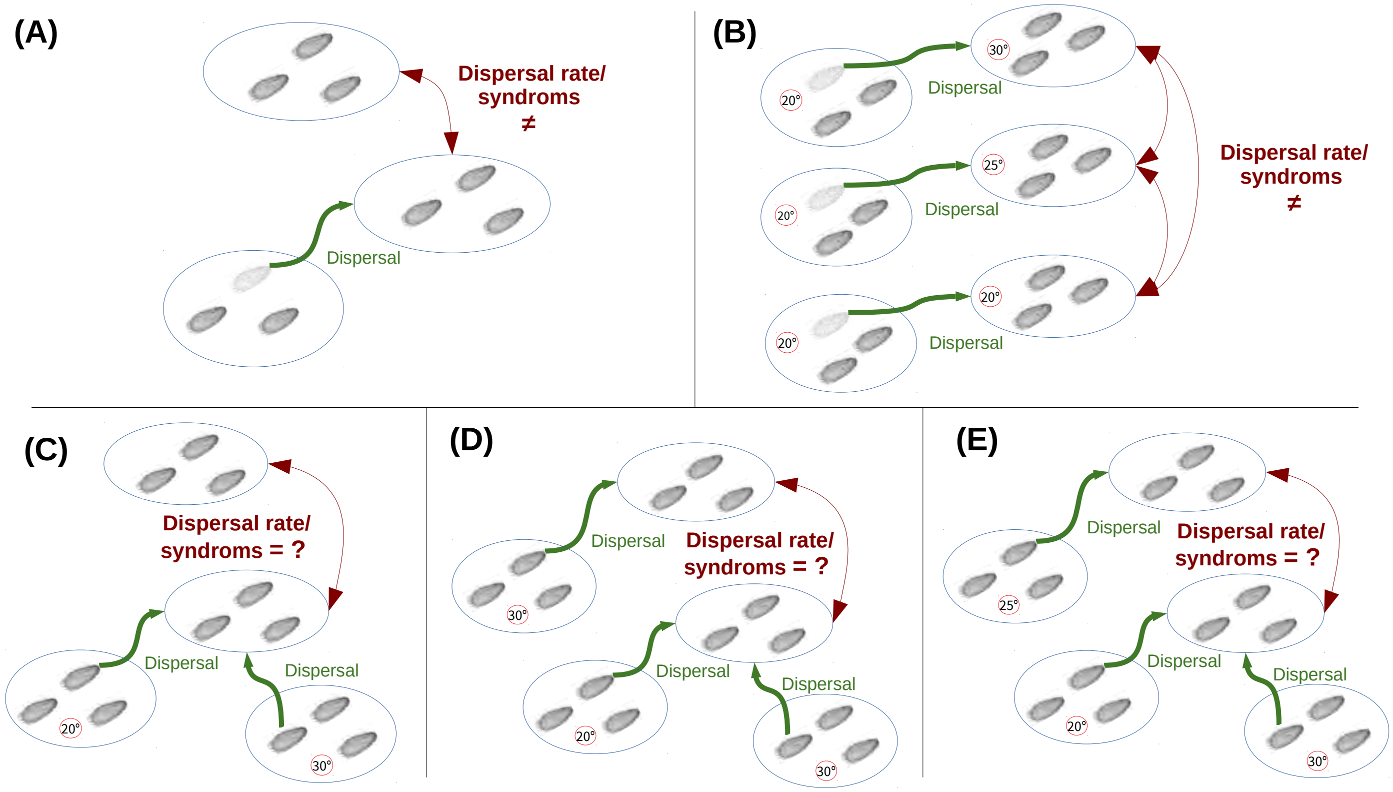


Figure 1: Main experimental expectations.
More detailed hypotheses are described in the Introduction. In each scheme, we represented immigrant cells that dispersed under different possible temperatures (Table 1 for details of treatments) and that arrived in focal systems where the social information they transmit is expected to impact dispersal. These schemes are not representative of the exact experimental setting (Material and Methods and Figure 2 for details). The C,D,E graphs represent alternative hypotheses for the use of conflicting social information sources.

A- Use of social information on temperature. We expected the dispersal response (rate and syndromes) to differ when social information was present compared to conditions without social information.

B- Context-dependent use of social information. For the same social information (here immigrants having dispersed at 20°C), we expected dispersal response (rate and syndromes) to differ among the different local contexts (*i.e.* local temperature).

C- Use of conflicting sources of social information: Hyp.1, prevention of social information use. When social information conflicts, we could first hypothesize that such information will not be used because too uncertain.

D- Use of conflicting sources of social information: Hyp.2, use of only one component of the information (here the supposedly more advantageous, 30°C). When social information conflicts, we could also hypothesize that only one component of the information will be used, probably the most advantageous (potentially determined by the local context).

E- Use of conflicting sources of social information: Hyp.3, averaged information use. When social information conflicts, we could finally hypothesize that averaged information will be used.

difference in the value of a trait between residents and dispersers.

Social information results from either adding immigrants from two different sources, which had both separately dispersed at the same temperature of 20°C or 25°C or 30°C; or adding informants from two different sources, which had separately dispersed at a temperature of 20°C and 30°C; or adding control medium from two different sources with no informants. We performed 300 experimental replicates, there were 20 replicates by treatment (combination of a local context and social information, Table 1) distributed over two blocks of three consecutive days (3 replicates by treatment the first two days and 4 the last day; December 15 to 17, 2020 and February 22 to 24, 2022).

		Local Temperature		
	Number of replicates per condition	**20°**	**25°**	**30°**
Social Information	**20°**	20	20	20
	25°	20	20	20
	30°	20	20	20
	20° / 30°	20	20	20
	None	20	20	20

Table 3.2: Distribution of experimental replicates.
Social information was always provided through two sources of immigrants. When only one temperature is displayed, it means, that the two sources were at the same temperatures. The same is true for the absence of information, in which case a cell-free medium from two different sources was added (Figure 2).

Each day, the used informant (from two distinct sources) and focal cells originated from three cultures (Figure 2) launched one week before the experimental day. In parallel, two control cultures with no cells were launched one week before each experimental day (Figure 2). These control cultures were used for information treatment control (*i.e.* absence of social information, two sources). All cultures were maintained in 1L bottles, at a constant temperature of 25°C. Cells were inoculated in 100mL of standardized media: an axenic-rich liquid growth media with 1% Difco proteose peptone and 0.1% yeast extract. Cells all originated from the same pre-culture (strain maintained over the long term in the laboratory), all cultures were inoculated with 2mL of this pre-culture. Dispersal experiments were then performed using cells from these different cultures (Figure 2).

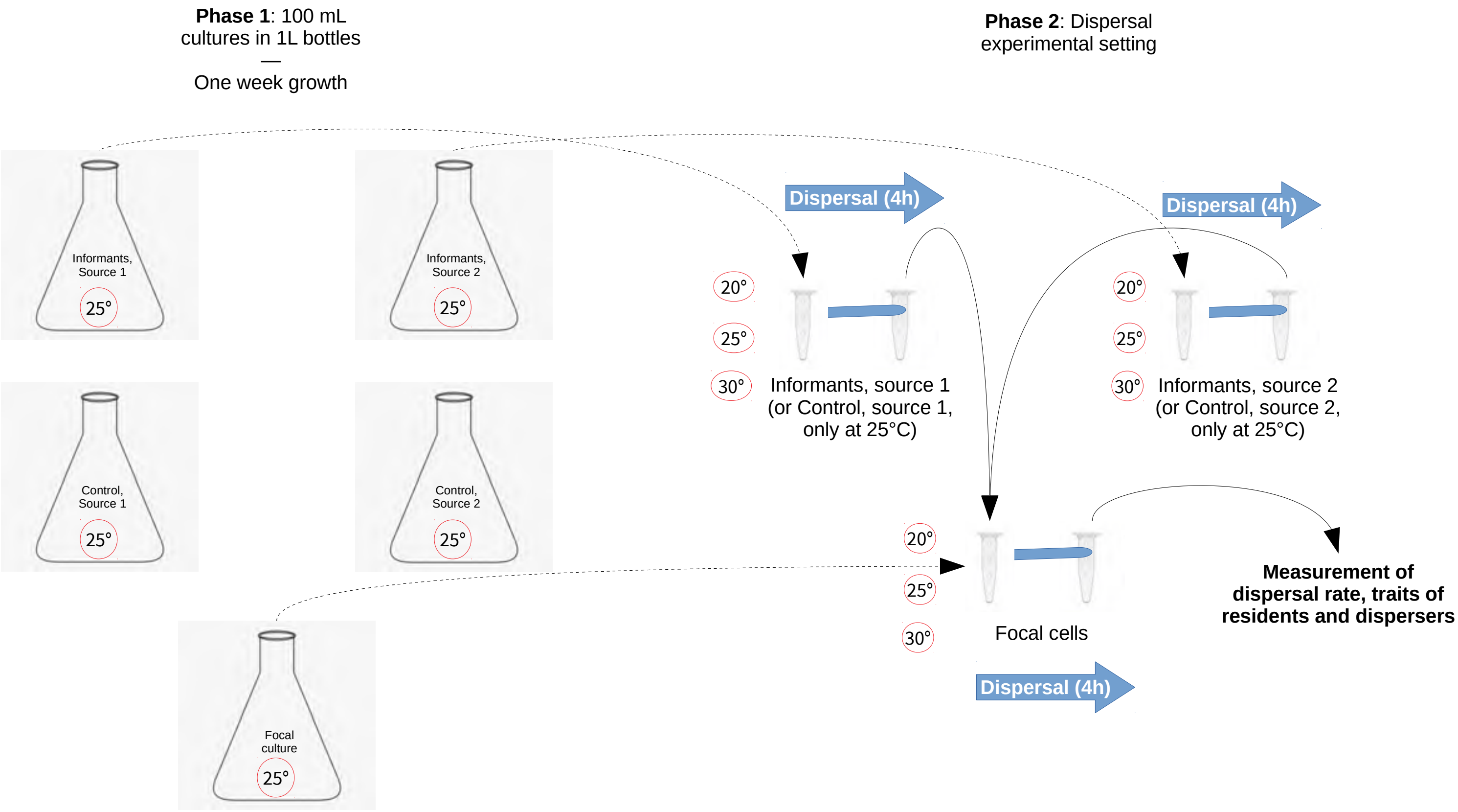


Figure 2: Experimental design.
The experiment took place in two phases. First, the different cultures were maintained for one week (at 25°C) to constitute one source of focal cells, two sources of informants, and two control sources (without cells inside). These cultures were then used for dispersal experiments: we transferred cells from these cultures to the departure patch of dispersal systems, with 1h of accommodation for the cells we just added, and then 4h during which dispersal is allowed. Dispersal experiments take place either at 20, 25 or 30°C (depending on treatment: Table 1), with first the dispersal of informants during the morning, followed by the dispersal of focal cells in the afternoon. Informant dispersers (*i.e.* immigrants) from the two sources were then inoculated in the same quantity in the focal system (30 minutes before the beginning of dispersal) in a negligible amount compared to the focal cells. We measured the dispersal rate and syndromes of informant and focal cells right after the dispersal experiment, to study the response to the different possible treatments (Table 1).

Dispersal experiments were led the same way as in Jacob et al. (2015b and 2019b). For this reason, I quote below the adequate portion of the material and method from these papers (slight modifications have been made and are indicated by being outside the quotation marks):

(Jacob et al. 2015b:) “To measure dispersal rate in T. thermophila, we used standard two-patch systems consisting of two habitat patches (1.5-mL standard microtubes), connected by a corridor (4-mm internal diameter silicon tube, 2.5 cm long) and filled" (Jacob et al. 2019b:) "with water solution (Tris Hcl, 10mMol) without resources (harsh matrix), as used in a previous study (Fronhofer et al. 2018). To do so, all two-patch systems were initially filled with water (in patches and corridor), and" media (same as in culture) "was added in each patch while keeping corridors closed to avoid diffusion of nutrients in the corridors." (Jacob et al. 2015b:) "At the beginning of each experiment, cells were placed in the start patch and the corridor was opened to allow dispersal towards the target tube. At the end of the dispersal time, the corridor was clamped to separate residents (cells remaining in the start patch) from dispersers (cells that moved to the target patch), and both patches were sampled (see further). For any given two-patch system, dispersal rate was computed as the proportion of the cells present in the target patch (target/(start+target)). This measure of dispersal, used in several previous studies (Fjerdingstad et al. 2007; Schtickzelle et al. 2009; Chaine et al. 2010), has been shown to be insensitive to density-dependent effects on growth that might lead to differences in growth rate between patches over the timeframe of the experiment (Pennekamp et al. 2014a). Moreover, temperatures used in Pennekamp et al. (2014a) were higher than in our study, which means generation time is longer in our work (about 1/2 – 1generation at 23°C; Chaine et al. 2010) and density effects should therefore be even smaller."

Experimental procedures were also highly similar to the ones described in Jacob et al. (2015b). For that reason, I again quote the adequate sections from this article below (slight modifications have been made and are indicated by being outside the quotation marks):

"All manipulations were performed in sterile conditions under a laminar flow hood." In each informants dispersal system target patchs, "we measured 5 samples (10 μL) each pipetted into one chamber of a multichambered counting slide (Kima precision cell 301890), and took digital pictures under dark-field microscopy (Fjerdingstad et al. 2007; Schtickzelle et al. 2009; Chaine et al. 2010). Digital pictures were analysed using IMAGEJ software (version 1.47, National Institutes of Health, USA, http://imagej.-nih.gov/ij; see Pennekamp and Schtickzelle 2013) to obtain the overall number of cells on the picture, later transformed into density per mL."

In addition to photos, we also took 16s videos of the departure and arrival patches (one of each patch for the informant cells dispersal systems and two of each patch for focal cells dispersal systems). These videos were analyzed a posteriori with the BEMOVI software (Pennekamp et al. 2014b, 2015) to obtain a precise measure of mean cells' traits in the sample (size, shape, velocity, and movement linearity of cells) and cells density. Densities obtained from photos were only used for fast densities computation of informants dispersers, which were then inoculated in standardized concentrations in focal dispersal systems (next section for details). Densities obtained from videos are more precise and were used for subsequent statistical analyses.

“All experiments we conducted focused on the addition of ‘immigrants’ into a new population, but experiments differed in the conditions that immigrants experienced prior dispersal. To obtain immigrants, we introduced cells” (100 000 cells mL-1) “in one side of a two-patch system” (Figure 2). We let them 1 hour in this system before beginning dispersal procedure to let them accommodate to the local temperature treatment. After 4 h during which these cells where able to disperse, “we collected cells that dispersed to the target patch (*i.e.* dispersers). These disperser cells were then used as immigrants who had actually undergone dispersal of their own accord. Then, we transferred” 1500 immigrant cells (1000 cells mL-1) “into a new focal population that consisted in” 150 000 cells (100 000 cells mL-1) “in the start patch of a two-patch system as described above” (Figure 2). Before beginning dispersal procedure, this focal population was let half an hour alone in the system and half an hour with informants cells to accommodate to the local temperature treatment and to the presence of informants. “We then let cells disperse for” 4 h “(much less than 1 generation at 23 °C, Chaine et al. 2010).”

“Additionally, during the experiment, we quantified dispersal rate without immigrants in addition to treatments with immigrants presented above.” These control replicates were performed the exact same way than replicates with informants (see figure S3 and S4). “This control allowed us to test whether the range of dispersal rates differed according to the presence or absence of immigrants.”

“Since cells were not individually distinguishable when mixed, we could not determine whether cells that had dispersed at the end of our experiments were initially from the focal population or introduced immigrants. Immigrants could have different dispersal decisions than individuals from the focal populations. However, the” 1500 “immigrants introduced in our experiments represent only” 1% “of the resulting focal population” (*i.e.* 1500 immigrants + 150 000 residents). “Even in the hypothetical case where all these immigrants systematically either disperse or stay after their introduction to a new population, such a small proportion would have had little effect on our quantitative measure of dispersal.”

The treatment effects on dispersal rates and syndromes of focal cells were then statistically analyzed. We began to test for the use of social information by comparing the dispersal responses (dispersal rate, dispersal syndromes for cells’ size, shape, velocity, or linearity) between the treatment without social information and the others, each one separately (testing expectation of Figure 1A). Each comparison was also realized at the three different local temperatures separately, to test for possible context-dependent use of social information. In this latter case, we applied a Bonferonni correction for multiple testing on tests of the same nature performed for different local temperatures. We detected an important random effect of the date (Figure S2; analysis of deviance test between null models, *i.e.* linear regressions, with and without random effects for models on dispersal rate and each of the 4 dispersal syndromes; $p < 0.001$ in all comparisons). As a consequence, we also realized each comparison for each of the experimental dates separately. In this latter case, we applied a Bonferonni correction for multiple testing on tests of the same nature performed for different experimental dates. We used the Wilcoxon test to compare distributions of replicates as the sample sizes per treatment were rather low (about 10 replicates per day, and 20 replicates per temperature treatment). We then analyzed how conflicting social information sources were used, by comparing the dispersal responses between the treatment with conflicting sources with all other treatments (testing hypotheses from Figure 1C,D,E). The statistical method we used was the same as in the previous paragraph.

We then more particularly wanted to test how dispersal responses depended on continuous temperature treatments (local temperature and immigrants' temperature of dispersal, with three possible values: 20, 25, and 30°C, *i.e.* sample size of 180 dispersal experiments), and on the interaction between the local context and social information (testing expectation from Figure 1B). To do so, we performed a MANOVA analysis to consider all dispersal responses as a whole since these traits are highly intercorrelated (Figure S3). These dispersal responses were expressed as a function of the local temperature, the immigrants' temperature of dispersal, their quadratic transformation (to test for non-linear relationships), and the date of the experiment (because of its random effect, previous section for details). We also included the double interactions between the local temperature, the immigrants' temperature of dispersal, and their quadratic components. We also added the date as an interaction in all interactions, as random effects on the local temperature slope were identified for all dispersal responses (analysis of deviance test between null models with random effects on intercept only or intercept and slope: $p < 0.001$ for all comparisons; Figure S2). The results were then analyzed (Table S1) using F-tests for each response variable separately, and Pillai's test for the MANOVA as a whole (as recommended in Hand and Taylor 1987).
Yet, this method is likely to be flawed due to over-parametrization (due to the interactions with the date, representing each 5 degrees of freedom). To complement this analysis we also used a principal component analysis (PCA) to describe the dispersal response by using the PCA axes (independent of one another), allowing us to avoid any problem of correlation between response variables. However, the PCA axes obtained are quite difficult to interpret because they result from the combination of multiple responses of dispersion at the same time (details in the table of loadings from the PCA, Table S2). We then used the first two axes (explaining respectively 38.5 and 31% of the variance, against less than 14% for the other axes) as descriptors of the dispersal response, in distinct mixed linear regression models with a random effect of the date on the intercept and local temperature slope. We then used analyses of deviance (Wald chi-squared tests) for each model to test for significant effects of treatment.

Finally, we explored the path of effects by investigating the existing correlation between the initial temperature treatment (on social information), the traits of immigrants (supposedly informing on these initial conditions), and the dispersal responses. Traits of immigrants were computed as the average traits of dispersers' cells coming from both studied informant sources. First, we verified if immigrants' temperature of dispersal was correlated with their traits. To describe their traits we performed a PCA on the four measured traits (size, shape, velocity, and linearity of the cells) since they correlate with one another (Pearson correlation tests; size and shape: cor=-0.63 and p<0.001, velocity and linearity: cor=0.66 and p<0.001, but also size and velocity: cor=0.33 and p<0.001, shape and linearity: cor=0.23 and p=0.015). We retained the first two axes (respectively 46.2 and 39,5% of explained variance, against less than 8% for the other two) for the further analyses (Figure S7). The first axis mainly represents variation in cells' size, velocity, and linearity (respective loadings: 0.54, 0.61, 0.49), and the second axis mainly represents variation in cells' shape and linearity (respective loadings: 0.67, 0.51). We then used mixed linear regression for each axis to test the effect of the temperature of dispersal on these traits (with the date as a random effect on the intercept).

Second, we tested whether the immigrants' traits influence dispersal responses. To do so, we performed a MANOVA on all dispersal responses together depending on the two PCA axes describing the immigrants' traits, and the date, without interactions.

Lastly, we tested for the potential indirect effect of the initial temperature treatment (*i.e.* social information) on dispersal response through variation in immigrant traits. To do so, we performed d-separation tests between these three parameters on each dispersal response separately, with two separate tests for each PCA axis describing the immigrant's traits.

Results

Using social information about temperature and dealing with conflicting sources

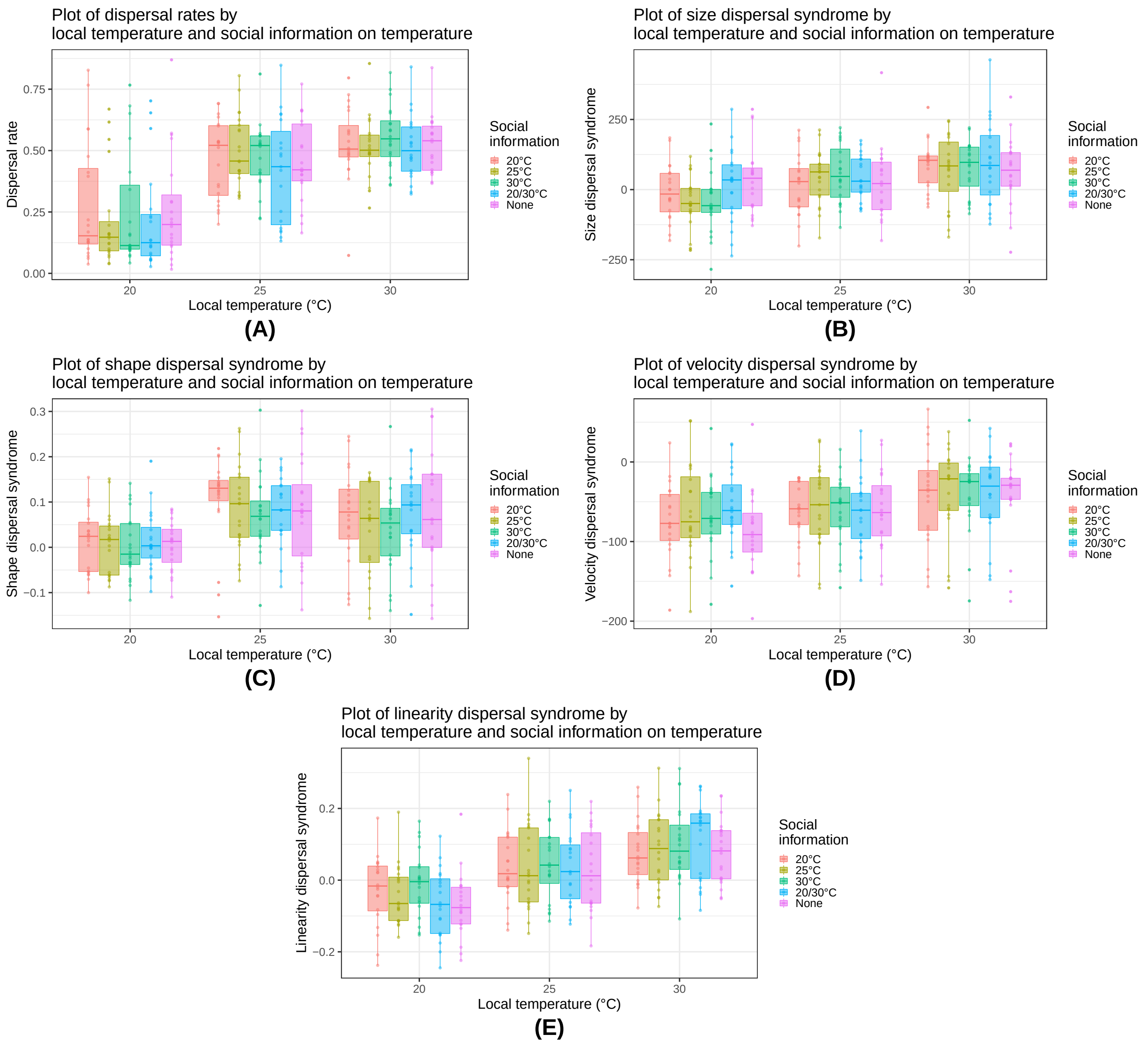
We found no significant differences in dispersal responses between the treatment with no social information and treatments with social information (Figure 3), except for the 23 February: the velocity of residents' cells increased relatively to the dispersing cells for information on immigrants having dispersed at 30°C compared to a situation without information (p=0.046, Figure S4). Yet, such an effect is likely to be not conserved because dispersal responses are non-independent (Figure S3) and such multiple comparisons among dispersal responses should also necessitate a correction.

We found no significant differences in dispersal responses between the treatment with conflicting sources of information and other treatments (Figure 3).

Local temperature, remote temperature and interactions

We first found all dispersal responses to depend on the date, with a particular deviation from other responses on the 16 December (Figure S2).

We then found the dispersal response to depend on the local temperature (both in the MANOVA and mixed linear regression on PCA axes). The dispersal rate increases with temperature (Figure 3A), but



(A) **(B)** **(C)** **(D)** **(E)**

Figure 3: Dispersal responses of focal cells depending on the local temperature and the social information treatment.

These graphs display how the different dispersal responses (A: Dispersal rate, B: Cells' size dispersal syndrome, C: Cells' shape dispersal syndrome, D: Cells' velocity dispersal syndrome, E: Cells' linearity dispersal syndrome) vary in function of the local temperature (20, 25 or 30°C) and the immigrants' temperature of dispersal (*i.e.* social information: either immigrants' from two sources having both dispersed at 20, 25 or 30°C, or having separately dispersed at 20 and 30°C, or no immigrants added, referred to as "None" in the legend).

in a non-linear way with a plateau on the two highest temperatures (date-dependent effect: variation in the intensity of the slope, no such relation on December 16, Figure S2A). The size of resident cells increases relative to that of dispersers when temperature increases (Figure 3B, date-dependent effect: variation in the intensity of the slope, no such relation on December 15: Figure S2B). The elongation of resident cells increases relative to that of dispersing cells for intermediate temperature (Figure 3C), with date-dependent variations (more or less comparable difference in elongation between 25 and 30°C, no such relationship on December 16: Figure S2C). The velocity of the resident cells increases relative to that of the dispersers when the temperature increases (slope more or less strong depending on the date, no such relation on December 16: Figure S2D). The linearity of the resident cells increases relative to that of the dispersers when the temperature increases (slope more or less strong depending on the date, or appearance of a plateau for higher temperatures, no such relation on December 16: Figure S2E).

The results from the MANOVA analysis suggest that there might be slight effects of temperature treatment. First, there is a tendency to have a different response to the information depending on the date (Pillai's test, p=0.095). Looking at the effects of the variables one by one, it seems that this variation would concern the response in terms of dispersal rate (Table S1, Figure S5). Then, a trend is observed in the shape of the response to social information that seems to depend on local temperature and date (Pillai's test, p=0.052), this trend seems to be associated with the response in terms of dispersal syndrome on the shape of the cells (Figure S6). No other trends regarding the effects of social information appeared to emerge from the MANOVA, or the models on the PCA axes describing the dispersal responses.

Is immigrants' traits potential cues?

The first PCA axis describing immigrant cell size, speed, and linearity did not depend on immigrants' dispersal temperature (p=0.22). Conversely, the axis describing the shape and linearity of immigrant cell movements depended significantly on this temperature (p<0.001): as temperature increases the cells are less elongated and have a less linear movement. We then found that the dispersal responses of the focal cells depended on the first axis describing the immigrant traits (Pillai test, p<0.001), but not on the second axis (Pillai test, p=0.55). When deviance analyses were performed on each dispersal variable separately the same results were observed. Thus, when the size of the immigrant cells, the velocity, and the linearity of their movement increases, the dispersal rate of the focal cells decreases, as well as the difference in size and linearity between the resident and dispersing focal cells, while the difference in elongation and velocity between the resident and dispersing focal cells increases.

In accordance with the observations that only the second axis was being affected by the temperature of dispersal and only the first one was being impacted by focal cells' dispersal responses, none of the d-separation tests were found significant (all p>0.1).

Discussion

The dispersal responses constantly depended on the local temperature. Contrary to what we initially expected, we found the dispersal rate to increase when the local temperature increased. The high growth rate at high temperature could be of little benefit to the individual, as the greater number of offspring may be coupled with much lower survival of the latter due to a too high associated density and thus to a too strong intra-specific competition (Fox and Morin 2002). Dispersal at high temperature may have been a behavior selected to avoid such costs, such potential positive density-dependence has already been observed in our model species for sufficiently high densities (Fronhofer et al. 2015b). We also observed that the traits of resident cells increased relative to those of the dispersers as the local temperature increased. The size, elongation, linearity, and velocity of the resident cell movements increased relative to those of the dispersers: this could reflect behavior on the part of the residents to escape the local condition and seek to disperse. Indeed, such traits are associated with greater efficiency in movement (Pennekamp et al. 2019), probably reflecting a search for displacement, consistent with the fact that high local temperature could be actively avoided by individuals.

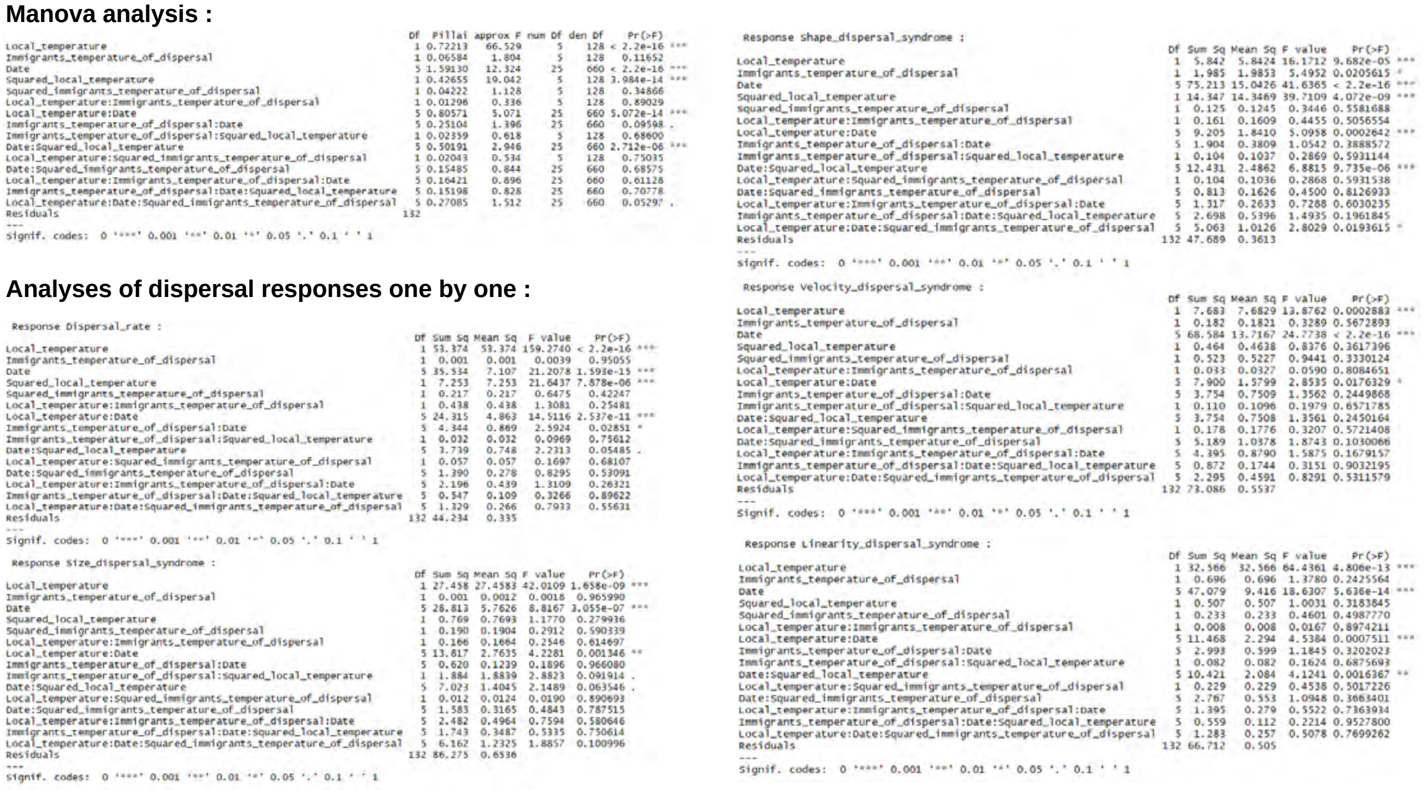
It appears that there was no consistent effect of social information on dispersal responses. Some variation among days, potentially indicating information used in different ways, were observed, but with no strong statistical support (Table S1, Figure S4, S5, S6). The interpretation of such effects is also particularly difficult in an experimental setting where we have been careful to control the different environmental parameters: they may result from variation in environmental parameters we did not have a perfect control on, probably related to the culture conditions for which variations in density were observed, that potentially correlate with other parameters (as resource availability, the stress level of cells, with possible chemical cues: Fronhofer et al. 2015b).

The decrease in elongation and movement linearity of immigrant cells having dispersed in high temperatures could be interpreted as a direct effect of temperature (Melo et al. 2020, Morel-Journel et al. 2020), and could reflect stressful conditions for the cells, in particular for elongation (Melo et al. 2020). The effect of immigrant traits on dispersal responses could be understood as an effect of the physiological state of immigrants, a probable source of information for focal cells that could adapt their dispersal movements to such social information. Indeed, cells' size could be directly related to resources availability (DeLong and Vasseur 2012, Tan et al. 2021 for other protists on cells' size reduction), temperature stress (Melo et al. 2020 for cell size), or competition pressure (smaller cells associated to an important inter-specific competition: Tan et al. 2021, in other protists species). Such conditions could also be associated with specific chemical production (Madinger et al. 2010, for an example of constitutive secretion under different resource availability conditions) that could then constitute social cues. Yet, it is quite difficult here to identify the exact ultimate cause of such physiological variations. It could be due to other parameters than temperature as crowding (Fox and Morin 2002). Other experiments should

be conducted to precisely understand what causes such physiological changes (*i.e.* what information could be precisely transmitted here) and which cues related to these traits could be perceived by the focal cells.
The temperature did not appear to be indirectly transmitted by social cues here. This is quite surprising as the temperature is of particularly high importance for cells' physiological condition (Melo et al. 2020), for their movement (Jacob et al. 2017, 2018), and population growth rate (Jacob et al. 2017, 2018). We could have expected that the transmission of information on this parameter would therefore be advantageous. The fact that this parameter is not informed could be due to too important variation of this parameter in natural conditions (making such information of low value: Riotte-Lambert and Matthiopoulos 2019). Another possibility is the absence of perceptible social cues.

Unfortunately, this experiment did not allow us to answer our initial question on the use of conflicting information sources, potentially depending on the local context (Figure 1). It could be of great interest to use the experimental setting we designed here for other studies while using social information that is known to be used (as the matrix characteristics or the resource availability in environments in *Tetrahymena thermophila*: Jacob et al. 2015b). Here, for example, we could have manipulated the concentration of resources in the media (as in Jacob et al. 2015b) in the departure patch of informant and focal cells.

Supplementary Materials



Manova analysis :

```
                                                                     Df  Pillai approx F num Df den Df    Pr(>F)    
Local_temperature                                                     1 0.72213   66.529      5    128 < 2.2e-16 ***
Immigrants_temperature_of_dispersal                                   1 0.06584    1.804      5    128   0.11652    
Date                                                                  5 1.59130   12.324     25    660 < 2.2e-16 ***
Squared_local_temperature                                             1 0.42655   19.042      5    128 3.984e-14 ***
Squared_immigrants_temperature_of_dispersal                           1 0.04222    1.128      5    128   0.34866    
Local_temperature:Immigrants_temperature_of_dispersal                 1 0.01298    0.336      5    128   0.89029    
Local_temperature:Date                                                5 0.80571    5.071     25    660 5.072e-14 ***
Immigrants_temperature_of_dispersal:Date                              5 0.25104    1.396     25    660   0.09598 .  
Immigrants_temperature_of_dispersal:Squared_local_temperature         1 0.02359    0.618      5    128   0.68600    
Date:Squared_local_temperature                                        5 0.50191    2.946     25    660 2.712e-06 ***
Local_temperature:Squared_immigrants_temperature_of_dispersal         1 0.02043    0.534      5    128   0.75035    
Date:Squared_immigrants_temperature_of_dispersal                      5 0.15485    0.844     25    660   0.68575    
Local_temperature:Immigrants_temperature_of_dispersal:Date            5 0.16421    0.896     25    660   0.61128    
Immigrants_temperature_of_dispersal:Date:Squared_local_temperature    5 0.15198    0.828     25    660   0.70778    
Local_temperature:Date:Squared_immigrants_temperature_of_dispersal    5 0.27085    1.512     25    660   0.05297 .  
Residuals                                                           132                                             
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Analyses of dispersal responses one by one :

```
 Response Dispersal_rate :
                                                                    Df Sum Sq Mean Sq  F value    Pr(>F)    
Local_temperature                                                    1 53.374  53.374 159.2740 < 2.2e-16 ***
Immigrants_temperature_of_dispersal                                  1  0.001   0.001   0.0039   0.95055    
Date                                                                 5 35.534   7.107  21.2078 1.593e-15 ***
Squared_local_temperature                                            1  7.253   7.253  21.6437 7.878e-06 ***
Squared_immigrants_temperature_of_dispersal                          1  0.217   0.217   0.6475   0.42247    
Local_temperature:Immigrants_temperature_of_dispersal                1  0.438   0.438   1.3081   0.25481    
Local_temperature:Date                                               5 24.315   4.863  14.5116 2.537e-11 ***
Immigrants_temperature_of_dispersal:Date                             5  4.344   0.869   2.5924   0.02851 *  
Immigrants_temperature_of_dispersal:Squared_local_temperature        1  0.032   0.032   0.0969   0.75612    
Date:Squared_local_temperature                                       5  3.739   0.748   2.2313   0.05485 .  
Local_temperature:Squared_immigrants_temperature_of_dispersal        1  0.057   0.057   0.1697   0.68107    
Date:Squared_immigrants_temperature_of_dispersal                     5  1.390   0.278   0.8295   0.53091    
Local_temperature:Immigrants_temperature_of_dispersal:Date           5  2.196   0.439   1.3109   0.26321    
Immigrants_temperature_of_dispersal:Date:Squared_local_temperature   5  0.547   0.109   0.3266   0.89622    
Local_temperature:Date:Squared_immigrants_temperature_of_dispersal   5  1.329   0.266   0.7933   0.55631    
Residuals                                                          132 44.234   0.335                       
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

 Response Size_dispersal_syndrome :
                                                                    Df Sum Sq Mean Sq F value    Pr(>F)    
Local_temperature                                                    1 27.458 27.4583 42.0109 1.658e-09 ***
Immigrants_temperature_of_dispersal                                  1  0.001  0.0012  0.0018  0.965990    
Date                                                                 5 28.813  5.7626  8.8167 3.055e-07 ***
Squared_local_temperature                                            1  0.769  0.7693  1.1770  0.279936    
Squared_immigrants_temperature_of_dispersal                          1  0.190  0.1904  0.2912  0.590339    
Local_temperature:Immigrants_temperature_of_dispersal                1  0.166  0.1664  0.2546  0.614697    
Local_temperature:Date                                               5 13.817  2.7635  4.2281  0.001346 ** 
Immigrants_temperature_of_dispersal:Date                             5  0.620  0.1239  0.1896  0.966080    
Immigrants_temperature_of_dispersal:Squared_local_temperature        1  1.884  1.8839  2.8823  0.091914 .  
Date:Squared_local_temperature                                       5  7.023  1.4045  2.1489  0.063546 .  
Local_temperature:Squared_immigrants_temperature_of_dispersal        1  0.012  0.0124  0.0190  0.890693    
Date:Squared_immigrants_temperature_of_dispersal                     5  1.583  0.3165  0.4843  0.787515    
Local_temperature:Immigrants_temperature_of_dispersal:Date           5  2.482  0.4964  0.7594  0.580646    
Immigrants_temperature_of_dispersal:Date:Squared_local_temperature   5  1.743  0.3487  0.5335  0.750614    
Local_temperature:Date:Squared_immigrants_temperature_of_dispersal   5  6.162  1.2325  1.8857  0.100996    
Residuals                                                          132 86.275  0.6536                      
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

```
 Response Shape_dispersal_syndrome :
                                                                    Df Sum Sq Mean Sq F value    Pr(>F)    
Local_temperature                                                    1  5.842  5.8424 16.1712 9.682e-05 ***
Immigrants_temperature_of_dispersal                                  1  1.985  1.9853  5.4952 0.0205615 *  
Date                                                                 5 75.213 15.0426 41.6365 < 2.2e-16 ***
Squared_local_temperature                                            1 14.347 14.3469 39.7109 4.072e-09 ***
Squared_immigrants_temperature_of_dispersal                          1  0.125  0.1245  0.3446 0.5581688    
Local_temperature:Immigrants_temperature_of_dispersal                1  0.161  0.1609  0.4455 0.5056554    
Local_temperature:Date                                               5  9.205  1.8410  5.0958 0.0002642 ***
Immigrants_temperature_of_dispersal:Date                             5  1.904  0.3809  1.0542 0.3888572    
Immigrants_temperature_of_dispersal:Squared_local_temperature        1  0.104  0.1037  0.2869 0.5931144    
Date:Squared_local_temperature                                       5 12.431  2.4862  6.8815 9.735e-06 ***
Local_temperature:Squared_immigrants_temperature_of_dispersal        1  0.104  0.1036  0.2868 0.5931538    
Date:Squared_immigrants_temperature_of_dispersal                     5  0.813  0.1626  0.4500 0.8126933    
Local_temperature:Immigrants_temperature_of_dispersal:Date           5  1.317  0.2633  0.7288 0.6030235    
Immigrants_temperature_of_dispersal:Date:Squared_local_temperature   5  2.698  0.5396  1.4935 0.1961845    
Local_temperature:Date:Squared_immigrants_temperature_of_dispersal   5  5.063  1.0126  2.8029 0.0193615 *  
Residuals                                                          132 47.689  0.3613                      
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

 Response Velocity_dispersal_syndrome :
                                                                    Df Sum Sq Mean Sq F value    Pr(>F)    
Local_temperature                                                    1  7.683  7.6829 13.8762 0.0002883 ***
Immigrants_temperature_of_dispersal                                  1  0.182  0.1821  0.3289 0.5672893    
Date                                                                 5 68.584 13.7167 24.7738 < 2.2e-16 ***
Squared_local_temperature                                            1  0.464  0.4638  0.8376 0.3617396    
Squared_immigrants_temperature_of_dispersal                          1  0.523  0.5227  0.9441 0.3330124    
Local_temperature:Immigrants_temperature_of_dispersal                1  0.033  0.0327  0.0590 0.8084651    
Local_temperature:Date                                               5  7.900  1.5799  2.8535 0.0176329 *  
Immigrants_temperature_of_dispersal:Date                             5  3.754  0.7509  1.3562 0.2449868    
Immigrants_temperature_of_dispersal:Squared_local_temperature        1  0.110  0.1096  0.1979 0.6571785    
Date:Squared_local_temperature                                       5  3.754  0.7508  1.3561 0.2450164    
Local_temperature:Squared_immigrants_temperature_of_dispersal        1  0.178  0.1776  0.3207 0.5721408    
Date:Squared_immigrants_temperature_of_dispersal                     5  5.189  1.0378  1.8743 0.1030066    
Local_temperature:Immigrants_temperature_of_dispersal:Date           5  4.395  0.8790  1.5875 0.1679157    
Immigrants_temperature_of_dispersal:Date:Squared_local_temperature   5  0.872  0.1744  0.3151 0.9032195    
Local_temperature:Date:Squared_immigrants_temperature_of_dispersal   5  2.295  0.4591  0.8291 0.5311579    
Residuals                                                          132 73.086  0.5537                      
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

 Response Linearity_dispersal_syndrome :
                                                                    Df Sum Sq Mean Sq F value    Pr(>F)    
Local_temperature                                                    1 32.566  32.566 64.4361 4.806e-13 ***
Immigrants_temperature_of_dispersal                                  1  0.696   0.696  1.3780 0.2425564    
Date                                                                 5 47.079   9.416 18.6307 5.636e-14 ***
Squared_local_temperature                                            1  0.507   0.507  1.0031 0.3183845    
Squared_immigrants_temperature_of_dispersal                          1  0.233   0.233  0.4601 0.4987770    
Local_temperature:Immigrants_temperature_of_dispersal                1  0.008   0.008  0.0167 0.8974211    
Local_temperature:Date                                               5 11.468   2.294  4.5384 0.0007511 ***
Immigrants_temperature_of_dispersal:Date                             5  2.993   0.599  1.1845 0.3202023    
Immigrants_temperature_of_dispersal:Squared_local_temperature        1  0.082   0.082  0.1624 0.6875693    
Date:Squared_local_temperature                                       5 10.421   2.084  4.1241 0.0016367 ** 
Local_temperature:Squared_immigrants_temperature_of_dispersal        1  0.229   0.229  0.4538 0.5017226    
Date:Squared_immigrants_temperature_of_dispersal                     5  2.767   0.553  1.0948 0.3663401    
Local_temperature:Immigrants_temperature_of_dispersal:Date           5  1.395   0.279  0.5522 0.7363934    
Immigrants_temperature_of_dispersal:Date:Squared_local_temperature   5  0.559   0.112  0.2214 0.9527800    
Local_temperature:Date:Squared_immigrants_temperature_of_dispersal   5  1.283   0.257  0.5078 0.7699262    
Residuals                                                          132 66.712   0.505                      
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Table S1: Study of dispersal responses (MANOVA) as a function of temperature treatments (local temperature and immigrants' temperature of dispersal, *i.e.* social information).
The MANOVA was analyzed through Pillai's tests. We also performed an analysis of deviance on each dispersal response separately.

Dispersal variables	**Loadings for the first PCA axis**	**Loadings for the second PCA axis**	**Loadings for the third PCA axis**	**Loadings for the fourth PCA axis**	**Loadings for the fifth PCA axis**
Dispersal rate	0.31	**-0.52**	**0.68**	-0.25	-0.30
Size dispersal syndrome	0.27	**-0.53**	**-0.72**	-0.28	-0.19
Shape dispersal syndrome	0.35	**0.51**	0.01	**-0.76**	0.14
Velocity dispersal syndrome	**0.53**	0.40	-0.07	0.39	**-0.62**
Linearity dispersal syndrome	**0.64**	-0.13	0.02	0.33	**0.67**

Table S2: Loadings of the principal component analysis (PCA) on all dispersal responses (focal cells).

The sign of the loading indicates the direction of correlation between the dispersal variable and the PCA axis. The loading is a good indicator of the contribution of the variable to a PCA axis (Jolliffe and Cadima 2016). We can consider that a variable has a high contribution to an axis if its contribution is superior to the contribution value if all variables had the same weight: as the sum of squared loadings is equal to one, it means here to have an absolute loading superior to 0.45. All such important contributions are highlighted in bold.

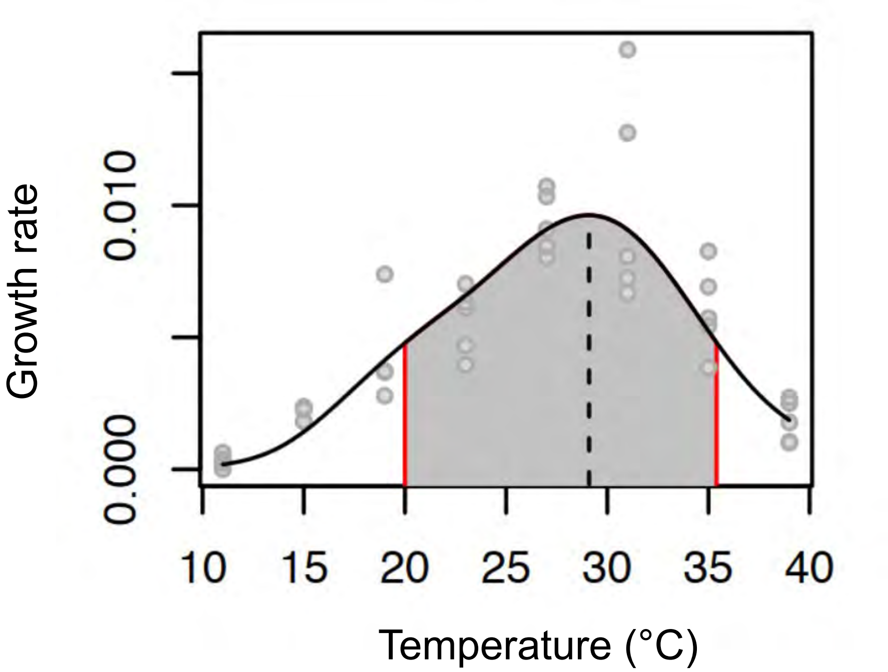


Figure S1: Thermal niche of the D13 strain.
This figure is extracted from Jacob et al. (2018) in PNAS. Each point represents a measure replicate. The dashed line represents the temperature at which the growth rate is maximal. The grey area (delimited by red lines) represents the temperature range including 80% of the thermal niche (area under the curve).

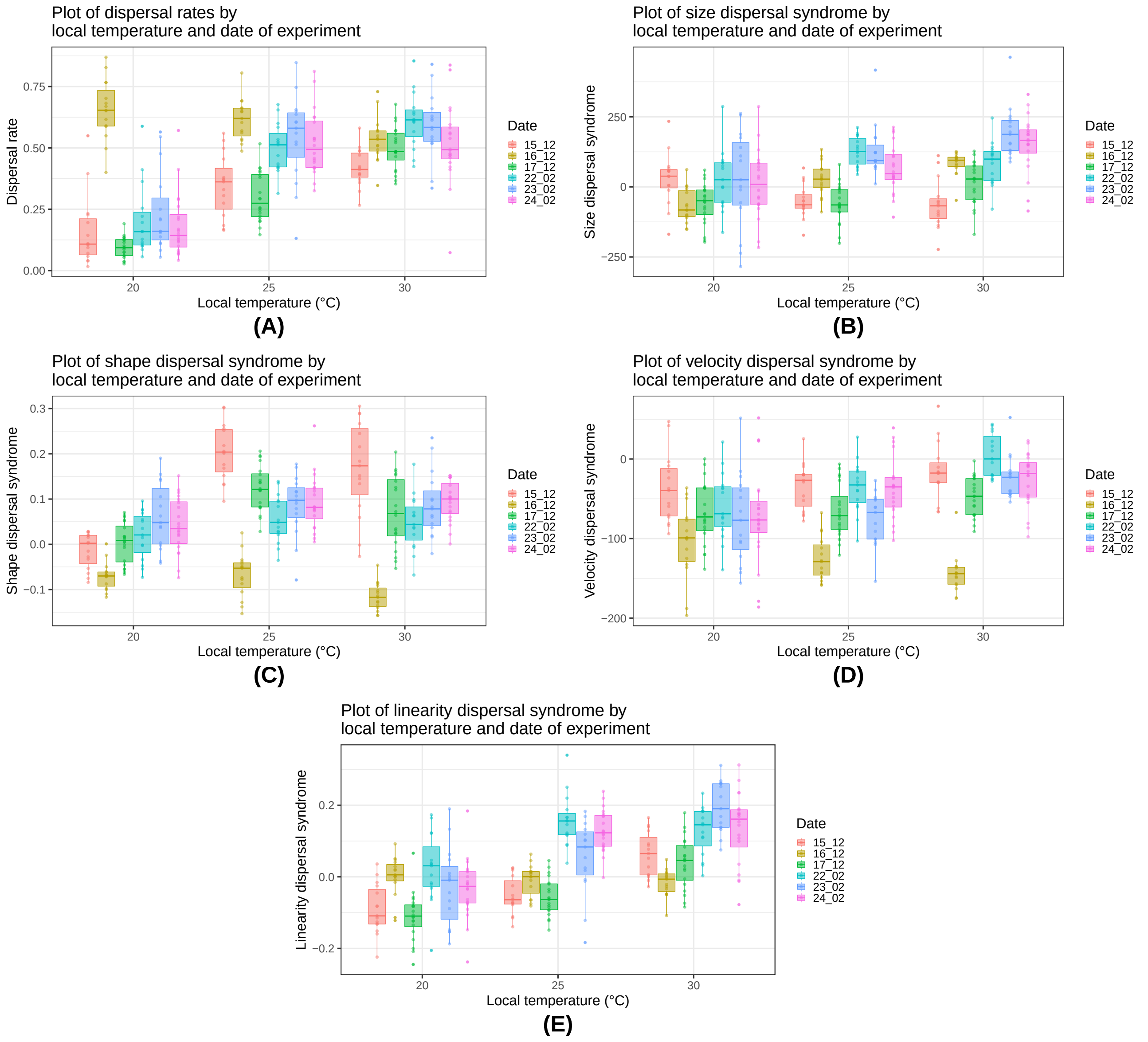


Figure S2: Dispersal responses of focal cells depending on the local temperature and the date of experiments.

These graphs display how the different dispersal responses (A: Dispersal rate, B: Cells' size dispersal syndrome, C: Cells' shape dispersal syndrome, D: Cells' velocity dispersal syndrome, E: Cells' linearity dispersal syndrome) vary in function of the local temperature (20, 25 or 30°C) and the experimental day.

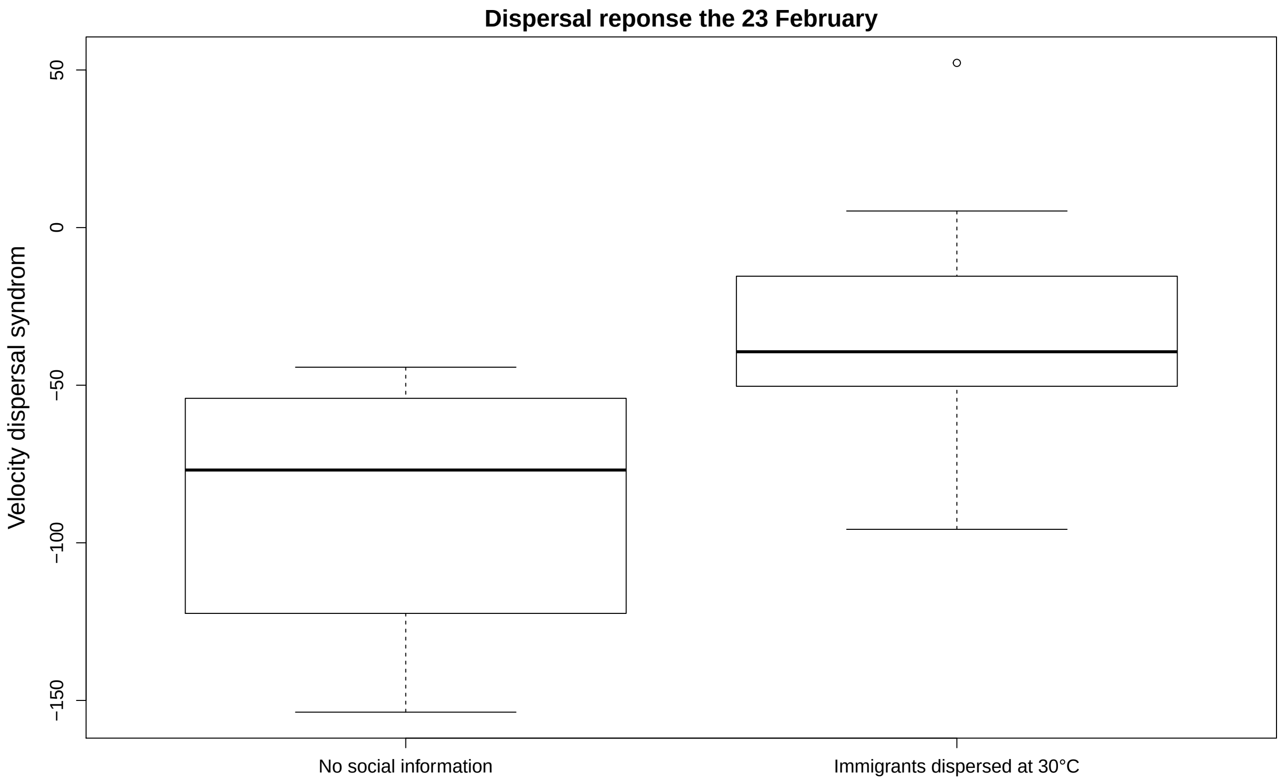


Figure S3: Correlations between dispersal response variables.
This figure was produced using the ‘ppcor’ and ‘corrplot’ R packages. Partial Spearman’s correlation tests were performed for each couple of variables (while other variables’ values). Values of the correlation coefficient are displayed by colors (the darker the color, the stronger the correlation). The size of the circles is proportional to the p-value (the bigger it is the lower the p-value), only the correlations with a p-value lower than 0.05 are represented by circles.

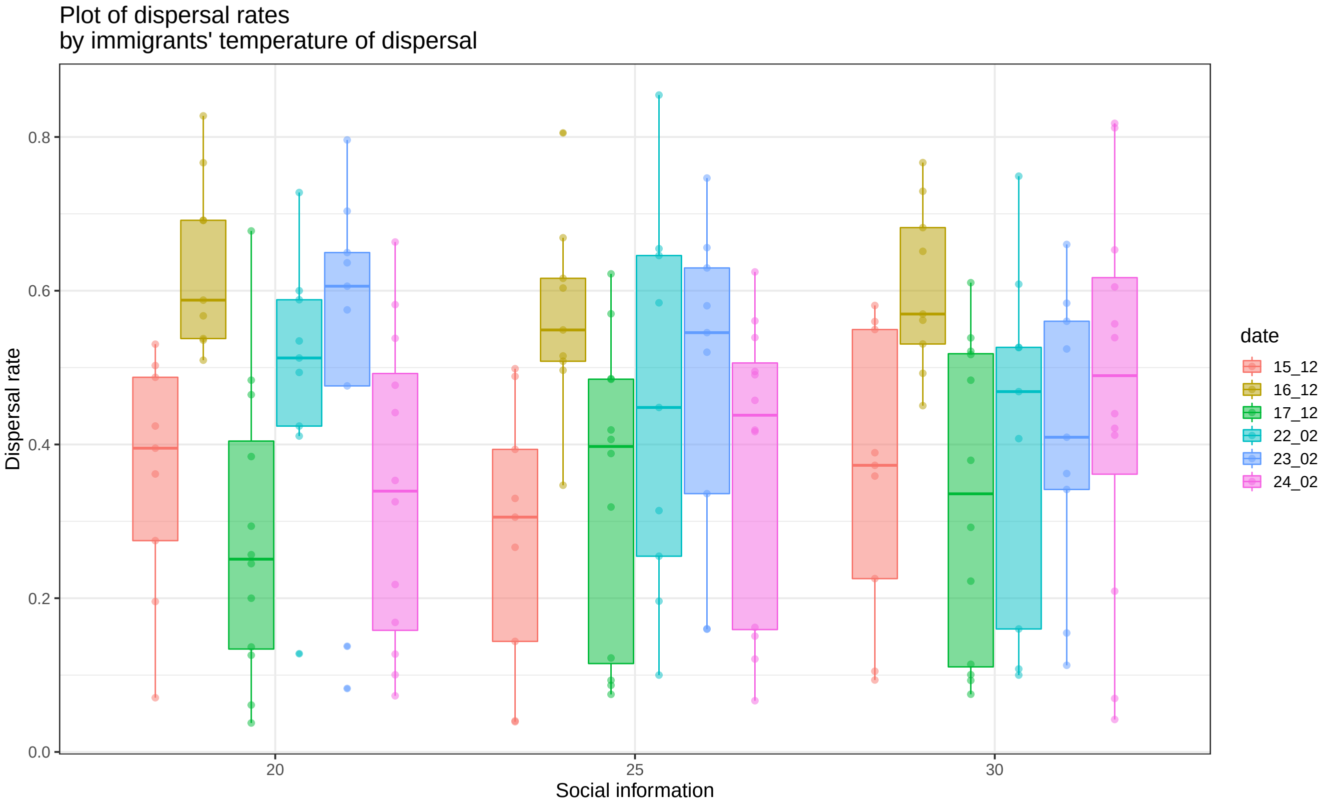
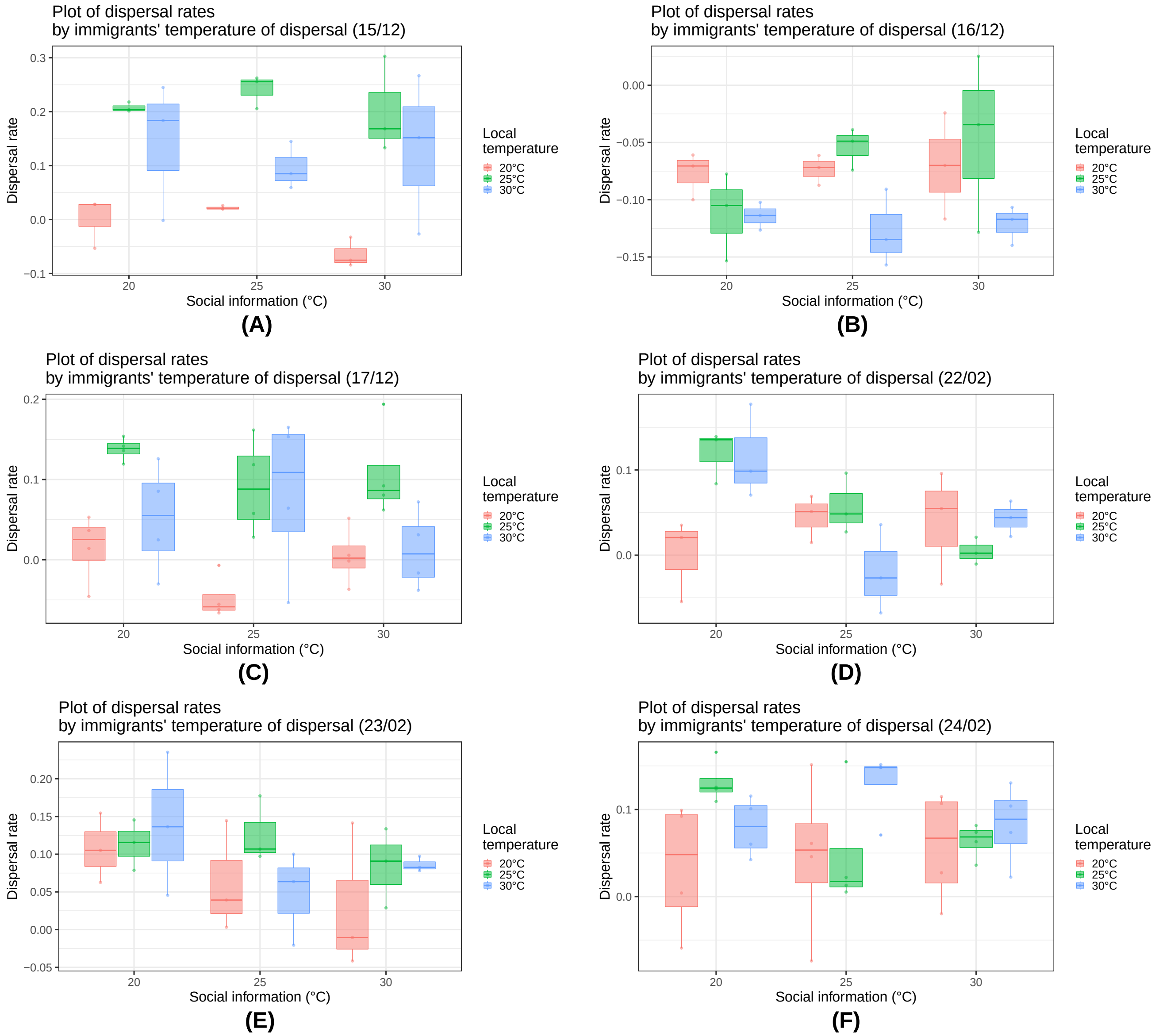


Figure S4: Use of social information detected the 23 February.
Comparison of the distribution of velocity dispersal syndromes without information and with information about immigrants having dispersed at 30°C the 23 February. The Wilcoxon test comparing these two distributions was found significant (p= 0.046).



(A) (B)

(C) (D)

(E) (F)

Figure S5: Dispersal rate of focal cells depending on the social information (immigrants' temperature of dispersal, in °C) and the date of experiments.
The shape of the relationship between the dispersal rate and the social information at the different local temperature depended on the experimental date (represented by different colors).

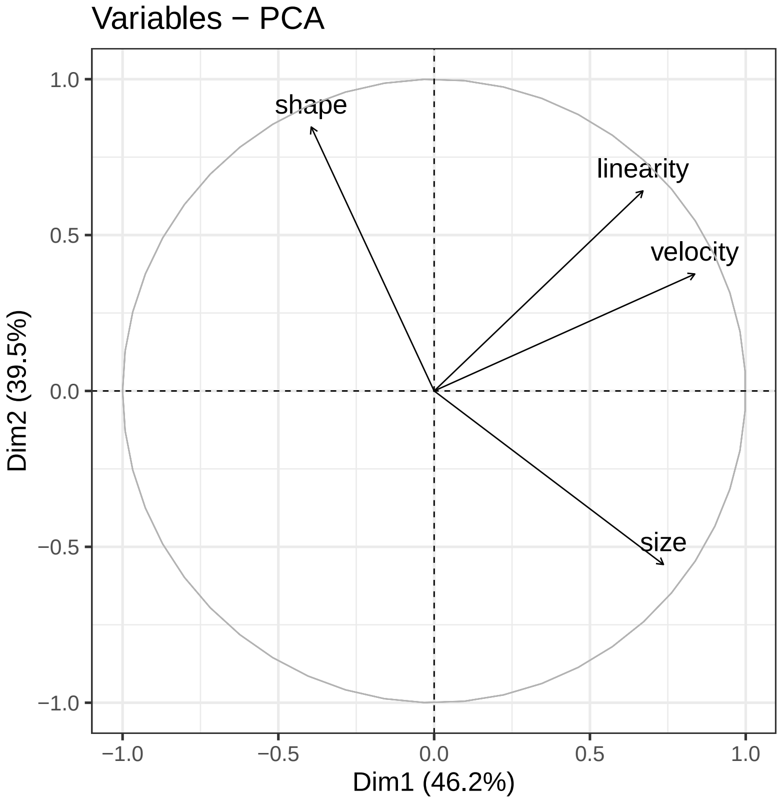


Figure S6: Immigrants' traits PCA graph of variables (first and second axes).
Each arrow is associated with a trait displayed at its extremity. Arrows indicate strength and sense of correlation among variables and between variables and the PCA axes. The axes explained variances are displayed on the x-axis and y-axis (percentages).

Appendix 4: Spatial distribution of dispersers and residents in the study site of common lizards

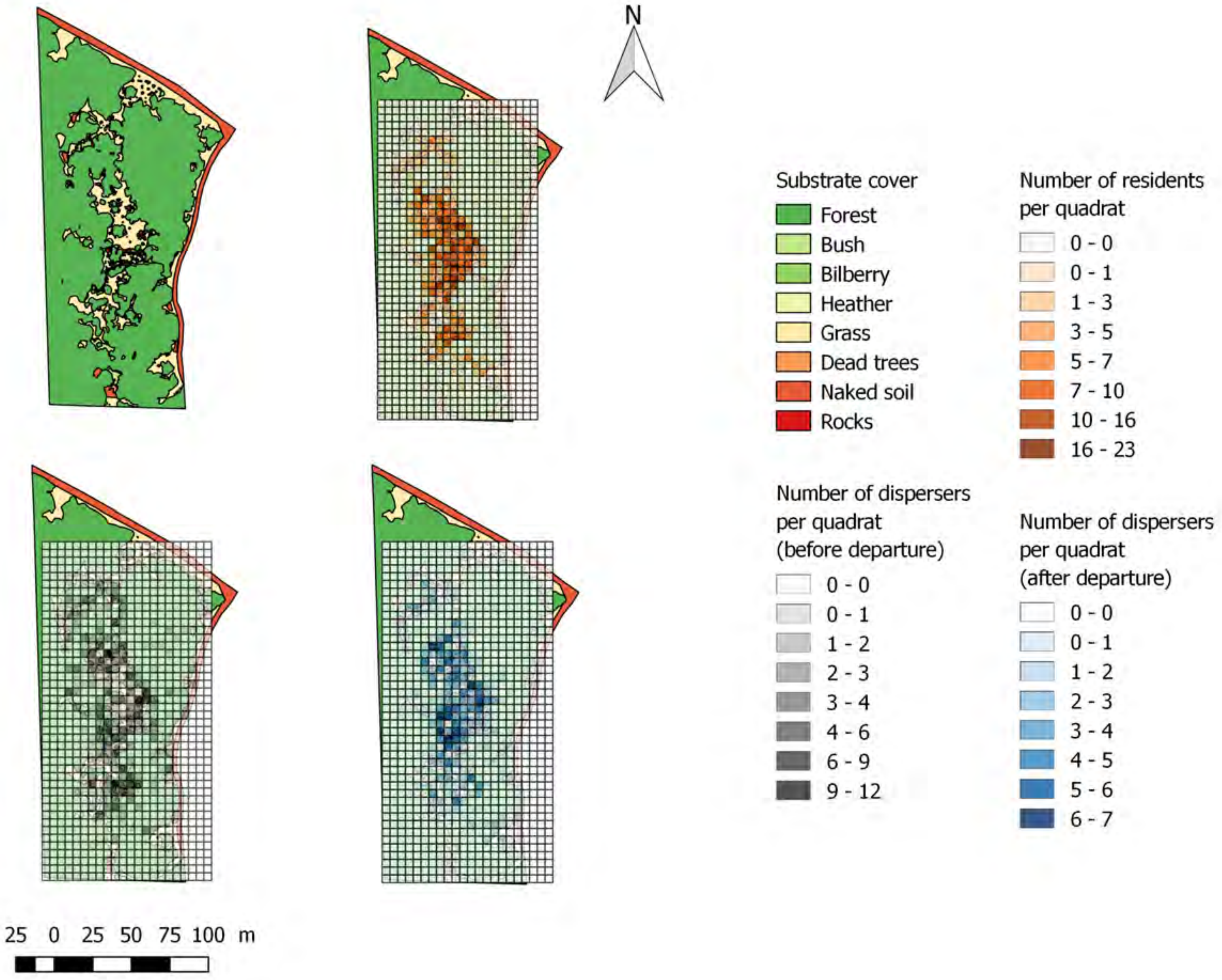


Figure 1: Spatial distribution of residents and dispersers in the common lizard study site. The map on the top left displays the study site and the substrate cover on it. The three over maps display the spatial distribution of individuals that did not disperse (residents), and those who dispersed (dispersers), with their distribution at birth (*i.e.* before departure) and after dispersal (*i.e.* after departure). Each quadrat is 5x5m long. The map was produced with QGIS 2.18.25.

Appendix 5: Influence of local social information on dispersal distances

During this thesis, we explored the relationships between the natal dispersal distance (*i.e.* the distance between the natal area and the home-range area as an individual over the age of one year, defined in Chapters 1 and 3) and the environmental context in the natal area (same variables than in Chapter 1). To do so, we used the long-term monitoring of common lizards, with a method highly similar to Chapter 1. Only the model implementation differed, with the use of a linear regression to study such relationships, without random effect on year as it revealed non-significant before the model implementation (analysis of deviance test between null models with and without random effects).

We aimed at investigating the relative importance of multiple factors (the social context, including the condition of mothers that is a potential proxy for kin competition, non-social context, and focal neonate's phenotype: same as in Chapter 1) in determining dispersal distances. We specifically expected dispersal distance to depend on kin competition proxies (Rousset and Gandon 2002, *e.g.* Long et al. 2008, Bitume et al. 2013, Hardouin et al. 2015, Aguillon and Duckworth 2015). We more particularly wanted to test whether social information gathered in the natal area influenced such distance, possibly in a similar way than for emigration decisions (investigating in Chapter 1), with a greater distancing from environments associated with higher emigration rates.

We analyzed the dispersal distance of 381 individuals (with a random sampling among siblings, to avoid bias from non-independence in sibling dispersal movements). The model had an overall fit quite low (r-squared of 0.07). We found the dispersal distance to depend on the natal social context, with particularly high effect size and variance explained by the mother's body size (SVL: snout-to-vent length), the average neonates' corpulence in the natal area, and to a lesser extent the density and the average adults' age in the natal area (Table 1; F-values and partial R-squared for estimation of variables effect sizes and explained variance). The dispersal distance tended to decrease when the density (Figure 1-A) and the average adult's age (Figure 1-B) increased. The dispersal distance decreased when the average neonates' corpulence increased (Figure 1-D), but also when the average adults' corpulence decreased (Figure 1-C). Finally, we observed a non-linear relationship between the mothers' body size and the dispersal distance of focal neonates (Figure 1-E): the dispersal distance was minimal for minimal and maximal values of the mother's body size.

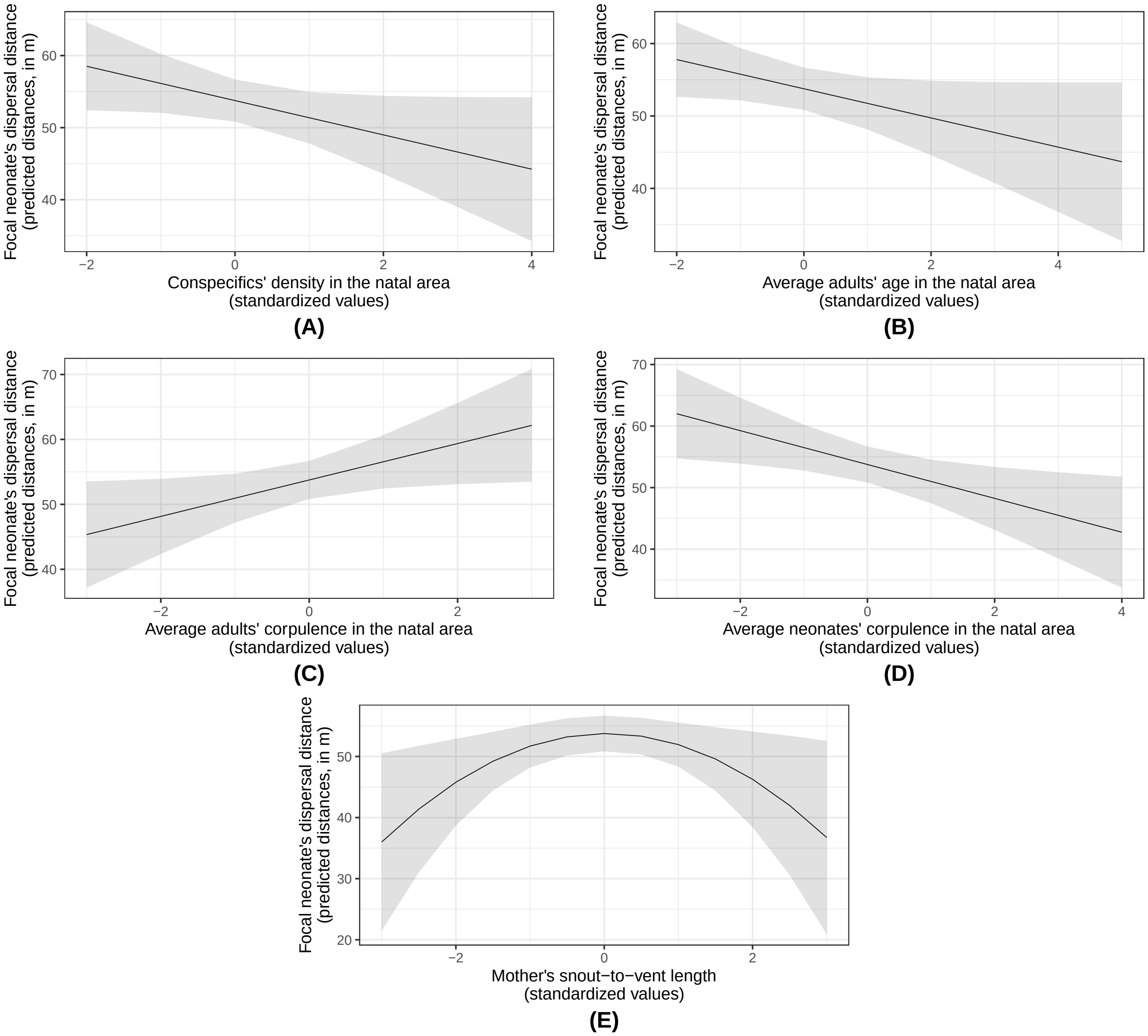


Figure 1: Significant correlations between the social context in the natal area and the dispersal distance.

These graphs displayed predicted dispersal distance (in m) as a function of the social context in the natal area (A: Density, B: Average adults' age, C: Average adults' corpulence, D: Average neonates' corpulence, E: Mother's snout-to-vent length). Predicted values were computed from coefficient estimates of the linear regressions (Table 1), by using the R package 'ggeffects' (Lüdecke 2018). Grey areas display confidence intervals computed from variance in coefficient estimates.

	Parameter	Coefficient	SE	df	F-value	P-value	Partitioning of R-squared (%)
Individual's phenotype	Sex (baseline level: female)	0.608	2.170	1	0.078	0.779	0.28
	Corpulence	1.391	1.111	1	1.568	0.211	5.58
Mother's phenotype	Mother's SVL	0.120	1.317	1	0.008	0.927	0.02
	Mother's SVL (squared)	**-1.932**	**0.816**	**1**	**5.605**	**0.018***	**19.73**
	Mother's corpulence	-1.749	1.384	1	1.596	0.207	5.68
	Mother's corpulence (squared)	0.142	0.687	1	0.042	0.836	0.15
Social context	**Density**	**-2.379**	**1.262**	**1**	**12.57**	**0.060•**	**4.2**
	Adults' age	**-2.014**	**1.073**	**1**	**3.519**	**0.061•**	**12.46**
	Proportion of subadults	-1.088	1.177	1	0.854	0.355	3.04
	Adults sex-ratio	-0.257	1.308	1	0.038	0.844	0.13
	Neonates sex-ratio	1.459	1.066	1	1.871	0.172	6.65
	Adults' corpulence	**2.803**	**1.340**	**1**	**4.374**	**0.037***	**15.45**
	Neonates' corpulence	**-2.749**	**1.103**	**1**	**6.215**	**0.013***	**21.84**
	Adults' SVL	0.027	1.410	1	<0.001	0.984	<0.01
Abiotic environment	Substrate features	-0.358	1.246	1	0.082	0.774	0.29

Table 3.3: Linear regression studying dispersal distance as a function of the natal environment and the neonate's phenotype.
Results of the linear regression on focal neonates' dispersal traveled distance are displayed here. SVL refers to snout-to-vent length. For each variable, we displayed the associated coefficient and the standard error (SE) on this coefficient. An analysis of deviance was performed to test for the significance of each variable effect (likelihood ratio tests). For each test, the F-value statistic and the associated p-values are displayed. We also computed partial r-squared, expressed as the percentage of contribution to the overall r-squared. All significant ($p<0.05$) or marginally significant ($0.05<p<0.1$) variables are in bold font. Asterisks indicate the degree of significance. • : $0.05<p<0.1$, * : $0.01<p<0.05$, ** : $0.001<p<0.01$, *** : $p<0.001$

These results suggest an influence of social information on the distance traveled by dispersers. First, they could be interpreted as the necessity to maintain a considerable distance from potentially competitive habitats for individuals. Such distancing was frequently observed for competition on resources (Houston and Francis 1995, Adriaensen et al. 1998, Aguillon and Duckworth 2015), or with positive density-dependence of dispersal distance (Matthysen 2005, *e.g.* Bitume et al. 2013). Such competition avoidance would be translated here through the avoidance by distancing from areas with particularly corpulent or young adults. Second, some of these results suggest maintaining proximity with a potentially advantageous habitat, with social cues such as high age (potentially reflecting better life expectancy, *e.g.* Wiklund 1996), high density (being interpreted as a cue for habitat quality, Matthysen 2005, *e.g.* Pyle and Nettleship 2001, Serrano et al. 2021), high body condition of individuals of the same age (potentially reflecting resource availability in our model species, Mugabo et al. 2010). Yet, these results could alternatively result from social fence dynamics, as observed for density (Hestbeck 1982, *e.g.* Lambin 1994, Stoen et al. 2006): crowding and highly competitive conditions could inhibit movements and result in a low traveled distance. The latter hypothesis could be easily tested by exploring if the social context between the departure and arrival habitats impacts the dispersal distance (Brevet et al., analyses in progress). Finally, the non-linear relationship we observe for the mother's body size could be due to a trade-off between kin competition and habitat quality. Such an effect would have been potentially observed in Merrick and Koprowski (2017), with a negative effect of maternal body mass for females' dispersal distance, which could benefit from high habitat quality (reflected by the mother condition), and a positive effect on males, potentially escaping kin competition and/or inbreeding with high-quality mothers. When the body size is particularly low the individuals experience low kin competition pressure, and therefore it does not particularly distance themselves from their original habitat. With an increase in the size of the mother from these low values the kin competition increases and thus the individual could tend to isolate itself more from its mother by putting a greater distance to its original habitat or benefit from good conditions through maternal effect, with better performance for dispersal (observed for dispersal propensity in our model species: Lena et al. 1998a, Meylan et al. 2002). Increasing the size of the mother probably also reflects a better quality of the habitat, so the relationship to distance reverses for a sufficiently large size. The focal individual moved less away from the habitat of origin probably to remain in favorable conditions despite the risk of kin competition (observed for mothers treated with the corticosterone stress hormone in our model species: Meylan et al. 2004). Part of this non-linear relationship could also be due to variation in maternal age (as body size and age are highly correlated in reptiles: Halliday and Verrell 1988), with less avoidance of aged mothers as it reduces the kin competition level (Ronce et al. 1998).

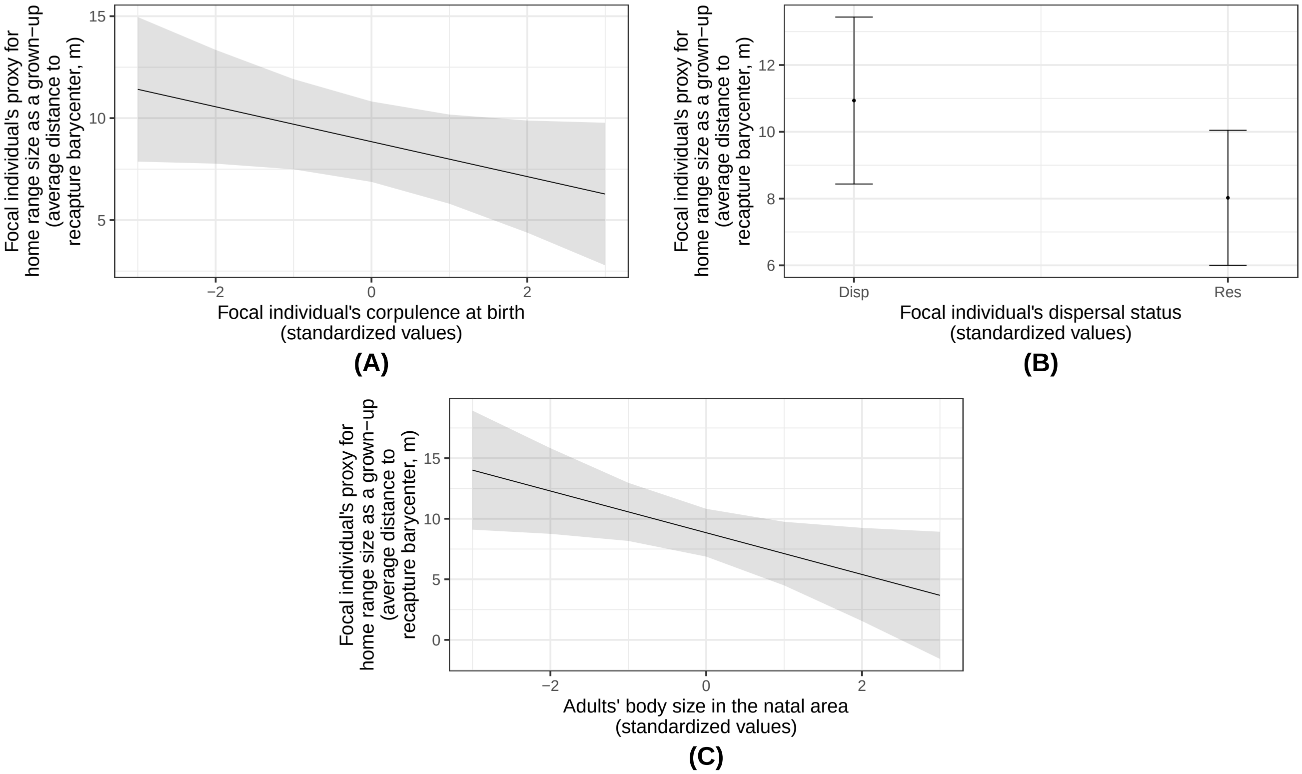
Such results should be complemented by more research on the role of the selected habitat in such traveled distance (Brevet et al., work in progress).

Appendix 6: Influence of local social information on living areas dimensions

During this thesis, we explored the existing relationships between the environmental context in the natal area or the phenotype of the individual at birth (with the same variables as in Chapter 1), and the dimensions of the home range of the same individual when older than one year (referred to as the established home range later in the text). For this, we used the long-term monitoring of common lizards by mark-recapture (Chapter 1). These data allowed us to estimate the dimensions of the home range by calculating the average distance of all recapture points as an adult or subadult from the barycenter of these recapture points (only for individuals with a least three recapture locations as an adult or subadult). The relationships were then analyzed using a mixed linear regression model, with a random effect on year (tested significant before the model implementation: analysis of deviance test between null models with and without random effects). The remaining method is identical to what was done in Chapter 1.
The objective was to test whether natal habitat and physical conditions had an impact on space use later in the life of the individual. We expected potential silver spoon effects, with the physical condition of the individual at birth potentially conditioning its performance in adulthood (Stamps et al. 2006). We also expected to see potential imprints of the natal habitat on the individual, with the competitive conditions experienced by the individual at a young age also impacting these performances in adulthood (Benard and McCauley 2008 for examples on dispersal).

We analyzed the home range dimensions of 294 individuals (with a random sampling among siblings, to avoid bias from non-independence in sibling movements). The model had an overall fit quite low (r-squared of 0.095). We found the home range dimensions to depend on the average adults' body size (SVL: snout-to-vent length) and the early phenotype of focal individuals (Table 1). Home range dimensions tended to decrease when the focal individual's corpulence at birth increased (Figure 1-A). Home range dimensions were high for dispersers compared to residents individuals (Figure 1-B, the dispersal status being defined in Chapters 1 and 3). Finally, the home range dimensions decreased when the average adults' body size in the natal area increased.

These results suggest that the natal context influenced space use as an adult, by shaping home range dimensions. First, the body condition at birth impacted the established home range dimension, with a decrease in home range size when the body condition at birth increased. As natal conditions are very



(A) **(B)**

(C)

Figure 1: Significant correlations between the social context in the natal area or the focal individual's phenotype at birth and the established home-range dimension.
These graphs displayed predicted established home range dimensions (in m) as a function of the focal individual's phenotype at birth (A: Corpulence, B: Dispersal status) and the social context in the natal area (C: Adults' snout-to-vent length). Predicted values were computed from coefficient estimates of the linear regressions (Table 1), by using the R package 'ggeffects' (Lüdecke 2018). Grey areas display confidence intervals computed from variance in coefficient estimates.

	Parameter	Coefficient	SE	df	χ^2	P-value
Individual's phenotype	**Dispersal status**	**-2.914**	**1.015**	**1**	**8.240**	**0.004****
	Sex (baseline level: female)	0.675	0.966	1	0.489	0.484
	Corpulence	**-0.856**	**0.493**	**1**	**3.008**	**0.082•**
Mother's phenotype	Mother's SVL	0.032	0.574	1	0.003	0.954
	Mother's SVL (squared)	-0.185	0.329	1	0.318	0.572
	Mother's corpulence	0.301	0.613	1	0.241	0.622
	Mother's corpulence (squared)	-0.055	0.300	1	0.034	0.852
Social context	Density	0.324	0.642	1	0.255	0.613
	Adults' age	-0.287	0.520	1	0.306	0.580
	Proportion of subadults	0.496	0.577	1	0.740	0.389
	Adults sex-ratio	-0.986	0.669	1	2.168	0.140
	Neonates sex-ratio	-0.443	0.475	1	0.871	0.350
	Adults' corpulence	0.766	0.712	1	1.157	0.281
	Neonates' corpulence	1.007	0.625	1	2.595	0.107
	Adults' SVL	**-1.723**	**0.793**	**1**	**4.716**	**0.029***
Abiotic environment	Substrate features	-0.767	0.544	1	1.986	0.158

Table 3.4: Linear regression studying the dimension of established home range as a function of the natal environment and the phenotype at birth.
Results of the linear regression on focal individuals' size of a living area (estimated by the average distance to the barycenter of recapture locations as an individual over the age of one year) are displayed here. SVL refers to snout-to-vent length. For each variable, we displayed the associated coefficient and the standard error (SE) on this coefficient. An analysis of deviance was performed to test for the significance of each variable effect (likelihood ratio tests). For each test, the F-value statistic and the associated p-values are displayed. All significant (p<0.05) or marginally significant (0.05<p<0.1) variables are in bold font. Asterisks indicate the degree of significance. • : 0.05<p<0.1, * : 0.01<p<0.05, ** : 0.001<p<0.01, *** : p<0.001

likely to have long-term consequences on the individual's performance (Stamps et al. 2006), individuals in good condition at birth should also be good competitors later in life. Such good competitors could then more efficiently exploit local resources, and might therefore need a smaller living area than poor competitors. Second, home range dimensions at adult age depended on the natal dispersal status, dispersers having larger home ranges. There could be several possible explanations. First, the residents could have better environmental imprinting (Davis and Stamps 2004) and benefit from it by reducing their living area. Second, the residents may reduce their home range to avoid encounters of kin (*e.g.* Bull and Cooper 1999), more probable for non-dispersers, and therefore reduce kin competition. Third, it could be directly linked to differences in traits between dispersers or residents (dispersal syndromes), dispersers being potentially more active, with a higher propensity to explore their environment (Raffard et al. 2022, *e.g.* Cote et al. 2012 in our model species), hence the higher home at adult age. Finally, the home range dimension depended on the social context in the natal area (Davis and Stamps 2004, Benard and McCauley 2008), with smaller home range estimates when the average adults' body size increased in the natal area. That could results from initial habitat imprinting, high adults' body size probably being associated with competitive environments, driving the individual to restrain its home range (*e.g.* Schradin et al. 2010, Le Roex et al. 2022), with potential carry-over effects on its space use as an adult (*e.g.* Van Allen and Rudolf 2016). An alternative explanation is that such individuals with low body size reflect low local resource availability in our model species (Mugabo et al. 2010, 2011), therefore neonates confronted with such context could have enlarged their home range size to find sufficient resources (*e.g.* Aronsson et al. 2020) and might have maintained such behavior as an adult through carry-over effects.

Further analyses are in progress on the determinism of the home-range dimension, notably testing for the effect of the social environment experienced throughout the individual's adult life (by averaging the contexts observed in its life range over all the years in which the individual of interest was captured). This greatly expands the data set and should allow for confirming the trends observed above, as well as finding more precise relationships between the home range dimension and the social context an individual is currently confronted with. With this larger data set, it will also be possible to test for possible interactions between the phenotype of the individual and its social context. It can also allow us to get a more precise measure of the home range dimensions by using only individuals recaptured at least 5 times, and even maybe by using most convex polygon areas (with a Jenrich-Turner correction for small sample size, Jennrich and Turner 1969) to obtain better estimates.

Appendix 7: Proposal for studies on the influence of social information during movements

1 - Identifying and distinguishing the cues and information used during movements

The model species used during this thesis could be good candidates to explore the relationships between social information and social cues in movement decisions. The phenotype of common lizards is known to depend on the context the individual is experiencing. In particular, such variations in color patterns have been well-evidenced. First, UV coloration potentially reflects sex, age, and body condition (Martin et al. 2013, Bonnaffé et al. 2018), correlating with males quality (influencing reproductive success: Badiane et al. 2020), or their dominance in agonistic interactions (badge of status: Martin et al. 2016, Kawamoto et al. 2021). Second, the general ventral coloration was found to be associated with different levels of aggressiveness and alternative reproductive strategies (Vercken et al. 2007b, Vercken and Clobert 2008a,b, Vercken et al. 2009, Vercken et al. 2012, Fitze et al. 2014). More precisely, carotenoid coloration correlates with body condition, sex, stress, resource availability, sex ratio, variation related to the level of aggressiveness, parasitism level (Cote et al. 2008c, 2010b, Fitze et al. 2009, Martin et al. 2013). Melanism coloration is for its part related to males' immune response (potentially reflecting their quality: Vroonen et al. 2013) or their performance (biting force and sprint speed: San-Jose et al. 2017). Carotenoid- and melanin-based coloration also correlates with environmental predictability (Maso et al. 2022), or the amount of stress hormone (San-José and Fitze 2013). Finally, variation in density may be associated with variation in ventral brightness (Meylan et al. 2007). Environmentally-induced variations in phenotype were also observed for behavioral traits, with the activity level depending on density, then probably used as a social cue for space use (Cote et al. 2008a), or high activity level observed in response to predator cues, then used as a cue for male quality during mate selection (Teyssier et al. 2014). In the same way, potential chemical cues may have been identified, with the use of scent marks as social cues informing on the relatedness (Léna et al. 1998b, 2000), density and sex (Aragon et al.

a,b), or predators' presence (Winandy et al. 2021).

A project on the role of these latter elements was initiated during the thesis and is still being processed. It mainly focused on behaviors and odors sampled during field sessions performed during this thesis (Introduction, Appendix 1 and 2 for details), but also with preliminary elements on coloration, as categories on the pattern of dorsal melanism and ventral coloration were recorded during the whole monitoring (Vercken et al. 2007b and Lepetz et al. 2009 for details). The aim was first to confirm the use of these potential social cues in movements, *i.e.* whether natal dispersal response on the averaged candidate cues in the natal area. For a second time, we plan to perform path analyses including these social cues and social information evidenced to impact dispersal during this thesis (Chapters 1 and 3), to investigate the potential information transmission path. As initiated by Cote et al. (2008a) or Winandy et al. (2021), other experiments could be led in controlled conditions to properly test for the relationship between social cues and social information. For example, we could imagine the use of playback videos on some behaviors, or chemicals or scents, we suspected to reflect information on density or the presence of predators (with an already evidenced strong association between the social cues and the social information of interest: for example slow motion and tail vibration in response to predator cues, Thoen et al. 1986, Van Damme et al. 1995) and see how an individual react in term of movements and if a similar response is observed when confronted to more direct cues (*e.g.* high number of individuals or predator scents).

Second, the use of water-soluble chemical compounds as social cues in *Tetrahymena thermophila* is also well-described with the use of heterospecific chemical cues (informing on predator presence: Hauzy et al. 2007), use of chemical cues on the density (Fronhofer et al. 2015b) or survival of conspecifics (Fronhofer et al. 2017a), and with chemotaxis responses to chemical cues produced by potential prey or conspecifics (Hellung-Larsen et al. 1986, 1990, Leick and Hellung-Larsen 1992). By directly using potential candidate components (Madinger et al. 2010), and studying movement responses we could lead promising experiments in microcosms with such organisms.

2 - Use of information from heterospecifics and temporally distant social information

The species used during this thesis could be good candidates for experiments aiming at better understanding the role of temporal and spatial distance in the use of social information. First, the role of an information distance from the origin could be experimentally tested for the use of immigrant-based information, possibly by using microcosms in *Tetrahymena thermophila* (Appendix 3, Jacob et al. 2015b, for details on possible settings). In such microcosms, we can vary the length of dispersal corridors (as in Laurent et al. 2020) to test for the influence of immigrants' traveled distance on information use, while keeping all other parameters controlled.

Second, the role of the temporal distance of information (*i.e.* time since the informant left the situation about which he informs) could be explored using *Tetrahymena thermophila* microcosms. We could vary the time of immigrants' arrival by keeping the immigrants in their arrival patch for variable periods, and testing for its effect on social information use while controlling all other parameters. The effect of temporal distance on social information use could also be further explored in our field monitoring, by studying the importance of aged immigrants (arrived at least one year before a focal individual birth) on natal dispersal decisions. We could lead preliminary path analyses to better understand the existing correlations between the habitat of origin of old immigrants, their traits, and the dispersal responses of focal neonates. Such a study could be complemented with experiments aimed at testing if the observed effects are indeed due to the dispersal status of conspecifics. For example, we could confront focal neonates to conspecifics group with similar traits (known to be used as social cues in dispersal decisions) but with some having dispersed and others being residents, to observe if the information is interpreted differently in both cases. Of note, during our monitoring, we indeed observed an important effect of the presence of adults or subadults immigrants on the dispersal probability of individuals. This probability increased with the proportion of former dispersers (arrived at least one year ago) in the natal area (Wilcoxon test, $p<0.001$), potentially informing on the connectivity with the nearby habitats but also possibly about their characteristics.

Third, microcosm experiments could be an ideal way of testing the diffusion of social information along information chains, potentially over long temporal or spatial distances. We could perform microcosm experiments of sequential transfer of information (Appendix 3 for details on microcosms we could use). The idea would be to vary the initial conditions (variation in only one parameter with all others fixed, such as resources availability or temperature) only for a first pool of microcosms, to collect the dispersers from these microcosms, and inoculate them in a second pool of microcosm for which the conditions are constant (*e.g.* the averaged condition of the initial condition treatments), and to observe their responses to the conveyed social information. Then, we could use the dispersers of this second pool to inoculate them in a third pool of microcosms, to test for a chain of transmission of the initial information (dispersal responses in this third pool depending on the initial environmental variations in the first pool), and possibly so on with a fourth, fifth, or sixth pool with constant conditions. The aim will be to first test for the use of indirectly transmitted social information (obtained through the perception of conspecific traits, having itself acquired social information) and to test for a potential decline of social information use along such information chain, as we could expect the value of information to decrease with the number of intermediaries (and therefore the intensity in information use, *e.g.* Carter et al. 2016, Crane et al. 2018).

3 - Investigating the use of conflicting social information sources

We need more theoretical and experimental frameworks to explore the social information conflicts during movement decisions. In particular, we need to explore if the "who" and "when" strategies (Kendal et al. 2009) indeed occurred in such social information conflicts. We can first explore it using our common lizard long-term monitoring, by investigating for example if the traits of immigrants modulate the use of the information they convey. For example, we might expect the information about good habitat quality conveyed by corpulent immigrants to be favored because their corpulence is likely to reflect their success at accessing food and competing. Second, we could more precisely test for such hypotheses by performing controlled experiments confronting two conflicting sources of information (or more) varying on a parameter that may change information reliability or value. Once realized, it could be particularly interesting to look at the interactions between these parameters, to test whether some are prioritized or whether non-additive effects emerge. For example, how the conformity to the major part of information conveyers depends on the personal experience about the information value (*e.g.* Stumpter 2008).

In more complex cases, with a high number of information sources co-existing with different variability among them (Chapter 3), we should continue to explore the effect of such uncertainty in information on movement decisions. In particular, we could investigate how it impacts the way the individual moves in space: more exploratory, erratic behavior, to locate the most interesting information? More return rate in case of too much time or distance of exploration without success? On the latter question, *Tetrahymena thermophila* could be a good model species, since 2D experimental systems make possible the continuous monitoring of movement dynamics are being developed (Schtickzelle and Jacob, in prep).

Finally, theoretical models could allow us to better predict the impact of such conflicts on demographic or evolutive parameters. A potentially interesting framework to work with has been developed by Chaine et al. (2013), with an individual-based model integrating both local and immigrant-based information and the impact of the use of such information on metapopulation dynamics. This model could be further developed by adding several sources of immigrant-based distant information, and by varying the way conflicts in such information are handled (preference over reliable cues, with parameters such as spatial or temporal distance, age of immigrants, success associated with the information, value compared to the present environment; decrease in social information use with the overall variability among information sources), to investigate their repercussion on demographic parameters and meta-population functioning.

4 - Investigating how social information influence the length of performed movements

To study the way traveled distance may vary with context initial and transience context, we could use our long-term monitoring on common lizards and microcosm experiments on *Tetrahymena thermophila*. We should first investigate how traveled distance is influenced partly by initial condition by comparing the selected habitat with the initial habitat, to explore if these habitats appear to be similar or dissimilar in general, and then investigate if the habitat dissimilarity or similarity evolves with traveled distance. Yet, to further understand the driver of similarity or dissimilarity choices (real advantage to conserve or change of habitat, dispersal related to the avoidance of kin) experiments should be led to investigate what dispersers are seeking. For example, we could propose to an individual two habitats at the same distance, one familiar, the other unfamiliar, and observe its preference (in the presence of kin or not in the initial habitat), and then vary the distance to access the familiar or unfamiliar habitat, to see how the preferences evolve.

We can also more specifically investigate the importance of habitat settlement. In the common lizard long-term monitoring, the randomness in habitat selection could be tested by measuring the distribution of dissimilarities between selected habitats after dispersal and the most probable habitats of arrival (theoretical distribution) considering the position of the initial habitat, the dispersal kernel (computed on all dispersers) and the limit of the study site (wood areas restricting displacements): if the distribution mean differs from 0, we could reject the null hypothesis of a random habitat selection. We could even explore if such habitat selection depends on phenotypes, initial contexts, or immigrant-based information (possibly also by adjusting dispersal kernel characteristics to these conditions). Microcosm experiments on *Tetrahymena thermophila* could also precise the way habitat selection is performed under specific conditions, especially when the arrival habitat is somehow unsatisfying (compared to the initial context, and most importantly compared to immigrant-based information). In particular, the use of 2D systems could allow us to test for potential habitat refusal (by investigating the return rates) when arriving in unsatisfying ones.

5 - Investigating the evolution of social information use

Microcosm experiments on *Tetrahymena thermophila* could again be particularly useful to investigate whether using social information for movement decisions is under selection. First, we could explore whether the existing genetic variability in social information use leads to better population performance. To do this, we can use clonal strains, in the same conditions, and focus only on the effect of social information in changing (different regimes of fluctuations and predictability of these changes) and heterogeneous systems (multipatch systems allowing movements and metapopulation dynamics), where the use of social information might provide a greater or lesser benefit for population maintenance. Moreover, the existence of multiple strains varying in their levels of cooperation and possibly in the propensity and the way they use social information (Jacob et al. 2015b), could allow testing for the genetically-based difference in social information use, by exploring the fitness consequences of the use of social information for these different strains while keeping similar experimental conditions. It could be also a way of exploring under which conditions social information used for movement decisions would lead to maladaptive decisions. Crossing these experiments with those aiming to better understand the importance of context in the use of social information for the same genotype (*i.e.* phenotypic plasticity, detailed in a previous section), could allow us to understand the respective part of plasticity and genetic determinism in the existing variability of response to this information (*e.g.* Morinay et al. 2018, Tolvanen et al 2020).

Bibliography

A

Abrahams MV. 1986. Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. Behav Ecol Sociobiol. 19(6):409–415. doi:10.1007/BF00300543.

Abrahms B, Seidel DP, Dougherty E, Hazen EL, Bograd SJ, Wilson AM, Weldon McNutt J, Costa DP, Blake S, Brashares JS, et al. 2017. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. Movement Ecology. 5(1):12. doi:10.1186/s40462-017-0104-2.

Adriaensen F, Verwimp N, Dhondt A. 1998. Between cohort variation in dispersal distance in the Eurasian Kestrel *Falco tinnunculus* as shown by ringing recoveries. Ardea. 86:147-152 https://www.semanticscholar.org/paper/Between-cohort-variation-in-dispersal-distance-in-Adriaensen-Verwimp/26fd81fd0c9123cd660fd196a61fb4c23d5895be.

Adrian C, Griffith SC, Naguib M, Schuett W. 2022. Wild zebra finches are attracted towards acoustic cues from conspecific social groups. Behav Ecol. doi:10.1093/beheco/arac013.

Aghasyan A, Avci A, Tuniyev B, Crnobrnja-Isailović J, Lymberakis P, Andrén C, Cogalniceanu D, Wilkinson J, Ananjeva NB, Üzüm N, Orlov NL, Podloucky R, Tuniyev S, Kaya U, Böhme W, Nettmann HK, Joger U, Cheylan M, Pérez Mellado V, Borczyk B, Sterijovski B, Westerström A, Schmidt B, Terbish K, Munkhbayar K, Nazarov R, Shi L, Zhao W, Bi J. 2019. *Zootoca vivipara*. The IUCN Red List of Threatened Species 2019: e.T61741A49741947. http://dx.doi.org/10.2305/IUCN.UK.2019-2.RLTS.T61741A49741947.en

Aguillon SM, Duckworth RA. 2015. Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. Behav Ecol Sociobiol. 69(4):625–633. doi:10.1007/s00265-015-1873-5.

Akesson S, Boström J, Liedvogel M, Muheim R. 2014. Animal Navigation. p. 151–178.

Albert A, Anderson JA. 1984. On the existence of maximum likelihood estimates in logistic regression models. Biometrika. 71(1):1–10. doi:10.1093/biomet/71.1.1.

Alley TR. 1982. Competition theory, evolution, and the concept of an ecological niche. Acta Biotheor. 31(3):165–179.

doi:10.1007/BF01857239.

Almagor M, Ron A, Bar-Tana J. 1981. Chemotaxis in *Tetrahymena thermophila*. Cell Motility. 1(2):261–268. doi:10.1002/cm.970010208.

And VL, Hellung-Larsen P. 1992. Chemosensory behaviour of Tetrahymena. BioEssays. 14(1):61–66. doi:10.1002/bies.950140113.

Andrade P, Pinho C, Lanuza GP i de, Afonso S, Brejcha J, Rubin C-J, Wallerman O, Pereira P, Sabatino SJ, Bellati A, et al. 2019 Feb 28. Regulatory changes in pterin and carotenoid genes underlie balanced color polymorphisms in the wall lizard. PNAS.:201820320. doi:10.1073/pnas.1820320116.

Anholt BR, Werner E, Skelly DK. 2000. Effect of Food and Predators on the Activity of Four Larval Ranid Frogs. Ecology. 81(12):3509–3521. doi:10.1890/0012-9658(2000)081[3509:EOFAPO]2.0.CO;2.

Antczak M, Ekner-Grzyb A, Majláth I, Majláthová V, Bona M, Hromada M, Tryjanowski P. 2019. Do males pay more? A male-biased predation of common lizard (*Zootoca vivipara*) by great grey shrike (*Lanius excubitor*). acta ethol. 22(3):155–162. doi:10.1007/s10211-019-00318-6.

Aragón P, López P, Martín J. 2001. Effects of Conspecific Chemical Cues on Settlement and Retreat-Site Selection of Male Lizards *Lacerta monticola*. Journal of Herpetology. 35(4):681–684. doi:10.2307/1565912.

Aragón P., Meylan S, Clobert J. 2006a. Dispersal status-dependent response to the social environment in the Common Lizard, *Lacerta vivipara*. Functional Ecology. 20(5):900–907. doi:10.1111/j.1365-2435.2006.01164.x.

Aragón P, Clobert J, Massot M. 2006b. Individual dispersal status influences space use of conspecific residents in the common lizard, *Lacerta vivipara*. Behav Ecol Sociobiol. 60(3):430–438. doi:10.1007/s00265-006-0183-3.

Aragón P, Massot M, Gasparini J, Clobert J. 2006c. Socially acquired information from chemical cues in the common lizard, *Lacerta vivipara*. Animal Behaviour. 72(5):965–974. doi:10.1016/j.anbehav.2005.11.023.

Armansin NC, Stow AJ, Cantor M, Leu ST, Klarevas-Irby JA, Chariton AA, Farine DR. 2020. Social Barriers in Ecological Landscapes: The Social Resistance Hypothesis. Trends in Ecology & Evolution. 35(2):137–148. doi:10.1016/j.tree.2019.10.001.

Armitage KB, Vuren DHV, Ozgul A, Oli MK. 2011. Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. Ecology. 92(1):218–227. doi:10.1890/10-0109.1.

Armsworth PR, Roughgarden JE. 2005. The Impact of Directed versus Random Movement on Population Dynamics and Biodiversity Patterns. The American Naturalist. 165(4):449–465. doi:10.1086/428595.

Aronsson M, Åkesson M, Low M, Persson J, Andrén H. 2020. Resource dispersion and relatedness interact to explain space use in a solitary predator. Oikos. 129(8):1174–1184. doi:10.1111/oik.07258.

Attaran A, Salahinejad A, Naderi M, Crane AL, Chivers DP, Niyogi S. 2021. Transgenerational effects of selenomethionine on behaviour, social cognition, and the expression of genes in the serotonergic pathway in zebrafish. Environmental Pollution. 286:117289. doi:10.1016/j.envpol.2021.117289.

Atton N, Hoppitt W, Webster MM, Galef BG, Laland KN. 2012. Information flow through threespine stickleback networks without social transmission. Proceedings of the Royal Society B: Biological Sciences. 279(1745):4272–4278. doi:10.1098/rspb.2012.1462.

Atton N, Galef BJ, Hoppitt W, Webster MM, Laland KN. 2014. Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. Proceedings of the Royal Society B: Biological Sciences. 281(1789):20140579. doi:10.1098/rspb.2014.0579.

Ausprey IJ, Rodewald AD. 2013. Post-Fledging Dispersal Timing and Natal Range Size of Two Songbird Species in an Urbanizing Landscape. Condor. 115(1):102–114. doi:10.1525/cond.2013.110176.

Avery RA. 1966. Food and feeding habits of the Common lizard (*Lacerta vivipara*) in the west of England. Journal of Zoology. 149(2):115–121. doi:10.1111/j.1469-7998.1966.tb03886.x.

Avery RA. 1975. Age-structure and longevity of Common lizard (*Lacerta vivipara*) populations. Journal of Zoology. 176(4):555–558. doi:10.1111/j.1469-7998.1975.tb03221.x.

B

Baines CB, McCauley SJ, Rowe L. 2014. The interactive effects of competition and predation risk on dispersal in an insect. Biology Letters. 10(6):20140287. doi:10.1098/rsbl.2014.0287.

Baines CB, Ferzoco IMC, McCauley SJ. 2019. Phenotype-by-environment interactions influence dispersal. Journal of Animal Ecology. 88(8):1263–1274. doi:10.1111/1365-2656.13008.

Baines CB, Diab S, McCauley SJ. 2020. Parasitism Risk and Infection Alter Host Dispersal. The American Naturalist. 196(2):119–131. doi:10.1086/709163.

Bairos-Novak KR, Mitchell MD, Crane AL, Chivers DP, Ferrari MCO. 2017. Trust thy neighbour in times of trouble: background risk alters how tadpoles release and respond to disturbance cues. Proceedings of the Royal

Society B: Biological Sciences. doi:10.1098/rspb.2017.1465.

Bairos-Novak KR, Crane AL, Chivers DP, Ferrari MCO. 2019. Better the devil you know? How familiarity and kinship affect prey responses to disturbance cues. Behav Ecol. 30(2):446–454. doi:10.1093/beheco/ary184.

Bairos-Novak KR, Ferrari MCO, Chivers DP. 2019. A novel alarm signal in aquatic prey: Familiar minnows coordinate group defences against predators through chemical disturbance cues. Journal of Animal Ecology. 88(9):1281–1290. doi:10.1111/1365-2656.12986.

Baker MB, Rao S. 2004. Incremental Costs and Benefits Shape Natal Dispersal: Theory and Example with *Hemilepistus Reaumuri*. Ecology. 85(4):1039–1051. doi:10.1890/02-0507.

Barnes MJ, Beale CM. 2021. Public information affects foraging patch use by mixed-species flocks of tits in high-risk, open environments. Ibis. 163(4):1443–1447. doi:10.1111/ibi.12952.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software. 67:1–48. doi:10.18637/jss.v067.i01.

Battesti M, Pasquaretta C, Moreno C, Teseo S, Joly D, Klensch E, Petit O, Sueur C, Mery F. 2015 Feb 22. Ecology of information: social transmission dynamics within groups of non-social insects. Proceedings of the Royal Society B: Biological Sciences. doi:10.1098/rspb.2014.2480.

Baude M, Danchin É, Mugabo M, Dajoz I. 2011. Conspecifics as informers and competitors: an experimental study in foraging bumble-bees. Proceedings of the Royal Society B: Biological Sciences. 278(1719):2806–2813. doi:10.1098/rspb.2010.2659.

Baudouin A, Gatti S, Levréro F, Genton C, Cristescu RH, Billy V, Motsch P, Pierre J-S, Le Gouar P, Ménard N. 2019. Disease avoidance, and breeding group age and size condition the dispersal patterns of western lowland gorilla females. Ecology. 100(9):e02786. doi:10.1002/ecy.2786.

Bauer S, McNamara JM, Barta Z. 2020. Environmental variability, reliability of information and the timing of migration. Proceedings of the Royal Society B: Biological Sciences. 287(1926):20200622. doi:10.1098/rspb.2020.0622.

Bauwens D, Thoen C. 1981. Escape Tactics and Vulnerability to Predation Associated with Reproduction in the Lizard *Lacerta vivipara*. Journal of Animal Ecology. 50(3):733–743. doi:10.2307/4133.

Bauwens D, Verheyen R. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. Ecography. 10:120–127. doi:10.1111/j.1600-0587.1987.tb00748.x.

Beason RC. 2005. Mechanisms of Magnetic Orientation in Birds. Integrative and Comparative Biology. 45(3):565–573. doi:10.1093/icb/45.3.565.

Behr DM, McNutt JW, Ozgul A, Cozzi G. 2020. When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore. Journal of Animal Ecology. 89(10):2356–2366. doi:10.1111/1365-2656.13300.

Behr O, von Helversen O. 2004. Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). Behav Ecol Sociobiol. 56(2):106–115. doi:10.1007/s00265-004-0768-7.

Bell WJ. 1990. Orientation cues: information for searching. In: Bell WJ, editor. Searching Behaviour: The behavioural ecology of finding resources. Dordrecht: Springer Netherlands. p. 27–35. https://doi.org/10.1007/978-94-011-3098-1_2.

Belliure J, Meylan S, Clobert J. 2004. Prenatal and postnatal effects of corticosterone on behavior in juveniles of the common lizard, *Lacerta vivipara*. Journal of Experimental Zoology Part A: Comparative Experimental Biology. 301A(5):401–410. doi:10.1002/jez.a.20066.

Beltman JB, Haccou P. 2005. Speciation through the learning of habitat features. Theoretical Population Biology. 67(3):189–202. doi:10.1016/j.tpb.2005.01.001.

Benard MF, McCauley SJ. 2008. Integrating across Life-History Stages: Consequences of Natal Habitat Effects on Dispersal. The American Naturalist. 171(5):553–567. doi:10.1086/587072.

Ben-Shachar MS, Lüdecke D, Makowski D. 2020. effectsize: Estimation of Effect Size Indices and Standardized Parameters. Journal of Open Source Software. 5(56):2815. doi:10.21105/joss.02815.

Ben-Shaul Y. 2015. Extracting Social Information from Chemosensory Cues: Consideration of Several Scenarios and Their Functional Implications. Frontiers in Neuroscience. 9. doi:10.3389/fnins.2015.00439

van Bergen Y, Coolen I, Laland KN. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. Proceedings of the Royal Society of London Series B: Biological Sciences. 271(1542):957–962. doi:10.1098/rspb.2004.2684.

Bernardo J. 1996. Maternal Effects in Animal Ecology. American Zoologist. 36(2):83–105. doi:10.1093/icb/36.2.83.

Bernays EA, Wcislo WT. 1994. Sensory Capabilities, Information Processing, and Resource Specialization. The Quarterly Review of Biology. 69(2):187–204. doi:10.1086/418539.

Berner D, Thibert-Plante X. 2015. How mechanisms of habitat preference evolve and promote divergence with gene flow. Journal of Evolutionary Biology. 28(9):1641–1655. doi:10.1111/jeb.12683.

Bestion E, Teyssier A, Aubret F, Clobert J, Cote J. 2014. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. Proceedings of the Royal Society of London B: Biological Sciences. 281(1792):20140701. doi:10.1098/rspb.2014.0701.

Bestion E, Clobert J, Cote J. 2015. Dispersal response to climate change: scaling down to intraspecific variation. Ecology Letters. 18(11):1226–1233. doi:10.1111/ele.12502.

Bhatt D, Kumar A, Singh Y, Payne RB. 2000. Territorial songs and calls of the oriental magpie robin Copsychus saularis. Current Science. 78(6):722–728.

Biernaskie JM, Perry JC, Grafen A. 2018. A general model of biological signals, from cues to handicaps. Evolution Letters. 2(3):201–209. doi:10.1002/evl3.57.

Biewener A, Patek S. 2018. Animal Locomotion. Oxford University Press.

Bitume EV, Bonte D, Ronce O, Bach F, Flaven E, Olivieri I, Nieberding CM. 2013. Density and genetic relatedness increase dispersal distance in a subsocial organism. Ecology Letters. 16(4):430–437. doi:10.1111/ele.12057.

Bivand RS, Wong DWS. 2018. Comparing implementations of global and local indicators of spatial association. TEST. 27(3):716–748. doi:10.1007/s11749-018-0599-x.

Blaustein AR. 1988. Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. Behav Genet. 18(4):449–464. doi:10.1007/BF01065514.

Bleu J, Massot M, Haussy C, Meylan S. 2012. Experimental litter size reduction reveals costs of gestation and delayed effects on offspring in a viviparous lizard. Proceedings of the Royal Society B: Biological Sciences. 279(1728):489–498. doi:10.1098/rspb.2011.0966.

Blount JD, McGraw KJ. 2008. Signal Functions of Carotenoid Colouration. In: Britton G, Liaaen-Jensen S, Pfander H, editors. Carotenoids: Volume 4: Natural Functions. Basel: Birkhäuser. p. 213–236. https://doi.org/10.1007/978-3-7643-7499-0_11.

Bocedi G, Heinonen J, Travis JMJ. 2012. Uncertainty and the Role of Information Acquisition in the Evolution of Context-Dependent Emigration. The American Naturalist. 179(5):606–620. doi:10.1086/665004.

Bohenek JR, Resetarits WJ. 2018. Are direct density cues, not resource competition, driving life history trajectories in a polyphenic salamander? Evol Ecol. 32(4):335–357. doi:10.1007/s10682-018-9941-8.

Bollinger EK, Harper SJ, Barrett GW. 1993. Inbreeding Avoidance Increases Dispersal Movements of the Meadow Vole. Ecology. 74(4):1153–1156. doi:10.2307/1940485.

Bolnick DI. 2001. Intraspecific competition favours niche width expansion in *Drosophila melanogaster*. Nature. 410(6827):463–466. doi:10.1038/35068555.

Bolnick DI, Nosil P. 2007. Natural Selection in Populations Subject to a Migration Load. Evolution. 61(9):2229–2243. doi:10.1111/j.1558-5646.2007.00179.x.

Bond ML, Wolff JO. 1999. Does Access to Females or Competition among Males Limit Male Home-Range Size in a Promiscuous Rodent? J Mammal. 80(4):1243–1250. doi:10.2307/1383174.

Bonte D, Dyck HV, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M, et al. 2012. Costs of dispersal. Biological Reviews. 87(2):290–312. doi:10.1111/j.1469-185X.2011.00201.x.

Boogert NJ, Zimmer C, Spencer KA. 2013 Apr 23. Pre- and post-natal stress have opposing effects on social information use. Biology Letters. doi:10.1098/rsbl.2012.1088.

Borg JM, Channon A. 2021. The Effect of Social Information Use Without Learning on the Evolution of Social Behavior. Artif Life. 26(4):431–454. doi:10.1162/artl_a_00328.

Börger L, Franconi N, Ferretti F, Meschi F, De Michele G, Gantz A, Coulson T. 2006 Jul 17. An Integrated Approach to Identify Spatiotemporal and Individual-Level Determinants of Animal Home Range Size. The American Naturalist. doi:10.1086/507883.

Boudjemadi K, Lecomte J, Clobert J. 1999. Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. Journal of Animal Ecology. 68(6):1207–1224. doi:10.1046/j.1365-2656.1999.00363.x.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews. 80(2):205–225. doi:10.1017/S1464793104006645.

Bowler DE, Benton TG. 2009. Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. Journal of Animal Ecology. 78(6):1234–1241. doi:10.1111/j.1365-2656.2009.01580.x.

Boyd C, Grünbaum D, Hunt GL Jr, Punt AE, Weimerskirch H, Bertrand S. 2016. Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. Behavioral Ecology. 27(4):1223–1234. doi:10.1093/beheco/arw039.

Brandl HB, Griffith SC, Schuett W. 2018. Wild zebra finches do not use social information from conspecific reproductive success for nest site choice and clutch size decisions. Behav Ecol Sociobiol. 72(7):114. doi:10.1007/s00265-018-2533-3.

Breithaupt T, Thiel M. 2010. Chemical Communication in Crustaceans. Springer Science & Business Media.

Brena PF, Mourier J, Planes S, Clua EE. 2018. Concede or clash? Solitary sharks competing for food assess rivals to decide. Proceedings of the Royal Society B: Biological Sciences. 285(1875):20180006. doi:10.1098/rspb.2018.0006.

Bretman A, Westmancoat JD, Gage MJG, Chapman T. 2011. Males Use Multiple, Redundant Cues to Detect Mating Rivals. Current Biology. 21(7):617–622. doi:10.1016/j.cub.2011.03.008.

Bro-Jørgensen J. 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. Trends in Ecology & Evolution. 25(5):292–300. doi:10.1016/j.tree.2009.11.003.

Brophy T, Luong LT. 2022. The influence of infection status and parasitism risk on host dispersal and susceptibility to infection in *Drosophila nigrospiracula*. Parasitology. 149(5):587–592. doi:10.1017/S0031182021001979.

Brown GE, Demers EEM, Goldman JA, Singh A, Chivers DP, Ferrari MCO. 2020. Unpredictable risk enhances induced neophobia in northern red-bellied dace. Animal Behaviour. 168:121–127. doi:10.1016/j.anbehav.2020.08.012.

Brown GE, Crane AL, Demers EE, Chivers DP, Ferrari MCO. 2022. Uncertain foraging opportunities and predation risk exert additive effects on induced neophobia in cichlids. Animal Behaviour. 186:21–28. doi:10.1016/j.anbehav.2022.01.

Bull CM, Cooper SJB. 1999. Relatedness and avoidance of inbreeding in the lizard, *Tiliqua rugosa*. Behav Ecol Sociobiol. 46(6):367–372. doi:10.1007/s002650050631.

Burnham KP, Anderson DR. 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research. 33(2):261–304. doi:10.1177/0049124104268644.

Burton OJ, Phillips BL, Travis JMJ. 2010. Trade-offs and the evolution of life-histories during range expansion. Ecology Letters. 13(10):1210–1220. doi:10.1111/j.1461-0248.2010.01505.x.

Buxton VL, Enos JK, Sperry JH, Ward MP. 2020. A review of conspecific attraction for habitat selection across taxa. Ecology and Evolution. 10(23):12690–12699. doi:10.1002/ece3.6922.

Byström P, Andersson J. 2005. Size-dependent foraging capacities and intercohort competition in an ontogenetic omnivore (Arctic char). Oikos. 110(3):523–536. doi:10.1111/j.0030-1299.2005.13543.x.

C

Calenge C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling. 197(3):516–519. doi:10.1016/j.ecolmodel.2006.03.017.

Calsbeek R, Sinervo B. 2002. An experimental test of the ideal despotic distribution. Journal of Animal Ecology. 71(3):513–523. doi:10.1046/j.1365-2656.2002.00619.x.

Camacho C, Canal D, Potti J. 2015. Testing the matching habitat choice hypothesis in nature: phenotype-environment correlation and fitness in a songbird population. Evol Ecol. 29(6):873–886. doi:10.1007/s10682-015-9793-4.

Camacho C, Canal D, Potti J. 2016. Natal habitat imprinting counteracts the diversifying effects of phenotype-dependent dispersal in a spatially structured population. BMC Evol Biol. 16(1):158. doi:10.1186/s12862-016-0724-y.

Camacho C, Martínez-Padilla J, Canal D, Potti J. 2019. Long-term dynamics of phenotype-dependent dispersal within a wild bird population. Behav Ecol. 30(2):548–556. doi:10.1093/beheco/ary195.

Campos SM, Strauss C, Martins EP. 2017. In Space and Time: Territorial Animals are Attracted to Conspecific Chemical Cues. Ethology. 123(2):136–144. doi:10.1111/eth.12582.

Campos SM, Pruett JA, Soini HA, Zúñiga-Vega JJ, Goldberg JK, Vital-García C, Hews DK, Novotny MV, Martins EP. 2020. Volatile fatty acid and aldehyde abundances evolve with behavior and habitat temperature in *Sceloporus lizards*. Behav Ecol. 31(4):978–991. doi:10.1093/beheco/araa044.

Campos SM, Belkasim SS. 2021. Chemical Communication in Lizards and a Potential Role for Vasotocin in Modulating Social Interactions. Integr Comp Biol. 61(1):205–220. doi:10.1093/icb/icab044.

Candolin U. 2003. The use of multiple cues in mate choice. Biological Reviews. 78(4):575–595. doi:10.1017/S1464793103006158.

Canteloup C, Hoppitt W, van de Waal E. 2020. Wild primates copy higher-ranked individuals in a social transmission experiment. Nat Commun. 11(1):459. doi:10.1038/s41467-019-14209-8.

Caro TM. 1995. Pursuit-deterrence revisited. Trends in Ecology & Evolution. 10(12):500–503. doi:10.1016/S0169-

5347(00)89207-1.

Caro SP, Balthazart J, Bonadonna F. 2015. The perfume of reproduction in birds: Chemosignaling in avian social life. Hormones and Behavior. 68:25–42. doi:10.1016/j.yhbeh.2014.06.001.

Carrascal LM, Senar JC, Mozetich I, Uribe F, Domenech J. 1998. Interactions among Environmental Stress, Body Condition, Nutritional Status, and Dominance in Great Tits. The Auk. 115(3):727–738. doi:10.2307/4089420.

Carter AJ, Lee AEG, Marshall HH, Ticó MT, Cowlishaw G. 2015. Phenotypic assortment in wild primate networks: implications for the dissemination of information. Royal Society Open Science. 2(5):140444. doi:10.1098/rsos.140444.

Carter AJ, Torrents Ticó M, Cowlishaw G. 2016. Sequential phenotypic constraints on social information use in wild baboons. Berman C, editor. eLife. 5:e13125. doi:10.7554/eLife.13125.

Cauchoix M, Chaine AS, Barragan-Jason G. 2020. Cognition in Context: Plasticity in Cognitive Performance in Response to Ongoing Environmental Variables. Frontiers in Ecology and Evolution. 8:106. doi:10.3389/fevo.2020.00106.

Cayuela H, Grolet O, Joly P. 2018. Context-dependent dispersal, public information, and heterospecific attraction in newts. Oecologia. 188(4):1069–1080. doi:10.1007/s00442-018-4267-3.

Cayuela H, Valenzuela-Sánchez A, Teulier L, Martínez-Solano Í, Léna J-P, Merilä J, Muths E, Shine R, Quay L, Denoël M, et al. 2020. Determinants and Consequences of Dispersal in Vertebrates with Complex Life Cycles: A Review of Pond-Breeding Amphibians. The Quarterly Review of Biology. 95(1):1–36. doi:10.1086/707862.

Chaine AS, Schtickzelle N, Polard T, Huet M, Clobert J. 2010. Kin-Based Recognition and Social Aggregation in a Ciliate. Evolution. 64(5):1290–1300. doi:10.1111/j.1558-5646.2009.00902.x.

Chaine AS, Legendre S, Clobert J. 2013. The co-evolution of multiply-informed dispersal: information transfer across landscapes from neighbors and immigrants. PeerJ. 1:e44. doi:10.7717/peerj.44.

Chamaillé-Jammes S, Massot M, Aragón P, Clobert J. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. Global Change Biology. 12(2):392–402. doi:10.1111/j.1365-2486.2005.01088.x.

Chaput-Bardy A, Grégoire A, Baguette M, Pagano A, Secondi J. 2010. Condition and Phenotype-Dependent Dispersal in a Damselfly, *Calopteryx splendens*. PLOS ONE. 5(5):e10694. doi:10.1371/journal.pone.0010694.

Choleris E, Clipperton-Allen AE, Phan A, Kavaliers M. 2009. Neuroendocrinology of social information processing in rats and mice. Frontiers in Neuroendocrinology. 30(4):442–459. doi:10.1016/j.yfrne.2009.05.003.

Chouinard-Thuly L, Reader SM. 2019. Population differences in how wild Trinidadian guppies use social information and socially learn. :786772. doi:10.1101/786772.

Civantos E. 2011 Feb 15. Home-range ecology, aggressive behaviour, and survival in juvenile lizards, *Psammodromus algirus*. Canadian Journal of Zoology. doi:10.1139/z00-083.

Claramunt S. 2021. Flight efficiency explains differences in natal dispersal distances in birds. Ecology. 102(9):e03442. doi:10.1002/ecy.3442.

Cliff HB, Jones ME, Johnson CN, Pech RP, Biemans BT, Barmuta LA, Norbury GL. 2022. Rapid gain and loss of predator recognition by an evolutionarily naïve lizard. Austral Ecology. doi:10.1111/aec.13148.

Clobert J, Massot M, Lecomte J, Sorci G, Fraipont M de, Barbault R. 1994. Chapter 9. Determinants of Dispersal Behavior: The Common Lizard as a Case Study. Princeton University

Clobert J, Ims RA, Rousset F. 2004. 13 - Causes, Mechanisms and Consequences of Dispersal. In: Hanski I, Gaggiotti OE, editors. Ecology, Genetics and Evolution of Metapopulations. Burlington: Academic Press. p. 307–335.

Clobert J, Galliard J-FL, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters. 12(3):197–209. doi:10.1111/j.1461-0248.2008.01267.x.

Clobert J, Massot M, Le Galliard J-F. 2012. Multi-determinism in natal dispersal: the common lizard as a model system. p. 29–40.

Cohen J. 2013. Statistical Power Analysis for the Behavioral Sciences. Academic Press.

Coolen I, Bergen YV, Day RL, Laland KN. 2003. Species difference in adaptive use of public information in sticklebacks. Proceedings of the Royal Society of London Series B: Biological Sciences. 270(1531):2413–2419. doi:10.1098/rspb.2003.2525.

Cooper WE. 1994. Chemical discrimination by tongue-flicking in lizards: A review with hypotheses on its origin and its ecological and phylogenetic relationships. J Chem Ecol. 20(2):439–487. doi:10.1007/BF02064449.

Costanzo JP, Grenot C, Lee RE. 1995. Supercooling, ice inoculation and freeze tolerance in the European common lizard, *Lacerta vivipara*. J Comp Physiol B. 165(3):238–244. doi:10.1007/BF00260815.

Côte J, Boniface A, Blanchet S, Hendry AP, Gasparini J, Jacquin L. 2018. Melanin-based coloration and host–parasite interactions under global change. Proceedings of the Royal Society B: Biological Sciences. 285(1879):20180285. doi:10.1098/rspb.2018.0285.

Cote J, Clobert J. 2007a. Social information and emigration: lessons from immigrants. Ecology Letters. 10(5):411–417. doi:10.1111/j.1461-0248.2007.01032.x.

Cote J, Clobert J. 2007b. Social personalities influence natal dispersal in a lizard. Proceedings of the Royal Society of London B: Biological Sciences. 274(1608):383–390. doi:10.1098/rspb.2006.3734.

Cote J, Clobert J, Fitze PS. 2007. Mother–offspring competition promotes colonization success. PNAS. 104(23):9703–9708. doi:10.1073/pnas.0703601104.

Cote J, Boudsocq S, Clobert J. 2008a. Density, social information, and space use in the common lizard (*Lacerta vivipara*). Behav Ecol. 19(1):163–168. doi:10.1093/beheco/arm119.

Cote J, Dreiss A, Clobert J. 2008b. Social personality trait and fitness. Proceedings of the Royal Society of London B: Biological Sciences. 275(1653):2851–2858. doi:10.1098/rspb.2008.0783.

Cote J., Galliard J-FL, Rossi J-M, Fitze PS. 2008c. Environmentally induced changes in carotenoid-based coloration of female lizards: a comment on Vercken et al. Journal of Evolutionary Biology. 21(4):1165–1172. doi:10.1111/j.1420-9101.2008.01534.x.

Cote J, Clobert J. 2010. Risky dispersal: avoiding kin competition despite uncertainty. Ecology. 91(5):1485–1493. doi:10.1890/09-0387.1.

Cote J, Clobert J, Brodin T, Fogarty S, Sih A. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 365(1560):4065–4076. doi:10.1098/rstb.2010.0176.

Cote J, Clobert J. 2012. Dispersal syndromes in the common lizard: personality traits, information use, and context-dependent dispersal decisions. In: Dispersal. Ecology and Evolution. Oxford University Press. p. 152–160.

Cote J, Bestion E, Jacob S, Travis J, Legrand D, Baguette M. 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. Ecography. 40(1):56–73. doi:10.1111/ecog.02538.

Cotto O, Massot M, Ronce O, Clobert J. 2015. Dispersal as a source of variation in age-specific reproductive strategies in a wild population of lizards. Proceedings of the Royal Society B: Biological Sciences. 282(1820):20151741. doi:10.1098/rspb.2015.1741.

Coulon A, Fitzpatrick JW, Bowman R, Lovette IJ. 2010. Effects of Habitat Fragmentation on Effective Dispersal of Florida Scrub-Jays. Conservation Biology.
24(4):1080–1088. doi:10.1111/j.1523-1739.2009.01438.x.

Cozzi G, Maag N, Börger L, Clutton-Brock TH, Ozgul A. 2018. Socially informed dispersal in a territorial cooperative breeder. Journal of Animal Ecology. 87(3):838–849. doi:10.1111/1365-2656.12795.

Crane A, Ferrari MCO. 2013. Social learning of predation risk: A review and prospectus. In: Social Learning Theory: Phylogenetic Considerations across Animal, Plant, and Microbial Taxa. p. 53–82.

Crane AL, Ferrari MCO. 2017. Evidence for risk extrapolation in decision making by tadpoles. Sci Rep. 7(1):43255. doi:10.1038/srep43255.

Crane AL, Bairos-Novak KR, Sacco LH, Ferrari MCO. 2018. The socially mediated recovery of a fearful fish paired with periodically replaced calm models. Proceedings of the Royal Society B: Biological Sciences. 285(1888):20180739. doi:10.1098/rspb.2018.0739.

Crane AL, Meuthen D, Thapa H, Ferrari MCO, Brown GE. 2021. Early-life and parental predation risk shape fear acquisition in adult minnows. Anim Cogn. 24(3):471–481. doi:10.1007/s10071-020-01439-3.

Crespo-Miguel R, Jarillo J, Cao-García FJ. 2022. Dispersal-induced resilience to stochastic environmental fluctuations in populations with Allee effect. Phys Rev E. 105(1):014413. doi:10.1103/PhysRevE.105.014413.

Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R. 2009. Behavioural trait assortment in a social network: patterns and implications. Behav Ecol Sociobiol. 63(10):1495–1503. doi:10.1007/s00265-009-0802-x.

Cronin AL. 2013. Conditional Use of Social and Private Information Guides House-Hunting Ants. PLOS ONE. 8(5):e64668. doi:10.1371/journal.pone.0064668.

Crossley MS, Lagos-Kutz D, Davis TS, Eigenbrode SD, Hartman GL, Voegtlin DJ, Snyder WE. 2021. Precipitation change accentuates or reverses temperature effects on aphid dispersal. Ecological Applications. e2593. doi:10.1002/eap.2593.

Cullum JP, Nixon LJ, Morrison WR, Raupp MJ, Shrewsbury PM, Venugopal PD, Martinson H, Bergh JC, Leskey TC. 2020. Influence of Landscape Factors and Abiotic Conditions on Dispersal Behavior and Overwintering Site Selection by *Halyomorpha halys* (Hemiptera: Pentatomidae). J Econ Entomol. 113(4):2016–2021. doi:10.1093/jee/toaa077.

Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME, Hill GE, Jablonski NG, Jiggins CD, Kelber A, et al. 2017. The biology of color. Science. 357(6350):eaan0221. doi:10.1126/science.aan0221.

Czaczkes TJ, Grüter C, Jones SM, Ratnieks FLW. 2011. Synergy between social and private information increases foraging efficiency in ants. Biol Lett. 7(4):521–524. doi:10.1098/rsbl.2011.0067.

D

D'adamo P, Lozada M, Corley J. 2003. Conspecifics Enhance Attraction of *Vespula germanica* (Hymenoptera: Vespidae) Foragers to Food Baits. Ann Entomol Soc Am. 96(5):685–688.
doi:10.1603/0013-8746(2003)096[0685:CEAOVG]2.0.CO;2.

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. Trends in Ecology & Evolution. 20(4):187–193. doi:10.1016/j.tree.2005.01.010.

Damas-Moreira I, Oliveira D, Santos JL, Riley JL, Harris DJ, Whiting MJ. 2018. Learning from others: an invasive lizard uses social information from both conspecifics and heterospecifics. Biology Letters. 14(10):20180532. doi:10.1098/rsbl.2018.0532.

Danchin E, Boulinier T, Massot M. 1998. Conspecific Reproductive Success and Breeding Habitat Selection: Implications for the Study of Coloniality. Ecology. 79(7):2415–2428.
doi:10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2.

Danchin É, Giraldeau L-A, Valone TJ, Wagner RH. 2004. Public Information: From Nosy Neighbors to Cultural Evolution. Science. 305(5683):487–491. doi:10.1126/science.1098254.

Danielson BJ, Gaines MS. 1987. The Influences of Conspecific and Heterospecific Residents on Colonization. Ecology. 68(6):1778–1784. doi:10.2307/1939869.

Davey AJH, Hawkins SJ, Turner GF, Doncaster CP. 2005. Size-dependent microhabitat use and intraspecific competition in *Cottus gobio*. Journal of Fish Biology. 67(2):428–443. doi:10.1111/j.0022-1112.2005.00736.x.

David Morgan E. 2009. Trail pheromones of ants. Physiological Entomology. 34(1):1–17. doi:10.1111/j.1365-3032.2008.00658.x.

Davies NB, Madden JR, Butchart SHM. 2004. Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. Proceedings of the Royal Society of London Series B: Biological Sciences. 271(1554):2297–2304. doi:10.1098/rspb.2004.2835.

Davis JM. 2008. Patterns of Variation in the Influence of Natal Experience on Habitat Choice. The Quarterly Review of Biology. 83(4):363–380. doi:10.1086/592851.

Davis JM, Stamps JA. 2004. The effect of natal experience on habitat preferences. Trends in Ecology & Evolution. 19(8):411–416. doi:10.1016/j.tree.2004.04.006.

Dawson Pell FSE, Senar JC, Franks DW, Hatchwell BJ. 2021. Fine-scale genetic structure reflects limited and coordinated dispersal in the colonial monk parakeet, *Myiopsitta monachus*. Molecular Ecology. 30(6):1531–1544. doi:10.1111/mec.15818.

Day LB, Ismail N, Wilczynski W. 2003. Use of Position and Feature Cues in Discrimination Learning by the Whiptail Lizard (*Cnemidophorus inornatus*). Journal of Comparative Psychology. 117(4):440–448. doi:10.1037/0735-7036.117.4.440.

De Fraipont M, Clobert J, John H, Alder -, Meylan S. 2000. Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. Journal of Animal Ecology. 69(3):404–413. doi:10.1046/j.1365-2656.2000.00405.x.

De Marco R, Menzel R. 2005. Encoding spatial information in the waggle dance. J Exp Biol. 208(20):3885–3894. doi:10.1242/jeb.01832.

De Meester N, Bonte D. 2010. Information use and density-dependent emigration in an agrobiont spider. Behav Ecol. 21(5):992–998. doi:10.1093/beheco/arq088.

De Meester N, Derycke S, Rigaux A, Moens T. 2015. Active dispersal is differentially affected by inter- and intraspecific competition in closely related nematode species. Oikos. 124(5):561–570. doi:10.1111/oik.01779.

Delgado M del M, Ratikainen II, Kokko H. 2011. Inertia: the discrepancy between individual and common good in dispersal and prospecting behaviour. Biological Reviews. 86(3):717–732. doi:10.1111/j.1469-185X.2010.00167.x.

Delgado MM, Bartoń KA, Bonte D, Travis JMJ. 2014. Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. Proceedings of the Royal Society B: Biological Sciences. 281(1778):20132851. doi:10.1098/rspb.2013.2851.

DeLong JP, Vasseur DA. 2012. Size-density scaling in protists and the links between consumer–resource interaction parameters. Journal of Animal Ecology. 81(6):1193–1201. doi:10.1111/j.1365-2656.2012.02013.x.

Denno RF, Roderick GK. 1992. Density-Related Dispersal in Planthoppers: Effects of Interspecific Crowding. Ecology. 73(4):1323–1334. doi:10.2307/1940679.

Denton RD, Greenwald KR, Gibbs HL. 2017. Locomotor endurance predicts differences in realized dispersal between sympatric sexual and unisexual salamanders. Functional Ecology. 31(4):915–926. doi:10.1111/1365-2435.12813.

D'Ettorre P, Moore A. 2008. Chemical communication and the coordination of social interactions in insects. In: Sociobiology of Communication. p. 81–96.

Deygout C, Gault A, Duriez O, Sarrazin F, Bessa-Gomes C. 2010. Impact of food predictability on social facilitation by foraging scavengers. Behavioral Ecology. 21(6):1131–1139. doi:10.1093/beheco/arq120.

Dobson FS, Jones WT. 1985. Multiple Causes of Dispersal. The American Naturalist. 126(6):855–858.

Doerder FP, Brunk C. 2012. Natural populations and inbred strains of Tetrahymena. Methods Cell Biol. 109:277–300. doi:10.1016/B978-0-12-385967-9.00009-8.

Doligez B, Danchin E, Clobert J, Gustafsson L. 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. Journal of Animal Ecology. 68(6):1193–1206. doi:10.1046/j.1365-2656.1999.00362.x.

Doligez B, Danchin E, Clobert J. 2002. Public Information and Breeding Habitat Selection in a Wild Bird Population. Science. 297(5584):1168–1170. doi:10.1126/science.1072838.

Doligez B, Cadet C, Danchin E, Boulinier T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Animal Behaviour. 66(5):973–988. doi:10.1006/anbe.2002.2270.

Doligez B, Pärt T, Danchin E, Clobert J, Gustafsson L. 2004. Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. Journal of Animal Ecology. 73(1):75–87. doi:10.1111/j.1365-2656.2004.00782.x.

Dore AA, McDowall L, Rouse J, Bretman A, Gage MJG, Chapman T. 2018. The role of complex cues in social and reproductive plasticity. Behav Ecol Sociobiol. 72(8):124. doi:10.1007/s00265-018-2539-x.

Doughty P, Sinervo B, Burghardt GM. 1994. Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. Animal Behaviour. 47(1):227–229. doi:10.1006/anbe.1994.1029.

Dreiss AN, Cote J, Richard M, Federici P, Clobert J. 2010. Age- and sex-specific response to population density and sex ratio. Behav Ecol. 21(2):356–364. doi:10.1093/beheco/arp198.

Drullion D, Dubois F. 2008. Mate-choice copying by female zebra finches, *Taeniopygia guttata*: what happens when model females provide inconsistent information? Behav Ecol Sociobiol. 63(2):269–276. doi:10.1007/s00265-008-0658-5.

Dubois F, Drullion D, Witte K. 2012. Social information use may lead to maladaptive decisions: a game theoretic model. Behav Ecol. 23(1):225–231. doi:10.1093/beheco/arr179.

Duboscq J, Romano V, MacIntosh A, Sueur C. 2016. Social Information Transmission in Animals: Lessons from Studies of Diffusion. Front Psychol. 7. doi:10.3389/fpsyg.2016.01147.

Dudzinski KM, Thomas JA, Gregg JD. 2009. Communication in Marine Mammals. In: Perrin WF, Würsig B, Thewissen JGM, editors. Encyclopedia of Marine Mammals (Second Edition). London: Academic Press. p. 260–269.

Duffy GA, Pike TW, Laland KN. 2009. Size-dependent directed social learning in nine-spined sticklebacks. Animal Behaviour. 78(2):371–375. doi:10.1016/j.anbehav.2009.05.015.

Dukas R, Ratcliffe JM. 2009. Cognitive Ecology II. University of Chicago Press.

Duputié A, Massol F. 2013 Dec 6. An empiricist's guide to theoretical predictions on the evolution of dispersal. Interface Focus.

E

Ebenman B. 1987. Niche differences between age classes and intraspecific competition in age-structured populations. Journal of Theoretical Biology. 124(1):25–33. doi:10.1016/S0022-5193(87)80249-7.

Edelaar P, Siepielski AM, Clobert J. 2008. Matching Habitat Choice Causes Directed Gene Flow: A Neglected Dimension in Evolution and Ecology. Evolution. 62(10):2462–2472. doi:10.1111/j.1558-5646.2008.00459.x.

Edelaar P, Bolnick DI. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. Trends in Ecology & Evolution. 27(12):659–665. doi:10.1016/j.tree.2012.07.009.

Edelaar P, Jovani R, Gomez-Mestre I. 2017. Should I Change or Should I Go? Phenotypic Plasticity and Matching Habitat Choice in the Adaptation to Environmental Heterogeneity. The American Naturalist. 190(4):506–520. doi:10.1086/693345.

Edelaar P, Bolnick DI. 2019. Appreciating the Multiple Processes Increasing Individual or Population Fitness.

Trends in Ecology & Evolution. 0(0). doi:10.1016/j.tree.2019.02.001.

Eisenbach M, Tamada A, Omann GM, Segall JE, Firtel RA, Meili R, Gutnick D, Varon M, Lengeler JW, Murakami F. 2004. Chemotaxis. World Scientific Publishing Company.

Ellsworth EA, Belthoff JR. 1999. Effects of social status on the dispersal behaviour of juvenile western screech-owls. Animal Behaviour. 57(4):883–892. doi:10.1006/anbe.1998.1050.

Endriss SB, Vahsen ML, Bitume EV, Monroe JG, Turner KG, Norton AP, Hufbauer RA. 2018. The importance of growing up: juvenile environment influences dispersal of individuals and their neighbours. Ecology Letters. 0(0). doi:10.1111/ele.13166.

Erm P, Hall MD, Phillips BL. 2019. Anywhere but here: local conditions motivate dispersal in Daphnia. PeerJ. 7:e6599. doi:10.7717/peerj.6599.

Erovenko IV. 2019. The Evolution of Cooperation in One-Dimensional Mobile Populations with Deterministic Dispersal. Games. 10(1):2. doi:10.3390/g10010002.

Erovenko IV, Bauer J, Broom M, Pattni K, Rychtář J. 2019. The effect of network topology on optimal exploration strategies and the evolution of cooperation in a mobile population. Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences. 475(2230):20190399. doi:10.1098/rspa.2019.0399.

Erulkar SD. 1972. Comparative aspects of spatial localization of sound. Physiological Reviews. 52(1):237–360. doi:10.1152/physrev.1972.52.1.237.

Escobar CA, Labra A, Niemeyer HM. 2001. Chemical Composition of Precloacal Secretions of Liolaemus Lizards. J Chem Ecol. 27(8):1677–1690. doi:10.1023/A:1010470611061.

Escobar CM, Escobar CA, Labra A, Niemeyer HM. 2003. Chemical Composition of Precloacal Secretions of Two *Liolaemus fabiani* Populations: Are They Different? J Chem Ecol. 29(3):629–638. doi:10.1023/A:1022858919037.

Evans BS, Kilpatrick AM, Hurlbert AH, Marra PP. 2017. Dispersal in the Urban Matrix: Assessing the Influence of Landscape Permeability on the Settlement Patterns of Breeding Songbirds. Frontiers in Ecology and Evolution. 5. doi:10.3389/fevo.2017.00063

Ewing AW, Bennet-Clark HC. 1968. The Courtship Songs of Drosophila. Behaviour. 31(3–4):288–301. doi:10.1163/156853968X00298.

Expósito-Granados M, Parejo D, Martínez JG, Precioso M, Molina-Morales M, Avilés JM. 2017. Host nest site choice depends on risk of cuckoo parasitism in magpie hosts. Behav Ecol. 28(6):1492–1497. doi:10.1093/beheco/arx113.

F

Fagan WF, Lewis MA, Auger-Méthé M, Avgar T, Benhamou S, Breed G, LaDage L, Schlägel UE, Tang W, Papastamatiou YP, et al. 2013. Spatial memory and animal movement. Ecology Letters. 16(10):1316–1329. doi:10.1111/ele.12165.

Farkas SR, Shorey HH. 1972. Chemical Trail-Following by Flying Insects: A Mechanism for Orientation to a Distant Odor Source. Science. 178(4056):67–68. doi:10.1126/science.178.4056.67.

Farnworth B, Meitern R, Innes J, Waas JR. 2019. Increasing predation risk with light reduces speed, exploration and visit duration of invasive ship rats (*Rattus rattus*). Sci Rep. 9(1):3739. doi:10.1038/s41598-019-39711-3.

Farren A, Prodöhl P, Laming P, Reid N. 2010. Distribution of the common lizard (*Zootoca vivipara*) and landscape favourability for the species in Northern Ireland. Amphibia-Reptilia. 31(3):387–394. doi:10.1163/156853810791769428.

Fernald RD, Maruska KP. 2012. Social information changes the brain. Proceedings of the National Academy of Sciences. 109(supplement_2):17194–17199. doi:10.1073/pnas.1202552109.

Ferrari MCO, Horn ME, Chivers DP. 2019. Cognitive resonance: When information carry-over constrains cognitive plasticity. Functional Ecology. 33(4):703–711. doi:10.1111/1365-2435.13294.

Feyten LEA, Crane AL, Ramnarine IW, Brown GE. 2021. Predation risk shapes the use of conflicting personal risk and social safety information in guppies. Behav Ecol. 32(6):1296–1305. doi:10.1093/beheco/arab096.

Firth D. 1993. Bias Reduction of Maximum Likelihood Estimates. Biometrika. 80(1):27–38. doi:10.2307/2336755.

Fisher HS, Rosenthal GG. 2006. Female swordtail fish use chemical cues to select well-fed mates. Animal Behaviour. 72(3):721–725. doi:10.1016/j.anbehav.2006.02.009.

Fitze PS, Galliard JFL, Federici P, Richard M, Clobert J. 2005. Conflict over multiple-partner mating between males and females of the polygynandrous common lizards. Evolution. 59(11):2451–2459. doi:10.1111/j.0014-3820.2005.tb00954.x.

Fjerdingstad EJ, Schtickzelle N, Manhes P, Gutierrez A, Clobert J. 2007. Evolution of dispersal and life history strategies – Tetrahymena ciliates. BMC Evolutionary Biology. 7:133. doi:10.1186/1471-2148-7-133.

Fleishman L, Font E. 2019. Sensory processing in relation to signaling behavior. In: Behavior of Lizards: Evolutionary and Mechanistic Perspectives (V Bels & A Russell, Eds.), pp. 207-258. Taylor and Francis Publishing; Abingdon, UK.

Fletcher RJ. 2007. Species interactions and population density mediate the use of social cues for habitat selection. Journal of Animal Ecology. 76(3):598–606. doi:10.1111/j.1365-2656.2007.01230.x.

Fletcher RJ, Miller CW. 2008. The type and timing of social information alters offspring production. Biology Letters. 4(5):482–485. doi:10.1098/rsbl.2008.0306.

Fletcher RJ, Sieving KE. 2010. Social-Information use in Heterogeneous Landscapes: A Prospectus. Condor. 112(2):225–234. doi:10.1525/cond.2010.090236.

Flor M de la, Chen L, Manson-Bishop C, Chu T-C, Zamora K, Robbins D, Gunaratne G, Roman G. 2017. Drosophila increase exploration after visually detecting predators. PLOS ONE. 12(7):e0180749.
doi:10.1371/journal.pone.0180749.

Forsman A, Merilaita S. 1999. Fearful symmetry: pattern size and asymmetry affects aposematic signal efficacy. Evolutionary Ecology. 13(2):131–140. doi:10.1023/A:1006630911975.

Forsman JT, Thomson RL, Seppänen J-T. 2007. Mechanisms and fitness effects of interspecific information use between migrant and resident birds. Behav Ecol. 18(5):888–894. doi:10.1093/beheco/arm048.

Forsman JT, Hjernquist MB, Taipale J, Gustafsson L. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. Behavioral Ecology. 19(3):539–545. doi:10.1093/beheco/arn005.

Forsman JT, Mönkkönen M, Korpimäki E, Thomson RL. 2013. Mammalian nest predator feces as a cue in avian habitat selection decisions. Behav Ecol. 24(1):262–266. doi:10.1093/beheco/ars162.

Forsman JT, Kivelä SM, Jaakkonen T, Seppänen J-T, Gustafsson L, Doligez B. 2014. Avoiding perceived past resource use of potential competitors affects niche dynamics in a bird community. BMC Evolutionary Biology. 14(1):175. doi:10.1186/s12862-014-0175-2.

Foucaud J, Philippe A-S, Moreno C, Mery F. 2013. A genetic polymorphism affecting reliance on personal versus public information in a spatial learning task in *Drosophila melanogaster*. Proceedings of the Royal Society B: Biological Sciences. 280(1760):20130588. doi:10.1098/rspb.2013.0588.

Fox J, Weisberg S. 2018. An R Companion to Applied Regression. SAGE Publications.

Frankel J. 1999. Chapter 2 Cell Biology of *Tetrahymena thermophila*. In: Asai DJ, Forney JD, editors. Methods in Cell Biology. Vol. 62. Academic Press. p. 27–125.

Freeberg TM, Book DL, Jung H, Kyle SC. 2017. Communication, Cues, and Signals. In: Shackelford TK, Weekes-Shackelford VA, editors. Encyclopedia of Evolutionary Psychological Science. Cham: Springer International Publishing. p. 1206–1214. https://doi.org/10.1007/978-3-319-19650-3_2728.

Fretwell SD. 1972. Populations in a seasonal environment. Monogr Popul Biol. 5:1–217.

Fretwell SD, Lucas HL. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19(1):16–36. doi:10.1007/BF01601953.

Friard O, Gamba M. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution. 7(11):1325–1330. doi:10.1111/2041-210X.12584.

Fronhofer EA, Hovestadt T, Poethke H-J. 2013. From random walks to informed movement. Oikos. 122(6):857–866. doi:10.1111/j.1600-0706.2012.21021.x.

Fronhofer EA, Klecka J, Melián CJ, Altermatt F. 2015a. Condition-dependent movement and dispersal in experimental metacommunities. Ecology Letters. 18(9):954–963. doi:10.1111/ele.12475.

Fronhofer EA, Kropf T, Altermatt F. 2015b. Density-dependent movement and the consequences of the Allee effect in the model organism Tetrahymena. Journal of Animal Ecology.:712–722.
doi:10.1111/1365-2656.12315@10.1111/(ISSN)1365-2656.MovementEcology.

Fronhofer EA, Nitsche N, Altermatt F. 2017a. Information use shapes the dynamics of range expansions into environmental gradients. Global Ecology and Biogeography. 26(4):400–411. doi:10.1111/geb.12547.

Fronhofer EAA, Gut S, Altermatt F. 2017b. Evolution of density-dependent movement during replicated experimental range expansions. bioRxiv.:114330. Doi:10.1101/114330.

Fronhofer EA, Legrand D, Altermatt F, Ansart A, Blanchet S, Bonte D, Chaine A, Dahirel M, De Laender F, De Raedt J, et al. 2018. Bottom-up and top-down control of dispersal across major organismal groups. Nat Ecol Evol. 2(12):1859–1863. doi:10.1038/s41559-018-0686-0.

G

Gabirot M, López P, Martín J, de Fraipont M, Heulin B, Sinervo B, Clobert J. 2008. Chemical composition of femoral secretions of oviparous and viviparous types of male common lizards *Lacerta vivipara*. Biochemical

Systematics and Ecology. 36(7):539–544. doi:10.1016/j.bse.2008.03.006.

Gadagkar R. 2003. Is the peacock merely beautiful or also honest? Current Science. 85(7):1012–1020.

Gager Y. 2019. Information transfer about food as a reason for sociality in bats. Mammal Review. 49(2):113–120. doi:10.1111/mam.12146.

Galef B G, Whiskin EE. 2004. Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. Animal Behaviour. 68(4):897–902. doi:10.1016/j.anbehav.2003.10.029.

Galef BG, Dudley KE, Whiskin EE. 2008. Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. Animal Behaviour. 75(2):631–637. doi:10.1016/j.anbehav.2007.06.024.

Gallagher AJ, Creel S, Wilson RP, Cooke SJ. 2017. Energy Landscapes and the Landscape of Fear. Trends in Ecology & Evolution. 32(2):88–96. doi:10.1016/j.tree.2016.10.010.

Gandon S. 1999. Kin Competition, the Cost of Inbreeding and the Evolution of Dispersal. Journal of Theoretical Biology. 200(4):345–364. doi:10.1006/jtbi.1999.0994.

Garland T, Hankins E, Huey RB. 1990. Locomotor Capacity and Social Dominance in Male Lizards. Functional Ecology. 4(2):243–250. doi:10.2307/2389343.

Gautier P, Olgun K, Uzum N, Miaud C. 2006. Gregarious behaviour in a salamander: attraction to conspecific chemical cues in burrow choice. Behav Ecol Sociobiol. 59(6):836–841. doi:10.1007/s00265-005-0130-8.

Gignac GE, Szodorai ET. 2016. Effect size guidelines for individual differences researchers. Personality and Individual Differences. 102:74–78. doi:10.1016/j.paid.2016.06.069.

Gill SA, Bierema AM-K. 2013. On the Meaning of Alarm Calls: A Review of Functional Reference in Avian Alarm Calling. Ethology. 119(6):449–461. doi:10.1111/eth.12097.

Gil MA, Emberts Z, Jones H, Mary CMS. 2016 Dec 29. Social Information on Fear and Food Drives Animal Grouping and Fitness. The American Naturalist. doi:10.1086/690055.

Gil MA, Hein AM, Spiegel O, Baskett ML, Sih A. 2018. Social Information Links Individual Behavior to Population and Community Dynamics. Trends in Ecology & Evolution. 33(7):535–548. doi:10.1016/j.tree.2018.04.010.

Gil MA, Baskett ML, Schreiber SJ. 2019. Social information drives ecological outcomes among competing species. Ecology. 100(11):e02835. doi:10.1002/ecy.2835.

Giraldeau L-A, Valone TJ, Templeton JJ. 2002. Potential disadvantages of using socially acquired information. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 357(1427):1559–1566. doi:10.1098/rstb.2002.1065.

Goldman JA, Crane AL, Feyten LEA, Collins E, Brown GE. 2021. Disturbance cue communication is shaped by emitter diet and receiver background risk in Trinidadian guppies. Curr Zool. doi:10.1093/cz/zoab025.

González-Suárez M, Mugabo M, Decencière B, Perret S, Claessen D, Le Galliard J. 2011. Disentangling the effects of predator body size and prey density on prey consumption in a lizard. Functional Ecology. 25(1):158–165. doi:10.1111/j.1365-2435.2010.01776.x.

Goodale E, Beauchamp G, Magrath RD, Nieh JC, Ruxton GD. 2010. Interspecific information transfer influences animal community structure. Trends in Ecology & Evolution. 25(6):354–361. doi:10.1016/j.tree.2010.01.002.

Goossens S, Wybouw N, Van Leeuwen T, Bonte D. 2020. The physiology of movement. Mov Ecol. 8(1):5. doi:10.1186/s40462-020-0192-2.

Görtz H-D, Kuhlmann H-W, Möllenbeck M, Tiedtke A, Kusch J, Schmidt HJ, Miyake A. 1999. Intra- and Intercellular Communication Systems in Ciliates. Naturwissenschaften. 86(9):422–434. doi:10.1007/s001140050646.

Gosler A, Carruthers T. 1999. Body Reserves and Social Dominance in the Great *Tit Parus* major in Relation to Winter Weather in Southwest Ireland. Journal of Avian Biology. 30(4):447–459. doi:10.2307/3677017.

Grabowska J, Zięba G, Przybylski M, Smith C. 2019. The role of intraspecific competition in the dispersal of an invasive fish. Freshwater Biology. 64(5):933–941. doi:10.1111/fwb.13275.

Grafen A. 1988. On the uses of data on lifetime reproductive success. Reproductive success.:454–485.

Gray RD, Kennedy M. 1994. Perceptual constraints on optimal foraging: A reason for departures from the ideal free distribution? Animal Behaviour. 47(2):469–471. doi:10.1006/anbe.1994.1064.

Greenfield MD. 1997. Sexual Selection and the Evolution of Advertisement Signals. In: Owings DH, Beecher MD, Thompson NS, editors. Communication. Boston, MA: Springer US. p. 145–177. https://doi.org/10.1007/978-1-4899-1745-4_6.

Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour. 28(4):1140–1162. doi:10.1016/S0003-3472(80)80103-5.

Greenwood PJ, Harvey PH, Perrins CM. 1979. The Role of Dispersal in the Great Tit (*Parus major*): The Causes, Consequences and Heritability of Natal Dispersal. Journal of Animal Ecology. 48(1):123–142. doi:10.2307/4105.

Grenot CJ, Garcin L, Dao J, Hérold J-P, Fahys B, Tséré-Pagès H. 2000. How does the European common lizard, *Lacerta vivipara*, survive the cold of winter? Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology. 127(1):71–80. doi:10.1016/S1095-6433(00)00236-1.

Gruber J, Whiting MJ, Brown G, Shine R. 2017. The loneliness of the long-distance toad: invasion history and social attraction in cane toads (*Rhinella marina*). Biology Letters. 13(11):20170445. doi:10.1098/rsbl.2017.0445.

Grüter C, Leadbeater E. 2014. Insights from insects about adaptive social information use. Trends in Ecology & Evolution. 29(3):177–184. doi:10.1016/j.tree.2014.01.004.

Guttal V, Couzin ID. 2010. Social interactions, information use, and the evolution of collective migration. Proceedings of the National Academy of Sciences. 107(37):16172–16177. doi:10.1073/pnas.1006874107.

Gvoždík L, Castilla AM. 2001. A Comparative Study of Preferred Body Temperatures and Critical Thermal Tolerance Limits among Populations of *Zootoca vivipara* (Squamata: Lacertidae) along an Altitudinal Gradient. Journal of Herpetology. 35(3):486–492. doi:10.2307/1565967.

Gyllenberg M, Kisdi É, Utz M. 2008. Evolution of condition-dependent dispersal under kin competition. J Math Biol. 57(2):285–307. doi:10.1007/s00285-008-0158-2.

Gyllenberg M, Kisdi É, Utz M. 2011. Body condition dependent dispersal in a heterogeneous environment. Theoretical Population Biology. 79(4):139–154. doi:10.1016/j.tpb.2011.02.004.

H

Hakkarainen H, Ilmonen P, Koivunen V, Korpimäki E. 2001. Experimental increase of predation risk induces breeding dispersal of Tengmalm's owl. Oecologia. 126(3):355–359. doi:10.1007/s004420000525.

Halliday TR, Verrell PA. 1988. Body Size and Age in Amphibians and Reptiles. Journal of Herpetology. 22(3):253–265. doi:10.2307/1564148.

Hand DJ, Taylor CC. 1987. Multivariate analysis of variance and repeated measures: A practical approach for behavioural scientists. Boca Raton, FL: Chapman & Hall/CRC (Multivariate analysis of variance and repeated measures: A practical approach for behavioural scientists).

Hanna CJ, Eason PK. 2013. Juvenile crab spiders (*Mecaphesa asperata*) use indirect cues to choose foraging sites. Ethology Ecology & Evolution. 25(2):161–173. doi:10.1080/03949370.2012.742464.

Hardouin LA, Legagneux P, Hingrat Y, Robert A. 2015. Sex-specific dispersal responses to inbreeding and kinship. Animal Behaviour. 105:1–10. doi:10.1016/j.anbehav.2015.04.002.

Hart N, Lisney T, Collin S. 2006. Visual communication in elasmobranchs. p. 338–392.

Hauzy C, Hulot FD, Gins A, Loreau M. 2007. Intra- and interspecific density-dependent dispersal in an aquatic prey–predator system. Journal of Animal Ecology. 76(3):552–558. doi:10.1111/j.1365-2656.2007.01227.x.

Hazell SP, Gwynn DM, Ceccarelli S, Fellowes MDE. 2005. Competition and dispersal in the pea aphid: clonal variation and correlations across traits. Ecological Entomology. 30(3):293–298. doi:10.1111/j.0307-6946.2005.00703.x.

Hazlett BA. 2011. Chemical Cues and Reducing the Risk of Predation. In: Breithaupt T, Thiel M, editors. Chemical Communication in Crustaceans. New York, NY: Springer. p. 355–370. https://doi.org/10.1007/978-0-387-77101-4_18.

Heinen VK, Stephens DW. 2016. Blue jays, *Cyanocitta cristata*, devalue social information in uncertain environments. Animal Behaviour. 112:53–62. doi:10.1016/j.anbehav.2015.11.015.

Heinze G, Schemper M. 2002. A solution to the problem of separation in logistic regression. Statistics in Medicine. 21(16):2409–2419. doi:https://doi.org/10.1002/sim.1047.

Hellung-Larsen P, Leick V, Tommerup N. 1986. Chemoattraction in Tetrahymena: on the role of chemokinesis. The Biological Bulletin. 170(3):357–367. doi:10.2307/1541847.

Hellung-Larsen P, Leick V, Tommerup N, Kronborg D. 1990. Chemotaxis in Tetrahymena. European Journal of Protistology. 25(3):229–233. doi:10.1016/S0932-4739(11)80174-4.

Hermann SL, Bird SA, Ellis DR, Landis DA. 2021. Predation risk differentially affects aphid morphotypes: impacts on prey behavior, fecundity and transgenerational dispersal morphology. Oecologia. 197(2):411–419. doi:10.1007/s00442-021-05037-z.

Hestbeck JB. 1982. Population Regulation of Cyclic Mammals: The Social Fence Hypothesis. Oikos. 39(2):157–163. doi:10.2307/3544480.

Heulin B. 1985. Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara*. Can J Zool. 63(8):1773–1777. doi:10.1139/z85-266.

Heulin B. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. Vie et Milieu / Life & Environment.:177.

Heulin B, Osenegg-Leconte K, Michel D. 1997. Demography of a Bimodal Reproductive Species of Lizard (*Lacerta vivipara*): Survival and Density Characteristics of Oviparous Populations. Herpetologica. 53(4):432–444.

Higham JP. 2014. How does honest costly signaling work? Behav Ecol. 25(1):8–11. doi:10.1093/beheco/art097.

Hill RJ. 1983. The temperature-dependent emission of low frequency sound by motile cultures of the ciliate Tetrahymena thermophilia. Biochemical and Biophysical Research Communications. 117(1):190–195. doi:10.1016/0006-291X(83)91559-0.

Hill GE, McGraw KJ. 2006. Bird Coloration, Volume 2: Function and Evolution. Harvard University Press.

Hodl W, Amézquita A. 2001. Visual signaling in anuran amphibians. In: Anuran Communication. p. 121–141.

Holland MD, Hastings A. 2008. Strong effect of dispersal network structure on ecological dynamics. Nature. 456(7223):792–794. doi:10.1038/nature07395.

Holtmann B, Santos ESA, Lara CE, Nakagawa S. 2017. Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. Proceedings of the Royal Society B: Biological Sciences. 284(1864):20170943. doi:10.1098/rspb.2017.0943.

Hoppitt W, Laland KN. 2008. Chapter 3 Social Processes Influencing Learning in Animals: A Review of the Evidence. In: Advances in the Study of Behavior. Vol. 38. Academic Press. p. 105–165.

Horvathova T, Baláž M, Jandzik D. 2013. Reproduction and Morphology of the Common Lizard (*Zootoca vivipara*) from Montane Populations in Slovakia. Zoological science. 30:92–8. doi:10.2108/zsj.30.92.

Hotta T, Takeyama T, Heg D, Awata S, Jordan L, Kohda M. 2015. The use of multiple sources of social information in contest behavior: testing the social cognitive abilities of a cichlid fish. Frontiers in Ecology and Evolution. 3. doi:10.3389/fevo.2015.00085

Houston CS, Francis CM. 1995. Survival of Great Horned Owls in Relation to the Snowshoe Hare Cycle. Auk. 112(1):44–59. doi:10.2307/4088765.

Howland HC. 1974. Optimal strategies for predator avoidance: The relative importance of speed and manoeuvrability. Journal of Theoretical Biology. 47(2):333–350. doi:10.1016/0022-5193(74)90202-1.

Hromada M, Antczak M, Valone TJ, Tryjanowski P. 2008. Settling Decisions and Heterospecific Social Information Use in Shrikes. PLOS ONE. 3(12):e3930. doi:10.1371/journal.pone.0003930.

Huang P, Sieving KE, Mary CMS. 2012. Heterospecific information about predation risk influences exploratory behavior. Behav Ecol. 23(3):463–472. doi:10.1093/beheco/arr212.

Hughes NK, Price CJ, Banks PB. 2010. Predators Are Attracted to the Olfactory Signals of Prey. PLOS ONE. 5(9):e13114. doi:10.1371/journal.pone.0013114.

Hurvich CM, Tsai C-L. 1993. A Corrected Akaike Information Criterion for Vector Autoregressive Model Selection. Journal of Time Series Analysis. 14(3):271–279. doi:10.1111/j.1467-9892.1993.tb00144.x.

I/J

Insel TR, Fernald RD. 2004. How the brain processes social information: Searching for the Social Brain. Annual Review of Neuroscience. 27(1):697–722. doi:10.1146/annurev.neuro.27.070203.144148.

Jaakkonen T, Kivelä SM, Meier CM, Forsman JT. 2015. The use and relative importance of intraspecific and interspecific social information in a bird community. Behav Ecol. 26(1):55–64. doi:10.1093/beheco/aru144.

Jacob S, Bestion E, Legrand D, Clobert J, Cote J. 2015a. Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. Evol Ecol. 29(6):851–871. doi:10.1007/s10682-015-9776-5.

Jacob S, Chaine AS, Schtickzelle N, Huet M, Clobert J. 2015b. Social information from immigrants: multiple immigrant-based sources of information for dispersal decisions in a ciliate. Journal of Animal Ecology. 84(5):1373–1383. doi:10.1111/1365-2656.12380.

Jacob S, Wehi P, Clobert J, Legrand D, Schtickzelle N, Huet M, Chaine A. 2016a. Cooperation-mediated plasticity in dispersal and colonization. Evolution. 70(10):2336–2345. doi:10.1111/evo.13028.

Jacob S, Clobert J, Legrand D, Schtickzelle N, Chaine AS. 2016b. Social Information in Cooperation and Dispersal in Tetrahymena. In: Witzany G, Nowacki M, editors. Biocommunication of Ciliates. Cham: Springer International Publishing. p. 235–252. https://doi.org/10.1007/978-3-319-32211-7_14.

Jacob S, Legrand D, Chaine AS, Bonte D, Schtickzelle N, Huet M, Clobert J. 2017. Gene flow favours local adaptation under habitat choice in ciliate microcosms. Nature Ecology & Evolution. 1(9):1407–1410. doi:10.1038/s41559-017-0269-5.

Jacob S, Laurent E, Haegeman B, Bertrand R, Prunier JG, Legrand D, Cote J, Chaine AS, Loreau M, Clobert

J, et al. 2018. Habitat choice meets thermal specialization: Competition with specialists may drive suboptimal habitat preferences in generalists. PNAS. 115(47):11988–11993. doi:10.1073/pnas.1805574115.

Jacob S, Chaine AS, Huet M, Clobert J, Legrand D. 2019a. Variability in Dispersal Syndromes Is a Key Driver of Metapopulation Dynamics in Experimental Microcosms. Am Nat. 194(5):613–626. doi:10.1086/705410.

Jacob S, Laurent E, Morel-Journel T, Schtickzelle N. 2019b. Fragmentation and the context-dependence of dispersal syndromes: matrix harshness modifies resident-disperser phenotypic differences in microcosms. Oikos. doi:10.1111/oik.06857.

Jander R. 1975. Ecological Aspects of Spatial Orientation. Annual Review of Ecology and Systematics. 6(1):171–188. doi:10.1146/annurev.es.06.110175.001131.

Jandt JM, Tibbetts EA, Toth AL. 2014. Polistes paper wasps: a model genus for the study of social dominance hierarchies. Insect Soc. 61(1):11–27. doi:10.1007/s00040-013-0328-0.

Jennrich RI, Turner FB. 1969. Measurement of non-circular home range. Journal of Theoretical Biology. 22(2):227–237. doi:10.1016/0022-5193(69)90002-2.

Johansson BG, Jones TM. 2007. The role of chemical communication in mate choice. Biological Reviews. 82(2):265–289. doi:10.1111/j.1469-185X.2007.00009.x.

Johnson RP. 1973. Scent marking in mammals. Animal Behaviour. 21(3):521–535. doi:10.1016/S0003-3472(73)80012-0.

Johnson MA, Cook EG, Kircher BK. 2019. Phylogeny and Ontogeny of Display Behavior. In: Behavior of Lizards. CRC Press. 29 p.

Johst K, Brandl R. 1997. The effect of dispersal on local population dynamics. Ecological Modelling. 104(1):87–101. doi:10.1016/S0304-3800(97)00112-9.

Jolliffe IT, Cadima J. 2016. Principal component analysis: a review and recent developments. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences. 374(2065):20150202. doi:10.1098/rsta.2015.0202.

Jonart LM, Hill GE, Badyaev AV. 2007. Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird. Animal Behaviour. 74(6):1675–1681. doi:10.1016/j.anbehav.2007.03.012.

Jones TB, Aplin LM, Devost I, Morand-Ferron J. 2017. Individual and ecological determinants of social information transmission in the wild. Animal Behaviour. 129:93–101. doi:10.1016/j.anbehav.2017.05.011.

Jones BC, DuVal EH. 2019. Mechanisms of Social Influence: A Meta-Analysis of the Effects of Social Information on Female Mate Choice Decisions. Frontiers in Ecology and Evolution. 7. doi:10.3389/fevo.2019.00390.

Josserand R, Dupoué A, Agostini S, Haussy C, Le Galliard J-F, Meylan S. 2017. Habitat degradation increases stress-hormone levels during the breeding season, and decreases survival and reproduction in adult common lizards. Oecologia. 184(1):75–86. doi:10.1007/s00442-017-3841-4.

Junker AD, Jacob S, Philippe H, Legrand D, Pearson CG. 2021. Plastic cell morphology changes during dispersal. iScience. 24(8):102915. doi:10.1016/j.isci.2021.102915.

K

Kaminski J, Riedel J, Call J, Tomasello M. 2005. Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. Animal Behaviour. 69(1):11–18. doi:10.1016/j.anbehav.2004.05.008.

Kappeler PM. 2022. Orientation in Time and Space. In: Kappeler PM, editor. Animal Behaviour: An Evolutionary Perspective. Cham: Springer International Publishing. p. 69–91. https://doi.org/10.1007/978-3-030-82879-0_5.

Kappeler PM, Schaik CP van. 2004. Sexual Selection in Primates: New and Comparative Perspectives. Cambridge University Press.

Kasuya E. 2000. Kin-biased dispersal behaviour in the mango shield scale, *Milviscutulus mangiferae*. Animal Behaviour. 59(3):629–632. doi:10.1006/anbe.1999.1334.

Kawamoto A, Le Galliard J-F, Badiane A. 2021. The role of social costs as a mechanism enforcing the honesty of ultraviolet-reflecting signals in a lizard. Biol J Linn Soc. 133(4):1126–1138. doi:10.1093/biolinnean/blab008.

Kawecki TJ, Ebert D. 2004. Conceptual issues in local adaptation. Ecology Letters. 7(12):1225–1241. doi:10.1111/j.1461-0248.2004.00684.x.

Kendal RL, Coolen I, Laland KN. 2004. The role of conformity in foraging when personal and social information conflict. Behav Ecol. 15(2):269–277. doi:10.1093/beheco/arh008.

Kendal R, Coolen I, Laland K. 2009 Nov 1. Adaptive trade-offs in the use of social and personal information. In Cognitive ecology II. doi:10.7208/chicago/9780226169378.003.0013.

Kennedy M, Gray RD. 1994. Agonistic Interactions and the Distribution of Foraging Organisms: Individual Costs and Social Information. Ethology. 96(2):155–165. doi:10.1111/j.1439-0310.1994.tb00891.x.

Kennedy M, Shave CR, Spencer HG, Gray RD. 1994. Quantifying the Effect of Predation Risk on Foraging Bullies: No Need to Assume an IFD. Ecology. 75(8):2220–2226. doi:10.2307/1940878.

Kern JM, Radford AN. 2017. Reduced social-information provision by immigrants and use by residents following dispersal. Current Biology. 27(23):R1266–R1267. doi:10.1016/j.cub.2017.10.045.

Khodadoost M, Pilorge T, Ortega A. 1987. Variations de la densité et de la taille corporelle en fonction de l'abondance et de la composition du peuplement de proies dans trois populations de lézards vivipares du Mont Lozère. Revue d'Ecologie, Terre et Vie. 42(2):193–201.

Kim S-Y, Torres R, Drummond H. 2009. Simultaneous positive and negative density-dependent dispersal in a colonial bird species. Ecology. 90(1):230–239. doi:10.1890/08-0133.1.

King AJ, Cowlishaw G. 2007. When to use social information: the advantage of large group size in individual decision making. Biology Letters. 3(2):137–139. doi:10.1098/rsbl.2007.0017.

Kingma SA. 2018. Food, friends or family: What drives delayed dispersal in group-living animals? Journal of Animal Ecology. 87(5):1205–1208. doi:10.1111/1365-2656.12874.

Kisdi E, Utz M, Gyllenberg M. 2012. Evolution of condition-dependent dispersal. p. 139–151.

Kivelä SM, Seppänen J-T, Ovaskainen O, Doligez B, Gustafsson L, Mönkkönen M, Forsman JT. 2014. The past and the present in decision-making: the use of conspecific and heterospecific cues in nest site selection. Ecology. 95(12):3428–3439. doi:10.1890/13-2103.1.

Kooijman SALM. 2000. Dynamic Energy and Mass Budgets in Biological Systems. 2nd ed. Cambridge: Cambridge University Press.

Koops MA. 1998 Dec 1. Misinformation and assessment uncertainty in the ecology of information use. Thesis. https://mspace.lib.umanitoba.ca/xmlui/handle/1993/1722.

Koops MA. 2004. Reliability and the value of information. Animal Behaviour. 67(1):103–111. doi:10.1016/j.anbehav.2003.02.008.

Korzan WJ, Höglund E, Watt MJ, Forster GL, Øverli Ø, Lukkes JL, Summers CH. 2007. Memory of opponents is more potent than visual sign stimuli after social hierarchy has been established. Behavioural Brain Research. 183(1):31–42. doi:10.1016/j.bbr.2007.05.021.

Kosmidis I, Firth D. 2021. Jeffreys-prior penalty, finiteness and shrinkage in binomial-response generalized linear models. Biometrika. 108(1):71–82. doi:10.1093/biomet/asaa052.

Kuefler D, Hudgens B, Haddad NM, Morris WF, Thurgate N. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology. 91(4):944–950. doi:10.1890/09-0614.1.

Kumar A. 2003. Acoustic communication in birds. Reson. 8(6):44–55. doi:10.1007/BF02837868.

Kümmerli R, Gardner A, West SA, Griffin AS. 2009. Limited dispersal, budding dispersal, and cooperation: an experimental study. Evolution. 63(4):939–949. doi:10.1111/j.1558-5646.2008.00548.x.

Kurvers RHJM, Van Oers K, Nolet BA, Jonker RM, Van Wieren SE, Prins HHT, Ydenberg RC. 2010. Personality predicts the use of social information. Ecology Letters. 13(7):829–837. doi:10.1111/j.1461-0248.2010.01473.x.

L

Labra A. 2006. Chemoreception and the Assessment of Fighting Abilities in the Lizard *Liolaemus monticola*. Ethology. 112(10):993–999. doi:10.1111/j.1439-0310.2006.01256.x.

LaDage LD, Roth TC, Cerjanic AM, Sinervo B, Pravosudov VV. 2012. Spatial memory: are lizards really deficient? Biology Letters. 8(6):939–941. doi:10.1098/rsbl.2012.0527.

Laidre ME, Johnstone RA. 2013. Animal signals. Current Biology. 23(18):R829–R833. doi:10.1016/j.cub.2013.07.070.

Laloi D, Richard M, Fédérici P, Clobert J, Teillac-Deschamps P, Massot M. 2009. Relationship between female mating strategy, litter success and offspring dispersal. Ecology Letters. 12(8):823–829. doi:10.1111/j.1461-0248.2009.01335.x.

Lambin X. 1994. Natal Philopatry, Competition for Resources, and Inbreeding Avoidance in Townsend's Voles (*Microtus Townsendii*). Ecology. 75(1):224–235. doi:10.2307/1939396.

Lambin X, Aars J, Piertney SB. 2001. Dispersal, intraspecific competition, kin competition, and kin facilitation: A review of the empirical evidence. Dispersal.

Langen TA. 1996. The mating system of the White-throated Magpie-jay *Calocitta formosa* and Greenwood's hypothesis for sex-biased dispersal. Ibis. 138(3):506–513. doi:10.1111/j.1474-919X.1996.tb08071.x.

Laurent E, Schtickzelle N, Jacob S. 2020. Fragmentation mediates thermal habitat choice in ciliate microcosms. Proceedings of the Royal Society B: Biological Sciences. 287(1919):20192818. doi:10.1098/rspb.2019.2818.

Le Galliard J-F, Ferrière, Clobert J. 2003a. Mother–offspring interactions affect natal dispersal in a lizard. Proceedings of the Royal Society of London B: Biological Sciences. 270(1520):1163–1169. doi:10.1098/rspb.2003.2360.

Le Galliard J-F, Bris ML, Clobert J. 2003b. Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. Functional Ecology. 17(6):877–885. doi:10.1046/j.0269-8463.2003.00800.x.

Le Galliard J-F, Clobert J, Ferrière R. 2004. Physical performance and darwinian fitness in lizards. Nature. 432(7016):502–505. doi:10.1038/nature03057.

Le Galliard J-F, Fitze P. S., Cote J, Massot M, Clobert J. 2005. Female common lizards (*Lacerta vivipara*) do not adjust their sex-biased investment in relation to the adult sex ratio. Journal of Evolutionary Biology. 18(6):1455–1463. doi:10.1111/j.1420-9101.2005.00950.x.

Le Galliard J-F, Fitze Patrick S., Ferrière R, Clobert J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. PNAS. 102(50):18231–18236. doi:10.1073/pnas.0505172102.

Le Galliard J-F, Ferrière R, Clobert J. 2005. Effect of patch occupancy on immigration in the common lizard. Journal of Animal Ecology. 74(2):241–249. doi:10.1111/j.1365-2656.2005.00912.x.

Le Galliard J-F, Ferrière R, Clobert J. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? Oikos. 111(2):368–376. doi:10.1111/j.0030-1299.2005.14163.x.

Le Galliard J-F, Cote J, Fitze PS. 2008. Lifetime and Intergenerational Fitness Consequences of Harmful Male Interactions for Female Lizards. Ecology. 89(1):56–64. doi:10.1890/06-2076.1.

Le Galliard J-F, Marquis O, Massot M. 2010. Cohort variation, climate effects and population dynamics in a short-lived lizard. Journal of Animal Ecology. 79(6):1296–1307. doi:10.1111/j.1365-2656.2010.01732.x.

Le Galliard J-F, Rémy A, Ims RA, Lambin X. 2012. Patterns and processes of dispersal behaviour in arvicoline rodents. Molecular Ecology. 21(3):505–523. doi:10.1111/j.1365-294X.2011.05410.x.

Le Galliard J-F, Paquet M, Cisel M, Montes-Poloni L. 2013. Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. Functional Ecology. 27(1):136–144. doi:10.1111/1365-2435.12017.

Le Gouar P, Mihoub J-B, Sarrazin F. 2012. Dispersal and Habitat Selection: Behavioural and Spatial Constraints for Animal Translocations. In: Reintroduction Biology: Integrating Science and Management. p. 138–164.

Lê S, Josse J, Husson F. 2008. FactoMineR: An R Package for Multivariate Analysis. Journal of Statistical Software. 25(1):1–18. doi:10.18637/jss.v025.i01.

Leadbeater E. 2015. What evolves in the evolution of social learning? Journal of Zoology. 295(1):4–11. doi:10.1111/jzo.12197.

Leadbeater E, Chittka L. 2009 Mar 4. Bumble-bees learn the value of social cues through experience. Biology Letters. doi:10.1098/rsbl.2008.0692

Lecomte J, Clobert J, Massot M. 1992. Sex identification in juveniles of *Lacerta vivipara*. Amphibia-Reptilia. 13(1):21–25. doi:10.1163/156853892X00193.

Lecomte J. 1993. Role du comportement dans l'organisation et la regulation des populations de lezards vivipares [These de doctorat]. Paris 11. https://www.theses.fr/1993PA112382.

Lecomte J, Clobert J, Massot M, Barbault R. 1994. Spatial and behavioural consequences of a density manipulation in the common lizard1. Écoscience. 1(4):300–310. doi:10.1080/11956860.1994.11682255.

Lecomte J, Boudjemadi K, Sarrazin F, Cally K, Clobert J. 2004. Connectivity and homogenisation of population sizes: an experimental approach in *Lacerta vivipara*. Journal of Animal Ecology. 73(1):179–189. doi:10.1111/j.1365-2656.2004.00796.x.

Lee AEG, Ounsley JP, Coulson T, Rowcliffe JM, Cowlishaw G. 2016. Information use and resource competition: an integrative framework. Proceedings of the Royal Society B: Biological Sciences. 283(1825):20152550. doi:10.1098/rspb.2015.2550.

Lefebvre L, Giraldeau L-A. 1996. Is social learning an adaptive specialization? In: Social learning in animals: The roots of culture. San Diego, CA, US: Academic Press. p. 107–128.

Legrand D, Trochet A, Moulherat S, Calvez O, Stevens VM, Ducatez S, Clobert J, Baguette M. 2015. Ranking the ecological causes of dispersal in a butterfly. Ecography. 38(8):822–831. doi:10.1111/ecog.01283.

Lehmann L, Perrin N. 2002. Altruism, Dispersal, and Phenotype-Matching Kin Recognition. The American Naturalist. 159(5):451–468. doi:10.1086/339458.

Leick V, Koppelhus U, Rosenberg J. 1994. Cilia-Mediated Oriented Chemokinesis in *Tetrahymena thermophila*. Journal of Eukaryotic Microbiology. 41(6):546–553. doi:10.1111/j.1550-7408.1994.tb01515.x.

Leick V. 1988. Gliding *Tetrahymena thermophila*: Oriented chemokinesis in a ciliate. European Journal of Protistology. 23(4):354–360. doi:10.1016/S0932-4739(88)80026-9.

Léna J-P, Clobert J, de Fraipont M, Lecomte J, Guyot G. 1998. The relative influence of density and kinship on dispersal in the common lizard. Behav Ecol. 9(5):500–507. doi:10.1093/beheco/9.5.500.

Léna JP, de Fraipont M, Léna JP. 1998. Kin recognition in the common lizard. Behav Ecol Sociobiol. 42(5):341–347. doi:10.1007/s002650050446.

Léna JP, Fraipont MD, Clobert J. 2000. Affinity towards maternal odour and offspring dispersal in the common lizard. Ecology Letters. 3(4):300–308. doi:10.1046/j.1461-0248.2000.00155.x.

Lepetz V, Massot M, Chaine AS, Clobert J. 2009. Climate warming and the evolution of morphotypes in a reptile. Global Change Biology. 15(2):454–466. doi:10.1111/j.1365-2486.2008.01761.x.

Leris I, Reader SM. 2016. Age and early social environment influence guppy social learning propensities. Animal Behaviour. 120:11–19. doi:10.1016/j.anbehav.2016.07.012.

Levins R. 1962. Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive Function. The American Naturalist. 96(891):361–373.

Levins R. 1968. Evolution in changing environments: some theoretical explorations. Princeton, N.J.: Princeton University Press.

Lhomme P, Carrasco D, Larsson M, Hansson B, Anderson P. 2018. A context-dependent induction of natal habitat preference in a generalist herbivorous insect. Behav Ecol. 29(2):360–367. doi:10.1093/beheco/arx173.

Li X-Y, Kokko H. 2019. Sex-biased dispersal: a review of the theory. Biological Reviews. 94(2):721–736. doi:10.1111/brv.12475.

Lidicker W, Stenseth N. 1992. To disperse or not to disperse: Who does it and why? In: Animal Dispersal. p. 21–36.

Lindstedt ER, Hamilton IM. 2013. Variation in social information use: the influences of information reliability and mass on decision making in a group-living fish *Gambusia affinis*. Journal of Fish Biology. 82(6):2095–2103. doi:10.1111/jfb.12105.

Lohmann KJ. 2010. Magnetic-field perception. Nature. 464(7292):1140–1142. doi:10.1038/4641140a.

Long ES, Diefenbach DR, Rosenberry CS, Wallingford BD. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. Behavioral Ecology. 19(6):1235–1242. doi:10.1093/beheco/arn082.

López P, Aragón P, Martin J. 1998. Iberian Rock Lizards (*Lacerta monticola cyreni*) Assess Conspecific Information Using Composite Signals from Faecal Pellets. Ethology. 104(10):809–820. doi:10.1111/j.1439-0310.1998.tb00033.x.

López P, Martín J. 2001. Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. Behav Ecol Sociobiol. 49(2):111–116. doi:10.1007/s002650000288.

López P, Amo L, Martín J. 2006. Reliable Signaling By Chemical Cues Of Male Traits And Health State In Male Lizards, *Lacerta monticola*. J Chem Ecol. 32(2):473–488. doi:10.1007/s10886-005-9012-9.

López P, Martín J. 2013. Effects of Microhabitat-Dependent Predation Risk on Vigilance during Intermittent Locomotion in Psammodromus algirus Lizards. Ethology. 119(4):316–324. doi:10.1111/eth.12068.

Lorenzon P, Clobert J, Oppliger A, John-Alder H. 1999. Effect of Water Constraint on Growth Rate, Activity and Body Temperature of Yearling Common Lizard (*Lacerta vivipara*). Oecologia. 118(4):423–430.

Lorenzon P, Clobert J, Massot M. 2001. The contribution of phenotypic plasticity to adaptation in *Lacerta vivipara*. Evolution. 55(2):392–404. doi:10.1111/j.0014-3820.2001.tb01302.x.

Lotem A, Wagner RH, Balshine-Earn S. 1999. The overlooked signaling component of nonsignaling behavior. Behavioral Ecology. 10(2):209–212. doi:10.1093/beheco/10.2.209.

Loukola OJ, Seppänen J-T, Forsman JT. 2012. Intraspecific social information use in the selection of nest site characteristics. Animal Behaviour. 83(3):629–633. doi:10.1016/j.anbehav.2011.12.004.

Lowe WH, McPeek MA. 2012. Can natural selection maintain long-distance dispersal? Insight from a stream salamander system. Evol Ecol. 26(1):11–24. doi:10.1007/s10682-011-9500-z.

Lüdecke D. 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. Journal of Open Source Software. 3(26):772. doi:10.21105/joss.00772.

Lurz PWW, Garson PJ, Wauters LA. 1997. Effects of temporal and spatial variation in habitat quality on red squirrel dispersal behaviour. Animal Behaviour. 54(2):427–435. doi:10.1006/anbe.1996.0486.

M

Macedonia JM, Evans CS. 1993. Essay on Contemporary Issues in Ethology: Variation among Mammalian Alarm Call Systems and the Problem of Meaning in Animal Signals. Ethology. 93(3):177–197. doi:10.1111/j.1439-0310.1993.tb00988.x.

MacLean SA, Bonter DN. 2013. The Sound of Danger: Threat Sensitivity to Predator Vocalizations, Alarm Calls, and Novelty in Gulls. PLOS ONE. 8(12):e82384. doi:10.1371/journal.pone.0082384.

Madinger CL, Collins K, Fields LG, Taron CH, Benner JS. 2010. Constitutive Secretion in *Tetrahymena thermophila*. Eukaryotic Cell. 9(5):674–681. doi:10.1128/EC.00024-10.

Majláthová V, Majláth I, Haklová B, Hromada M, Ekner A, Antczak M, Tryjanowski P. 2010. Blood parasites in two co-existing species of lizards (*Zootoca vivipara* and *Lacerta agilis*). Parasitol Res. 107(5):1121–1127. doi:10.1007/s00436-010-1981-0.

Manser MB. 2009. What do functionally referential alarm calls refer to? In: Dukas, R; Ratcliffe, J M. Cognitive Ecology, vol. 2. Chicago, US: University of Chicago Press, 229-248. Chicago, US: University of Chicago Press. p. 229–248.

Marchetti C, Drent PJ. 2000. Individual differences in the use of social information in foraging by captive great tits. Animal Behaviour. 60(1):131–140. doi:10.1006/anbe.2000.1443.

Marler P. 1967. Animal Communication Signals. Science. 157(3790):769–774. doi:10.1126/science.157.3790.769.

Marshall JT, Marshall ER. 1976. Gibbons and Their Territorial Songs. Science. 193(4249):235–237. doi:10.1126/science.193.4249.235.

Martin CW, Fodrie FJ, Heck KL, Mattila J. 2010. Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. Oecologia. 162(4):893–902. doi:10.1007/s00442-010-1564-x.

Martín J, López P. 2006. Interpopulational differences in chemical composition and chemosensory recognition of femoral gland secretions of male lizards *Podarcis hispanica*: implications for sexual isolation in a species complex. Chemoecology. 16(1):31–38. doi:10.1007/s00049-005-0326-4.

Martín J, López P. 2007 Jan 24. Scent may signal fighting ability in male Iberian rock lizards. Biology Letters. doi:10.1098/rsbl.2006.0589.

Martín J, Moreira PL, López P. 2007. Status-signalling chemical badges in male Iberian rock lizards. Functional Ecology. 21(3):568–576. doi:10.1111/j.1365-2435.2007.01262.x.

Martín J, López P. 2009. Multiple color signals may reveal multiple messages in male Schreiber's green lizards, *Lacerta schreiberi*. Behav Ecol Sociobiol. 63(12):1743–1755. doi:10.1007/s00265-009-0794-6.

Martín J, López P. 2015. Condition-dependent chemosignals in reproductive behavior of lizards. Hormones and Behavior. 68:14–24. doi:10.1016/j.yhbeh.2014.06.009.

Mas F, Haynes KF, Kölliker M. 2009. A chemical signal of offspring quality affects maternal care in a social insect. Proceedings of the Royal Society B: Biological Sciences. 276(1668):2847–2853. doi:10.1098/rspb.2009.0498.

Masó G, Kaufmann J, Clavero H, Fitze PS. 2019. Age-dependent effects of moderate differences in environmental predictability forecasted by climate change, experimental evidence from a short-lived lizard (*Zootoca vivipara*). Sci Rep. 9(1):1–10. doi:10.1038/s41598-019-51955-7.

Masó G, Ozgul A, Fitze PS. 2020. Decreased Precipitation Predictability Negatively Affects Population Growth through Differences in Adult Survival. The American Naturalist. 195(1):43–55. doi:10.1086/706183.

Mason RT, Parker MR. 2010. Social behavior and pheromonal communication in reptiles. J Comp Physiol A. 196(10):729–749. doi:10.1007/s00359-010-0551-3.

Massol F, Altermatt F, Gounand I, Gravel D, Leibold MA, Mouquet N. 2017. How life-history traits affect ecosystem properties: effects of dispersal in meta-ecosystems. Oikos. 126(4):532–546. doi:10.1111/oik.03893.

Massot M. 1992a. Movement patterns of the common lizard (*Lacerta vivipara*) in relation to sex and age. pp. 315-319. In: Korsos Z, Kiss I, editors. Proceedings of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica, 19-23 August 1991, Budapest, Hungary. Hungarian Natural History Museum, Budapest. 531 pp.

Massot M. 1992b. Determinisme de la dispersion chez le lezard vivipare [These de doctorat]. Paris 11.
http://www.theses.fr/1992PA112325.

Massot M, Clobert J, Pilorge T, Lecomte J, Barbault R. 1992. Density Dependence in the Common Lizard: Demographic Consequences of a Density Manipulation. Ecology. 73(5):1742–1756. doi:10.2307/1940026.

Massot M, Clobert J, Chambon A, Michalakis Y. 1994. Vertebrate Natal Dispersal: The Problem of Non-Independence of Siblings. Oikos. 70(1):172–176. doi:10.2307/3545714.

Massot M, Clobert J. 1995. Influence of maternal food availability on offspring dispersal. Behav Ecol Sociobiol. 37(6):413–418. doi:10.1007/BF00170589.

Massot, Clobert. 2000. Processes at the origin of similarities in dispersal behaviour among siblings. Journal of Evolutionary Biology. 13(4):707–719. doi:10.1046/j.1420-9101.2000.00202.x.

Massot M, Clobert J, Lorenzon P, Rossi J-M. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. Journal of Animal Ecology. 71(2):253–261. doi:10.1046/j.1365-2656.2002.00592.x.

Massot M, Clobert J, Ferrière R. 2008. Climate warming, dispersal inhibition and extinction risk. Global Change Biology. 14(3):461–469. doi:10.1111/j.1365-2486.2007.01514.x.

Massot M, Clobert J, Montes-Poloni L, Haussy C, Cubo J, Meylan S. 2011. An integrative study of ageing in a wild population of common lizards: Integrative study of ageing. Functional Ecology. 25(4):848–858. doi:10.1111/j.1365-2435.2011.01837.x.

Massot M, Aragón P. 2013. Phenotypic Resonance from a Single Meal in an Insectivorous Lizard. Current Biology. 23(14):1320–1323. doi:10.1016/j.cub.2013.05.047.

Matthysen E. 2005. Density-dependent dispersal in birds and mammals. Ecography. 28(3):403–416. doi:10.1111/j.0906-7590.2005.04073.x.

Matthysen E. 2012. Multicausality of dispersal: a review. In: Dispersal Ecology and Evolution. p. 3–18.

Mayer M, Zedrosser A, Rosell F. 2017. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. Animal Behaviour. 123:375–382. doi:10.1016/j.anbehav.2016.11.020.

Maynard-Smith J, Harper D. 2003. Animal Signals. Oxford University Press.

McCauley SJ. 2010. Body size and social dominance influence breeding dispersal in male *Pachydiplax longipennis* (Odonata). Ecological Entomology. 35(3):377–385. doi:10.1111/j.1365-2311.2010.01191.x.

McCauley SJ, Rowe L. 2010 Aug 23. Notonecta exhibit threat-sensitive, predator-induced dispersal. Biology Letters. doi:10.1098/rsbl.2009.1082.

McCune KB, Valente JJ, Jablonski PG, Lee S, Ha RR. 2022. Social behavior mediates the use of social and personal information in wild jays. Sci Rep. 12(1):2494. doi:10.1038/s41598-022-06496-x.

McDougall PT, Réale D, Sol D, Reader SM. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. Animal Conservation. 9(1):39–48. doi:10.1111/j.1469-1795.2005.00004.x.

McInerny C. 2013. Observations on a population of adders, slow-worms and common lizards on Loch Lomondside, Scotland. https://www.semanticscholar.org/paper/Observations-on-a-population-of-adders%2C-slow-worms-McInerny/be8f312b54683e2ad40244ad18e47fba351efbbf.

Melo VW de, Lowe R, Hurd PJ, Petchey OL. 2020. Phenotypic responses to temperature in the ciliate *Tetrahymena thermophila*. Ecology and Evolution. 10(14):7616–7626. doi:https://doi.org/10.1002/ece3.6486.

Merrick MJ, Koprowski JL. 2016 Nov 16. Evidence of natal habitat preference induction within one habitat type. Proceedings of the Royal Society B: Biological Sciences. doi:10.1098/rspb.2016.2106.

Merrick MJ, Koprowski JL. 2017. Altered natal dispersal at the range periphery: The role of behavior, resources, and maternal condition. Ecology and Evolution. 7(1):58–72. doi:10.1002/ece3.2612.

Mesoudi A, Chang L, Dall SRX, Thornton A. 2016. The Evolution of Individual and Cultural Variation in Social Learning. Trends in Ecology & Evolution. 31(3):215–225. doi:10.1016/j.tree.2015.12.012.

Mestre L, Bonte D. 2012. Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider. Behav Ecol. 23(4):759–764. doi:10.1093/beheco/ars024.

Meylan S, Belliure J, Clobert J, de Fraipont M. 2002. Stress and Body Condition as Prenatal and Postnatal Determinants of Dispersal in the Common Lizard (*Lacerta vivipara*). Hormones and Behavior. 42(3):319–326. doi:10.1006/hbeh.2002.1827.

Meylan S, Clobert J. 2004. Maternal Effects on Offspring Locomotion: Influence of Density and Corticosterone Elevation in the Lizard *Lacerta vivipara*. Physiological and Biochemical Zoology. 77(3):450–458. doi:10.1086/383508.

Meylan S, Fraipont MD, Clobert J. 2004. Maternal size and stress and offspring philopatry: An experimental study in the common lizard (*Lacerta vivipara*). Écoscience. 11(1):123–129. doi:10.1080/11956860.2004.11682816.

Meylan S, Clobert J, Sinervo B. 2007. Adaptive significance of maternal induction of density-dependent phenotypes. Oikos. 116(4):650–661. doi:10.1111/j.0030-1299.2007.15432.x.

Meylan S, Fraipont M de, Aragon P, Vercken E, Clobert J. 2009. Are dispersal-dependent behavioral traits produced by phenotypic plasticity? Journal of Experimental Zoology Part A: Ecological Genetics and Physiology. 311A(5):377–388. doi:10.1002/jez.533.

Meylan S, Lallemand F, Haussy C, Bleu J, Miles D. 2017. Arginine vasotocin inhibits social interactions and enhances essential activities in male common lizards (*Zootoca vivipara*). General and Comparative Endocrinology. 243:10–14. doi:10.1016/j.ygcen.2016.08.012.

Michelangeli M, Payne E, Spiegel O, Sinn DL, Leu ST, Gardner MG, Sih A. 2022. Personality, spatiotemporal ecological variation and resident/explorer movement syndromes in the sleepy lizard. Journal of Animal Ecology. 91(1):210–223. doi:10.1111/1365-2656.13616.

Miller CW, Fletcher RJ, Anderson BD, Nguyen LD. 2012. Natal social environment influences habitat selection later in life. Animal Behaviour. 83(2):473–477. doi:10.1016/j.anbehav.2011.11.022.

Milleret C, Ordiz A, Sanz-Pérez A, Uzal A, Carricondo-Sanchez D, Eriksen A, Sand H, Wabakken P, Wikenros C, Åkesson M, et al. 2019. Testing the influence of habitat experienced during the natal phase on habitat selection later in life in Scandinavian wolves. Sci Rep. 9(1):6526. doi:10.1038/s41598-019-42835-1.

Møller AP, Saino N, Taramino G, Galeotti P, Ferrario S. 1998. Paternity and Multiple Signaling: Effects of a Secondary Sexual Character and Song on Paternity in the Barn Swallow. The American Naturalist. 151(3):236–242. doi:10.1086/286114.

Moller A, Biard C, Blount J, Houston D, Ninni P, Saino N, Surai P. 2000. Carotenoid-dependent Signals: Indicators of Foraging Efficiency, Immunocompetence or Detoxification Ability? Avian and Poultry Biology Reviews. 11:137–159.

Monaghan P. 2008. Early growth conditions, phenotypic development and environmental change. Philosophical Transactions of the Royal Society B: Biological Sciences. 363(1497):1635–1645. doi:10.1098/rstb.2007.0011.

Mönkkönen M, Härdling R, Forsman JT, Tuomi J. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. Evolutionary Ecology. 13(1):93–106. doi:10.1023/A:1006590215306.

Mönkkönen M, Forsman JT, Kananoja T, Ylönen H. 2009. Indirect cues of nest predation risk and avian reproductive decisions. Biology Letters. 5(2):176–178. doi:10.1098/rsbl.2008.0631.

Moore AJ, Haynes KF, Preziosi RF, Moore PJ. 2002. The Evolution of Interacting Phenotypes: Genetics and Evolution of Social Dominance. The American Naturalist. 160(S6):S186–S197. doi:10.1086/342899.

Moore JC, Loggenberg A, Greeff JM. 2006. Kin competition promotes dispersal in a male pollinating fig wasp. Biology Letters. 2(1):17–19. doi:10.1098/rsbl.2005.0370.

Morales-González A, Fernández-Gil A, Quevedo M, Revilla E. 2021. Patterns and determinants of dispersal in grey wolves (*Canis lupus*). Biological Reviews. n/a(n/a). doi:10.1111/brv.12807.

Moran PAP. 1948. The Interpretation of Statistical Maps. Journal of the Royal Statistical Society Series B (Methodological). 10(2):243–251.

Moreira PL, López P, Martín J. 2008. Discrimination of conspecific faecal chemicals and spatial decisions in juvenile Iberian rock lizards (*Lacerta monticola*). acta ethol. 11(1):26–33. doi:10.1007/s10211-007-0038-6.

Morel-Journel T, Thuillier V, Pennekamp F, Laurent E, Legrand D, Chaine AS, Schtickzelle N. 2020. A multidimensional approach to the expression of phenotypic plasticity. Functional Ecology. 34(11):2338–2349. doi:10.1111/1365-2435.13667.

Morinay J, Forsman JT, Kivelä SM, Gustafsson L, Doligez B. 2018. Heterospecific Nest Site Copying Behavior in a Wild Bird: Assessing the Influence of Genetics and Past Experience on a Joint Breeding Phenotype. Frontiers in Ecology and Evolution. 5. doi:10.3389/fevo.2017.00167

Morinay J, Forsman JT, Doligez B. 2020a. Heterospecific song quality as social information for settlement decisions: an experimental approach in a wild bird. Animal Behaviour. 161:103–113.
doi:10.1016/j.anbehav.2020.01.002.

Morinay J, Forsman JT, Germain M, Doligez B. 2020b. Behavioural traits modulate the use of heterospecific social information for nest site selection: experimental evidence from a wild bird population. Proceedings of the Royal Society B. doi:10.1098/rspb.2020.0265.

Morosinotto C, Villers A, Thomson RL, Varjonen R, Korpimäki E. 2017. Competitors and predators alter settlement patterns and reproductive success of an intraguild prey. Ecological Monographs. 87(1):4–20.
doi:10.1002/ecm.1238.

Morris DW. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evol Ecol. 6(5):412–432. doi:10.1007/BF02270701.

Morris DW, Diffendorfer JE, Lundberg P. 2004. Dispersal among habitats varying in fitness: reciprocating migration through ideal habitat selection. Oikos. 107(3):559–575. doi:10.1111/j.0030-1299.2004.12894.x.

Morse DH. 1970. Territorial and Courtship Songs of Birds. Nature. 226(5246):659–661. doi:10.1038/226659a0.

Mortier F, Jacob S, Vandegehuchte ML, Bonte D. 2018 Feb 19. Habitat choice stabilizes metapopulation dynamics through increased ecological specialisation. bioRxiv.:267575. Doi:10.1101/267575.

Mugabo M, Marquis O, Perret S, Galliard JFL. 2010. Immediate and delayed life history effects caused by food deprivation early in life in a short-lived lizard. Journal of Evolutionary Biology. 23(9):1886–1898.
doi:10.1111/j.1420-9101.2010.02052.x.

Mugabo M, Marquis O, Perret S, Le Galliard J-F. 2011. Direct and socially-mediated effects of food availability late in life on life-history variation in a short-lived lizard. Oecologia. 166(4):949–960. doi:10.1007/s00442-011-1933-0.

Mugabo M, Perret S, Legendre S, Le Galliard J-F. 2013. Density-dependent life history and the dynamics of small populations. Journal of Animal Ecology. 82(6):1227–1239. doi:10.1111/1365-2656.12109.

Mugabo M, Perret S, Decencière B, Meylan S, Le Galliard J-F. 2015. Density-dependent immunity and parasitism risk in experimental populations of lizards naturally infested by ixodid ticks. Ecology. 96(2):450–460. doi:10.1890/14-0524.1.

Murai M, Backwell PRY. 2006. A conspicuous courtship signal in the fiddler crab *Uca perplexa*: female choice based on display structure. Behav Ecol Sociobiol. 60(5):736–741. doi:10.1007/s00265-006-0217-x.

N

Nagelkerke NJD. 1991. A note on a general definition of the coefficient of determination. Biometrika. 78(3):691–692. doi:10.1093/biomet/78.3.691.

Naguib M, Wiley RH. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Animal Behaviour. 62(5):825–837. doi:10.1006/anbe.2001.1860.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution. 4(2):133–142. doi:10.1111/j.2041-210x.2012.00261.x.

Nakano R, Skals N, Takanashi T, Surlykke A, Koike T, Yoshida K, Maruyama H, Tatsuki S, Ishikawa Y. 2008. Moths produce extremely quiet ultrasonic courtship songs by rubbing specialized scales. Proceedings of the National Academy of Sciences. 105(33):11812–11817. doi:10.1073/pnas.0804056105.

Nally RM, Walsh CJ. 2004. Hierarchical Partitioning Public-domain Software. Biodiversity and Conservation. 13(3):659–660. doi:10.1023/B:BIOC.0000009515.11717.0b.

Narins PM. 2001. Vibration Communication in Vertebrates. In: Barth FG, Schmid A, editors. Ecology of Sensing. Berlin, Heidelberg: Springer. p. 127–148.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. PNAS. 105(49):19052–19059. doi:10.1073/pnas.0800375105.

Neff EP. 2018. Zebrafish get oriented. Lab Anim. 47(9):233–233. doi:10.1038/s41684-018-0145-1.

Nelsen EM. 1978. Transformation in *Tetrahymena thermophila*: Development of an inducible phenotype. Developmental Biology. 66(1):17–31. doi:10.1016/0012-1606(78)90270-1.

Nelson RM, Greeff JM. 2011. Sex ratio dependent dispersal when sex ratios vary between patches. Journal of Theoretical Biology. 290:81–87. doi:10.1016/j.jtbi.2011.08.030.

Nelson-Flower MJ, Wiley EM, Flower TP, Ridley AR. 2018. Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance. Journal of Animal Ecology. 87(5):1227–1238. doi:10.1111/1365-2656.12814.

Németh Z, Moore FR. 2007. Unfamiliar stopover sites and the value of social information during migration. J Ornithol. 148(2):369–376. doi:10.1007/s10336-007-0209-2.

Nicolaus M, Edelaar P. 2018. Comparing the consequences of natural selection, adaptive phenotypic plasticity, and matching habitat choice for phenotype–environment matching, population genetic structure, and reproductive isolation in meta-populations. Ecology and Evolution. 8(8):3815–3827. doi:10.1002/ece3.3816.

Noble DWA, Byrne RW, Whiting MJ. 2014. Age-dependent social learning in a lizard. Biology Letters. 10(7):20140430. doi:10.1098/rsbl.2014.0430.

Nocera JJ, Forbes GJ, Giraldeau L-A. 2009. Aggregations from using inadvertent social information: a form of ideal habitat selection. Ecography. 32(1):143–152. doi:10.1111/j.1600-0587.2008.05614.x.

Noguera JC, Velando A. 2019. Bird embryos perceive vibratory cues of predation risk from clutch mates. Nat Ecol Evol. 3(8):1225–1232. doi:10.1038/s41559-019-0929-8.

Nomakuchi S, Park PJ, Bell MA. 2009. Correlation between exploration activity and use of social information in three-spined sticklebacks. Behav Ecol. 20(2):340–345. doi:10.1093/beheco/arp001.

Nowicki P, Vrabec V, Binzenhöfer B, Feil J, Zakšek B, Hovestadt T, Settele J. 2014. Butterfly dispersal in inhospitable matrix: rare, risky, but long-distance. Landscape Ecol. 29(3):401–412. doi:10.1007/s10980-013-9971-0.

O

O'brien RM. 2007. A Caution Regarding Rules of Thumb for Variance Inflation Factors. Qual Quant. 41(5):673–690. doi:10.1007/s11135-006-9018-6.

Olsson M, Wapstra E, Olofsson C. 2002. Offspring size-number strategies: Experimental manipulation of offspring size in a viviparous lizard (*Lacerta vivipara*). Functional Ecology. 16:135–140. doi:10.1046/j.0269-8463.2001.00600.x.

O'Mara MT, Dechmann DKN, Page RA. 2014. Frugivorous bats evaluate the quality of social information when choosing novel foods. Behav Ecol. 25(5):1233–1239. doi:10.1093/beheco/aru120.

Oro D, Bécares J, Bartumeus F, Arcos JM. 2021. High frequency of prospecting for informed dispersal and colonisation in a social species at large spatial scale. Oecologia. 197(2):395–409. doi:10.1007/s00442-021-05040-4.

Otsuki H, Yano S. 2014. Predation risk increases dispersal distance in prey. Naturwissenschaften. 101(6):513–516. doi:10.1007/s00114-014-1181-3.

Owings DH, Morton ES. 1998. Animal Vocal Communication: A New Approach. Cambridge University Press.

Page RA, Jones PL. 2016. Overcoming Sensory Uncertainty: Factors Affecting Foraging Decisions in Frog-Eating Bats. In: Bee MA, Miller CT, editors. Psychological Mechanisms in Animal Communication. Cham: Springer International Publishing. p. 285–312. https://doi.org/10.1007/978-3-319-48690-1_11.

P

Parejo D, White J, Danchin E. 2007. Settlement decisions in blue tits: difference in the use of social information according to age and individual success. Naturwissenschaften. 94(9):749–757. doi:10.1007/s00114-007-0253-z.

Parejo D, Danchin É, Silva N, White JF, Dreiss AN, Avilés JM. 2008. Do great tits rely on inadvertent social information from blue tits? A habitat selection experiment. Behav Ecol Sociobiol. 62(10):1569–1579. doi:10.1007/s00265-008-0586-4.

Parejo D, Avilés JM, Rodríguez J. 2012. Alarm calls modulate the spatial structure of a breeding owl community. Proceedings of the Royal Society B: Biological Sciences. 279(1736):2135–2141. doi:10.1098/rspb.2011.2601.

Parker GA, Sutherland WJ. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. Animal Behaviour. 34(4):1222–1242. doi:10.1016/S0003-3472(86)80182-8.

Pasqualone AA, Davis JM. 2011. The use of conspecific phenotypic states as information during reproductive decisions. Animal Behaviour. 82(2):281–284. doi:10.1016/j.anbehav.2011.05.002.

Payo-Payo A, Sanz-Aguilar A, Genovart M, Bertolero A, Piccardo J, Camps D, Ruiz-Olmo J, Oro D. 2018. Predator arrival elicits differential dispersal, change in age structure and reproductive performance in a prey population. Sci Rep. 8(1):1971. doi:10.1038/s41598-018-20333-0.

Pellerin F, Cote J, Bestion E, Aguilée R. 2019. Matching habitat choice promotes species persistence under climate change. Oikos. 128(2):221–234. doi:10.1111/oik.05309.

Pennekamp F, Schtickzelle N. 2013. Implementing image analysis in laboratory-based experimental systems for ecology and evolution: a hands-on guide. Methods in Ecology and Evolution. 4(5):483–492. doi:10.1111/2041-210X.12036.

Pennekamp F, Mitchell KA, Chaine A, Schtickzelle N. 2014a. Dispersal Propensity in *Tetrahymena thermophila* Ciliates—a Reaction Norm Perspective. Evolution. 68(8):2319–2330. doi:10.1111/evo.12428.

Pennekamp F, Schtickzelle N, Petchey OL. 2014b. Bemovi, software for extracting BEhaviour and MOrphology from VIdeos. bioRxiv.:011072. Doi:10.1101/011072.

Pennekamp F, Schtickzelle N, Petchey OL. 2015. BEMOVI, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. Ecology and Evolution. 5(13):2584–2595. doi:10.1002/ece3.1529.

Pennekamp F, Clobert J, Schtickzelle N. 2019. The interplay between movement, morphology and dispersal in Tetrahymena ciliates. PeerJ. 7:e8197. doi:10.7717/peerj.8197.

Pereira AG, Cruz A, Lima SQ, Moita MA. 2012. Silence resulting from the cessation of movement signals danger. Current Biology. 22(16):R627–R628. doi:10.1016/j.cub.2012.06.015.

Pérez-Cembranos A, Pérez-Mellado V. 2015. Local enhancement and social foraging in a non-social insular lizard. Anim Cogn. 18(3):629–637. doi:10.1007/s10071-014-0831-3.

Perrin N, Mazalov V. 1999. Dispersal and Inbreeding Avoidance. The American Naturalist. 154(3):282–292. doi:10.1086/303236.

Perrin N, Lehmann L. 2001. Is Sociality Driven by the Costs of Dispersal or the Benefits of Philopatry? A Role for Kin-Discrimination Mechanisms. The American Naturalist. 158(5):471–483. doi:10.1086/323114.

Perry G, Garland T. 2002. Lizard Home Ranges Revisited: Effects of Sex, Body Size, Diet, Habitat, and Phylogeny. Ecology. 83(7):1870–1885. doi:https://doi.org/10.1890/0012-9658(2002)083[1870:LHRREO]2.0.CO;2.

Peterson MA, Denno R. 1995. Chapter 6 – Density-Dependent Dispersal and Its Consequences for Population Dynamics.

Pike TW, Kendal JR, Rendell LE, Laland KN. 2010. Learning by proportional observation in a species of fish. Behav Ecol. 21(3):570–575. doi:10.1093/beheco/arq025.

Pike TW, Laland KN. 2010. Conformist learning in nine-spined sticklebacks' foraging decisions. Biology Letters. 6(4):466–468. doi:10.1098/rsbl.2009.1014.

Pilon G. 2020 Dec 16. Influence des capacités cognitives et du niveau d'incertitude sur l'utilisation d'information sociale chez le diamant mandarin. Thèse de doctorat. https://papyrus.bib.umontreal.ca/xmlui/handle/1866/24420.

Pilorge T, Castanet J. 1981. Détermination de l'age dans une population naturelle du lézard vivipare (*Lacerta vivipara* Jacquin 1787). Acta Oecol, (Oecol Gener) 2:3–16

Pilorge T. 1982. Régime alimentaire de *Lacerta vivipara* et *Rana temporaria* dans deux populations sympatriques du Puy-de-Dôme. Amphibia-Reptilia. 3(1):27–31. doi:10.1163/156853882X00130.

Pilorge T, Clobert J, Massot M. 1987. Life-History variations according to sex and age in *Lacerta vivipara*. In: Proceedings of the 4th Ordinary General Meeting of the Societas Europeae Herpetologica.

Pilorge T. 1987. Density, Size Structure, and Reproductive Characteristics of Three Populations of *Lacerta vivipara* (Sauria: Lacertidae). Herpetologica. 43(3):345–356.

Piper WH. 2011. Making habitat selection more "familiar": a review. Behav Ecol Sociobiol. 65(7):1329–1351. doi:10.1007/s00265-011-1195-1.

Piper WH, Palmer MW, Banfield N, Meyer MW. 2013. Can settlement in natal-like habitat explain maladaptive habitat selection? Proceedings of the Royal Society B: Biological Sciences. 280(1765):20130979. doi:10.1098/rspb.2013.0979.

Platzen D, Magrath RD. 2004. Parental alarm calls suppress nestling vocalization. Proceedings of the Royal Society of London Series B: Biological Sciences. 271(1545):1271–1276. doi:10.1098/rspb.2004.2716.

Poethke HJ, Weisser WW, Hovestadt T. 2010. Predator-Induced Dispersal and the Evolution of Conditional Dispersal in Correlated Environments. The American Naturalist. 175(5):577–586. doi:10.1086/651595.

Polis GA. 1984. Age Structure Component of Niche Width and Intraspecific Resource Partitioning: Can Age Groups Function as Ecological Species? The American Naturalist. 123(4):541–564.

Pollock MS, Pollock RJ, Chivers DP. 2006. Social Context Influences the Antipredator Behaviour of Fathead Minnows to Chemical Alarm Cues. Ethology. 112(8):801–806. doi:10.1111/j.1439-0310.2006.01222.x.

Ponchon A, Garnier R, Grémillet D, Boulinier T. 2015. Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. Diversity and Distributions. 21(1):88–100. doi:10.1111/ddi.12273.

Potrich D, Rugani R, Sovrano VA, Regolin L, Vallortigara G. 2019. Use of numerical and spatial information in ordinal counting by zebrafish. Sci Rep. 9(1):18323. doi:10.1038/s41598-019-54740-8.

Powell M. 2009 Jan 1. The BOBYQA Algorithm for Bound Constrained Optimization without Derivatives. Technical Report, Department of Applied Mathematics and Theoretical Physics.

Pusey AE. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution. 2(10):295–299. doi:10.1016/0169-5347(87)90081-4.

Pyke GH, Pulliam HR, Charnov EL. 1977. Optimal Foraging: A Selective Review of Theory and Tests. The Quarterly Review of Biology. 52(2):137–154. doi:10.1086/409852.

Pyke GH. 2019. Animal Movements – An Optimal Foraging Theory Approach. In: Choe JC, editor. Encyclopedia of Animal Behavior (Second Edition). Oxford: Academic Press. p. 149–156.

Pyle P, Nettleship D. 2001. Age at First Breeding and Natal Dispersal in a Declining Population of Cassin's Auklet. Auk. 118(4):996–1007. doi:10.1093/auk/118.4.996.

Q/R

Quinn JL, Whittingham MJ, Butler SJ, Cresswell W. 2006. Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. Journal of Avian Biology. 37(6):601–608. doi:10.1111/j.2006.0908-8857.03781.x.

Rafacz M, Templeton JJ. 2003. Environmental Unpredictability and the Value of Social Information for Foraging Starlings. Ethology. 109(12):951–960. doi:10.1046/j.0179-1613.2003.00935.x.

Raffard A, Campana J, Legrand D, Schtickzelle N, Jacob S. 2021. Dispersal syndromes affect ecosystem functioning in ciliate microcosms. bioRxiv.:2021.02.19.431939. doi:10.1101/2021.02.19.431939.

Raffard A, Bestion E, Cote J, Haegeman B, Schtickzelle N, Jacob S. 2022. Dispersal syndromes can link intraspecific trait variability and meta-ecosystem functioning. Trends in Ecology & Evolution. 37(4):322–331.

doi:10.1016/j.tree.2021.12.001.

Rasmussen J. 2015. The Ecological Importance of Extrinsic and Intrinsic Drivers of Animal Movement.

Rauber R, Manser MB. 2018. Experience of the signaller explains the use of social versus personal information in the context of sentinel behaviour in meerkats. Sci Rep. 8(1):11506. doi:10.1038/s41598-018-29678-y.

Reader SM, Lefebvre L. 2001. Social learning and sociality. Behavioral and Brain Sciences. 24(2):353–355. doi:10.1017/S0140525X01543964.

Reader SM, Kendal JR, Laland KN. 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. Animal Behaviour. 66(4):729–739. doi:10.1006/anbe.2003.2252.

Reader SM. 2014. Experiential effects on mirror systems and social learning: Implications for social intelligence. Behavioral and Brain Sciences. 37(2):217–218. doi:10.1017/S0140525X1300246X.

Reader SM. 2015. Causes of Individual Differences in Animal Exploration and Search. Topics in Cognitive Science. 7(3):451–468. doi:10.1111/tops.12148.

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society B: Biological Sciences. 365(1560):4051–4063. doi:10.1098/rstb.2010.0208.

Ridley AR. 2012. Invading together: the benefits of coalition dispersal in a cooperative bird. Behav Ecol Sociobiol. 66(1):77–83. doi:10.1007/s00265-011-1255-6.

Riehl C, Stern CA. 2015. How cooperatively breeding birds identify relatives and avoid incest: New insights into dispersal and kin recognition. BioEssays. 37(12):1303–1308. doi:10.1002/bies.201500120.

Rieucau G, Giraldeau L-A. 2009. Persuasive companions can be wrong: the use of misleading social information in nutmeg mannikins. Behav Ecol. 20(6):1217–1222. doi:10.1093/beheco/arp121.

Rieucau G, Giraldeau L-A. 2011. Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 366(1567):949–957. doi:10.1098/rstb.2010.0325.

Riotte-Lambert L, Matthiopoulos J. 2019 Nov 5. Environmental Predictability as a Cause and Consequence of Animal Movement. Trends in Ecology & Evolution. doi:10.1016/j.tree.2019.09.009.

Rivera-Gutierrez HF, Pinxten R, Eens M. 2011. Songs differing in consistency elicit differential aggressive response in territorial birds. Biology Letters. 7(3):339–342. doi:10.1098/rsbl.2010.0962.

Rivera-Hernández IAE, Crane AL, Pollock MS, Ferrari MCO. 2022 Jan 31. Disturbance cues function as a background risk cue but not as an associative learning cue in tadpoles. Anim Cogn. doi:10.1007/s10071-022-01599-4.

le Roex N, Mann GKH, Hunter LTB, Balme GA. 2022. Big competition for small spots? Conspecific density drives home range size in male and female leopards. Journal of Zoology. 316(3):178–187. doi:10.1111/jzo.12942.

Romano V, Martins AF, Ruiz-Miranda CR. 2019. Unraveling the dispersal patterns and the social drivers of natal emigration of a cooperative breeding mammal, the golden lion tamarin. American Journal of Primatology. 81(3):e22959. doi:10.1002/ajp.22959.

Romero-Diaz C, Campos SM, Herrmann MA, Soini HA, Novotny MV, Hews DK, Martins EP. 2021. Composition and compound proportions affect the response to complex chemical signals in a spiny lizard. Behav Ecol Sociobiol. 75(2):42.
doi:10.1007/s00265-021-02987-5.

Romero-González JE, Solvi C, Chittka L. 2020. Honey bees adjust colour preferences in response to concurrent social information from conspecifics and heterospecifics. Animal Behaviour. 170:219–228. doi:10.1016/j.anbehav.2020.10.008.

Ron R, Fragman-Sapir O, Kadmon R. 2018. Dispersal increases ecological selection by increasing effective community size. Proceedings of the National Academy of Sciences. 115(44):11280–11285. doi:10.1073/pnas.1812511115.

Ronce O, Clobert J, Massot M. 1998. Natal dispersal and senescence. PNAS. 95(2):600–605.
doi:10.1073/pnas.95.2.600.

Ronce O, Gandon S, Rousset F. 2000. Kin Selection and Natal Dispersal in an Age-Structured Population. Theoretical Population Biology. 58(2):143–159. doi:10.1006/tpbi.2000.1476.

Ronce O, Olivieri I, Clobert J, Danchin EGJ. 2001. Perspectives on the Study of Dispersal Evolution. In: Nichols JCEDAADJD, editor. Dispersal. Oxford University Press. p. 341–357.

Ronce O. 2007. How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution. Annual Review of Ecology, Evolution, and Systematics. 38(1):231–253. doi:10.1146/annurev.ecolsys.38.091206.095611.

Rosa P, Nguyen V, Dubois F. 2012. Individual differences in sampling behaviour predict social information use in zebra finches. Behav Ecol Sociobiol. 66(9):1259–1265. doi:10.1007/s00265-012-1379-3.

Rosenthal GG, Marshall NJ. 2011. Sensory systems, perception, and learning | Communication Behavior: Visual

Signals. In: Farrell AP, editor. Encyclopedia of Fish Physiology. San Diego: Academic Press. p. 692–698.

Roulin A. 2016. Condition-dependence, pleiotropy and the handicap principle of sexual selection in melanin-based colouration. Biol Rev Camb Philos Soc. 91(2):328–348. doi:10.1111/brv.12171.

Rousset F, Gandon S. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. Journal of Evolutionary Biology. 15(4):515–523. doi:10.1046/j.1420-9101.2002.00430.x.

Rowland WJ, Grindle N, Maclaren RD, Granquist R. 2002. Male preference for a subtle posture cue that signals spawning readiness in female sticklebacks. Animal Behaviour. 63(4):743–748. doi:10.1006/anbe.2001.1956.

Roy D. 1997. Communication signals and sexual selection in amphibians. Current Science. 72(12):923–927.

Royston P, Sauerbrei W. 2009. Bootstrap Assessment of the Stability of Multivariable Models. The Stata Journal. 9(4):547–570. doi:10.1177/1536867X0900900403.

Rozen-Rechels D, Dupoué A, Meylan S, Decencière B, Guingand S, Le Galliard J-F. 2018. Water restriction in viviparous lizards causes transgenerational effects on behavioral anxiety and immediate effects on exploration behavior. Behav Ecol Sociobiol. 72(2):23. doi:10.1007/s00265-018-2443-4.

Rozen-Rechels D, Rutschmann A, DupouÉ A, Blaimont P, Chauveau V, Miles DB, Guillon M, Richard M, Badiane A, Meylan S, et al. 2021. Interaction of hydric and thermal conditions drive geographic variation in thermoregulation in a widespread lizard. Ecological Monographs. 91(2):e01440. doi:10.1002/ecm.1440.

Rushing CS, Dudash MR, Marra PP. 2015. Habitat features and long-distance dispersal modify the use of social information by a long-distance migratory bird. Journal of Animal Ecology. 84(6):1469–1479. doi:10.1111/1365-2656.12395.

Rutschmann A, Miles DB, Le Galliard J-F, Richard M, Moulherat S, Sinervo B, Clobert J. 2016. Climate and habitat interact to shape the thermal reaction norms of breeding phenology across lizard populations. J Anim Ecol. 85(2):457–466. doi:10.1111/1365-2656.12473.

S

Saastamoinen M, Bocedi G, Cote J, Legrand D, Guillaume F, Wheat CW, Fronhofer EA, Garcia C, Henry R, Husby A, et al. 2018. Genetics of dispersal. Biological Reviews. 93(1):574–599. doi:10.1111/brv.12356.

Saïd S, Gaillard J-M, Widmer O, Débias F, Bourgoin G, Delorme D, Roux C. 2009. What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos. 118(9):1299–1306. doi:10.1111/j.1600-0706.2009.17346.x.

Samplonius JM, Both C. 2017. Competitor phenology as a social cue in breeding site selection. Journal of Animal Ecology. 86(3):615–623. doi:10.1111/1365-2656.12640.

Sánchez D, Nieh JC, Vandame R. 2008. Experience-based interpretation of visual and chemical information at food sources in the stingless bee *Scaptotrigona mexicana*. Animal Behaviour. 76(2):407–414. doi:10.1016/j.anbehav.2008.04.00

Sánchez-González JR, Nicieza AG. 2021. Individual differences in dominance-related traits drive dispersal and settlement in hatchery-reared juvenile brown trout. Sci Rep. 11(1):7277. doi:10.1038/s41598-021-86613-4.

San-Jose LM, Peñalver-Alcázar M, Huyghe K, Breedveld MC, Fitze PS. 2016. Inter-class competition in stage-structured populations: effects of adult density on life-history traits of adult and juvenile common lizards. Oecologia. 182(4):1063–1074. doi:10.1007/s00442-016-3738-7.

Sanz-Pérez A, Ordiz A, Sand H, Swenson JE, Wabakken P, Wikenros C, Zimmermann B, Åkesson M, Milleret C. 2018. No place like home? A test of the natal habitat-biased dispersal hypothesis in Scandinavian wolves. Royal Society Open Science. 5(12):181379. doi:10.1098/rsos.181379.

Sasaki T, Pratt SC. 2013. Ants learn to rely on more informative attributes during decision-making. Biology Letters. 9(6):20130667. doi:10.1098/rsbl.2013.0667.

Scandolara C, Lardelli R, Sgarbi G, Caprioli M, Ambrosini R, Rubolini D, Saino N. 2014. Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*). Behav Ecol. 25(1):180–190. doi:10.1093/beheco/art103.

Scheel D, Godfrey-Smith P, Lawrence M. 2016. Signal Use by Octopuses in Agonistic Interactions. Current Biology. 26(3):377–382. doi:10.1016/j.cub.2015.12.033.

Scheiner SM. 2016. Habitat Choice and Temporal Variation Alter the Balance between Adaptation by Genetic Differentiation, a Jack-of-All-Trades Strategy, and Phenotypic Plasticity. The American Naturalist. 187(5):633–646. doi:10.1086/685812.

Schmidt KA, Dall SRX, Van Gils JA. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos. 119(2):304–316. doi:10.1111/j.1600-0706.2009.17573.x.

Schmidt KA, Johansson J, Betts MG. 2015. Information-Mediated Allee Effects in Breeding Habitat Selection. The American Naturalist. doi:10.1086/683659.

Schmidt KA, Massol F. 2019. Habitat selection and the value of information in heterogenous landscapes. Oikos. 128(4):457–467. doi:10.1111/oik.05722.

Schneeberger K, Taborsky M. 2020. The role of sensory ecology and cognition in social decisions: Costs of acquiring information matter. Functional Ecology. 34(2):302–309. doi:10.1111/1365-2435.13488.

Schneider RAZ, Schneider RWS, Moore PA. 1999. Recognition of Dominance Status By Chemoreception in the Red Swamp Crayfish, *Procambarus clarkii*. J Chem Ecol. 25(4):781–794. doi:10.1023/A:1020888532513.

Schofield JA, Fenner AL, Pelgrim K, Bull CM, Schofield JA, Fenner AL, Pelgrim K, Bull CM. 2013. Male-biased movement in pygmy bluetongue lizards: implications for conservation. Wildl Res. 39(8):677–684. doi:10.1071/WR12098.

Schradin C, Schmohl G, Rödel HG, Schoepf I, Treffler SM, Brenner J, Bleeker M, Schubert M, König B, Pillay N. 2010. Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study. Animal Behaviour. 79(1):195–203. doi:10.1016/j.anbehav.2009.10.027.

Schtickzelle N, Mennechez G, Baguette M. 2006. Dispersal Depression with Habitat Fragmentation in the Bog Fritillary Butterfly. Ecology. 87(4):1057–1065. doi:10.1890/0012-9658(2006)87[1057:DDWHFI]2.0.CO;2.

Schtickzelle N, Fjerdingstad EJ, Chaine A, Clobert J. 2009. Cooperative social clusters are not destroyed by dispersal in a ciliate. BMC Evolutionary Biology. 9(1):251. doi:10.1186/1471-2148-9-251.

Searcy W, Nowicki S. 2010 Jan 1. Sexual Selection and the Evolution of Animal Signals. Encyclopedia of Neuroscience.:759–766. doi:10.1016/B978-008045046-9.01862-3.

Selonen V, Hanski IK, Desrochers A. 2007. Natal habitat-biased dispersal in the Siberian flying squirrel. Proceedings of the Royal Society B: Biological Sciences. 274(1621):2063–2068. doi:10.1098/rspb.2007.0570.

Senar JC. 2006. Color Displays as Intrasexual Signals of Aggression and Dominance. In: Bird coloration.

Seppänen J-T, Forsman JT, Mönkkönen M, Thomson RL. 2007. Social Information Use Is a Process Across Time, Space, and Ecology, Reaching Heterospecifics. Ecology. 88(7):1622–1633. doi:10.1890/06-1757.1.

Serrano D, Cortés-Avizanda A, Zuberogoitia I, Blanco G, Benítez JR, Ponchon C, Grande JM, Ceballos O, Morant J, Arrondo E, et al. 2021. Phenotypic and environmental correlates of natal dispersal in a long-lived territorial vulture. Sci Rep. 11(1):5424. doi:10.1038/s41598-021-84811-8.

Serrano D, Tella JL. 2003. Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. Journal of Animal Ecology. 72(3):400–410. doi:10.1046/j.1365-2656.2003.00707.x.

Serrano D, Tella JL, Donázar JA, Pomarol M. 2003. Social and Individual Features Affecting Natal Dispersal in the Colonial Lesser Kestrel. Ecology. 84(11):3044–3054. doi:10.1890/02-0231.

Serrano D, Forero MG, Donázar JA, Tella JL. 2004. Dispersal and Social Attraction Affect Colony Selection and Dynamics of Lesser Kestrels. Ecology. 85(12):3438–3447. doi:10.1890/04-0463.

Serrano D, Oro D, Ursúa E, Tella JL. 2005. Colony Size Selection Determines Adult Survival and Dispersal Preferences: Allee Effects in a Colonial Bird. The American Naturalist. 166(2):E22–E31. Doi:10.1086/431255.

Sharp SP, Simeoni M, Hatchwell BJ. 2008. Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. Proceedings of the Royal Society B: Biological Sciences. 275(1647):2125–2130. doi:10.1098/rspb.2008.0398.

Shaw AK. 2020. Causes and consequences of individual variation in animal movement. Mov Ecol. 8(1):12. doi:10.1186/s40462-020-0197-x.

Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013. Energy Landscapes Shape Animal Movement Ecology. The American Naturalist. 182(3):298–312. doi:10.1086/671257.

Sherman G, Visscher PK. 2002. Honeybee colonies achieve fitness through dancing. Nature. 419(6910):920–922. doi:10.1038/nature01127.

Shochat E, Abramsky Z, Pinshow B, Whitehouse MEA. 2002. Density-dependent habitat selection in migratory passerines during stopover: what causes the deviation from IFD? Evolutionary Ecology. 16(5):469–488. doi:10.1023/A:1020851801732.

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution. 19(7):372–378. doi:10.1016/j.tree.2004.04.009.

Sih A, Spiegel O, Godfrey S, Leu S, Bull CM. 2018. Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. Animal Behaviour. 136:195–205. doi:10.1016/j.anbehav.2017.09.008.

Sinervo B. 1990. The Evolution of Maternal Investment in Lizards: An Experimental and Comparative Analysis of Egg Size and Its Effects on Offspring Performance. Evolution. 44(2):279–294.
doi:https://doi.org/10.1111/j.1558-5646.1990.tb05198.x.

Sinervo B, Heulin B, Surget-Groba Y, Clobert J, Miles D, Corl A, Chaine A, Davis A. 2007. Models of Density-Dependent Genic Selection and a New Rock-Paper-Scissors Social System. The American naturalist. 170:663–80. doi:10.1086/522092.

Skellam JG. 1951. Random Dispersal in Theoretical Populations. Biometrika. 38(1/2):196–218. doi:10.2307/2332328.

Slatkin M. 1981. Estimating levels of gene flow in natural populations. Genetics. 99(2):323–335. doi:10.1093/genetics/99.2.323.

Smit JAH, van Oers K. 2019. Personality types vary in their personal and social information use. Animal Behaviour. 151:185–193. doi:10.1016/j.anbehav.2019.02.002.

Smith AT. 1974. The Distribution and Dispersal of Pikas: Influences of Behavior and Climate. Ecology. 55(6):1368–1376. doi:10.2307/1935464.

Smith JM. 1994. Must reliable signals always be costly? Animal Behaviour. 47(5):1115–1120. doi:10.1006/anbe.1994.1149.

Smith JE, Batzli GO. 2006. Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. Oikos. 112(1):209–217. doi:10.1111/j.0030-1299.2006.13431.x.

Smith R, Tan C, Srimani JK, Pai A, Riccione KA, Song H, You L. 2014. Programmed Allee effect in bacteria causes a tradeoff between population spread and survival. Proceedings of the National Academy of Sciences. 111(5):1969–1974. doi:10.1073/pnas.1315954111.

Smolla M, Alem S, Chittka L, Shultz S. 2016. Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. Biology Letters. doi:10.1098/rsbl.2016.0188.

Smolla M, Rosher C, Gilman RT, Shultz S. 2019 Jul 3. Reproductive skew affects social information use. Royal Society Open Science. doi:10.1098/rsos.182084.

Sorci G, Massot M, Clobert J. 1994. Maternal Parasite Load Increases Sprint Speed and Philopatry in Female Offspring of the Common Lizard. The American Naturalist. 144(1):153–164. doi:10.1086/285666.

Sorci G, Clobert J. 1995. Effects of maternal parasite load on offspring life-history traits in the common lizard (*Lacerta vivipara*). Journal of Evolutionary Biology. 8(6):711–723. doi:10.1046/j.1420-9101.1995.8060711.x.

Sorci G, Clobert J, Michalakis Y. 1996. Cost of Reproduction and Cost of Parasitism in the Common Lizard, *Lacerta vivipara*. Oikos. 76(1):121–130. doi:10.2307/3545754.

Sorci G, Clobert J. 1997. Environmental maternal effects on locomotor performance in the common lizard (*Lacerta vivipara*). Evol Ecol. 11(5):531–541. doi:10.1007/s10682-997-1509-y.

Sorci G, de Fraipont M, Clobert J. 1997. Host density and ectoparasite avoidance in the common lizard (*Lacerta vivipara*). Oecologia. 111(2):183–188. doi:10.1007/s004420050224.

Sorensen PW, Wisenden BD. 2015. Fish Pheromones and Related Cues. John Wiley & Sons.

Soto AP, McHenry MJ. 2020. Pursuit predation with intermittent locomotion in zebrafish. J Exp Biol. 223(24). doi:10.1242/jeb.230623.

Spencer WD. 2012. Home ranges and the value of spatial information. J Mammal. 93(4):929–947. doi:10.1644/12-MAMM-S-061.1.

Spiegel O, Leu ST, Bull CM, Sih A. 2017. What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecology Letters. 20(1):3–18. doi:10.1111/ele.12708.

Spottiswoode CN, Begg KS, Begg CM. 2016. Reciprocal signaling in honeyguide-human mutualism. Science. 353(6297):387–389. doi:10.1126/science.aaf4885.

Stamps JA. 1991. The effect of conspecifics on habitat selection in territorial species. Behav Ecol Sociobiol. 28(1):29–36. doi:10.1007/BF00172136.

Stamps J. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. p. 230–242.

Stamps JA, Krishnan VV, Reid ML. 2005. Search costs and habitat selection by dispersers. Ecology. 86(2):510–518. doi:10.1890/04-0516.

Stamps JA. 2006. The silver spoon effect and habitat selection by natal dispersers. Ecology Letters. 9(11):1179–1185. doi:10.1111/j.1461-0248.2006.00972.x.

Stamps JA, Davis JM. 2006. Adaptive effects of natal experience on habitat selection by dispersers. Animal Behaviour. 72(6):1279–1289. doi:10.1016/j.anbehav.2006.03.010.

Stamps JA, Swaisgood RR. 2007. Someplace like home: Experience, habitat selection and conservation biology. Applied Animal Behaviour Science. 102(3):392–409. doi:10.1016/j.applanim.2006.05.038.

Stamps J, Luttbeg B, Krishnan VV. 2009. Effects of Survival on the Attractiveness of Cues to Natal Dispersers. The American Naturalist. 173(1):41–46. doi:10.1086/593306.

Stamps JA, Krishnan VV, Willits NH. 2009. How Different Types of Natal Experience Affect Habitat Preference. The American Naturalist. 174(5):623–630. doi:10.1086/644526.

Steen R, Løw LM, Sonerud GA. 2011. Delivery of Common Lizards (Zootoca (Lacerta) vivipara) to nests of Eurasian Kestrels (*Falco tinnunculus*) determined by solar height and ambient temperature. Can J Zool. 89(3):199–205. doi:10.1139/Z10-109.

Steiger S, Schmitt T, Schaefer HM. 2011. The origin and dynamic evolution of chemical information transfer. Proceedings of the Royal Society B: Biological Sciences. 278(1708):970–979. doi:10.1098/rspb.2010.2285.

Stevens VM, Whitmee S, Le Galliard J-F, Clobert J, Böhning-Gaese K, Bonte D, Brändle M, Matthias Dehling D, Hof C, Trochet A, et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. Ecology Letters. 17(8):1039–1052. doi:10.1111/ele.12303.

Stienessen SC, Parrish JK. 2013. The effect of disparate information on individual fish movements and emergent group behavior. Behav Ecol. 24(5):1150–1160. doi:10.1093/beheco/art042.

Støen O-G, Zedrosser A, Sæbø S, Swenson JE. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. Oecologia. 148(2):356. doi:10.1007/s00442-006-0384-5.

Stoffel MA, Nakagawa S, Schielzeth H. 2021. partR2: partitioning R2 in generalized linear mixed models. PeerJ. 9:e11414. doi:10.7717/peerj.11414.

Strijbosch H, Rooy PTJC van, Voesenek L a. CJ. 1983. Homing behaviour of *Lacerta agilis* and *Lacerta vivipara* (Sauria, Lacertidae). Amphibia-Reptilia. 4(1):43–47. doi:10.1163/156853883X00256.

Strijbosch H, Creemers RCM. 1988. Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. Oecologia. 76(1):20–26. doi:10.1007/BF00379595.

Suh YH, Pesendorfer MB, Tringali A, Bowman R, Fitzpatrick JW. 2020. Investigating social and environmental predictors of natal dispersal in a cooperative breeding bird. Behav Ecol. 31(3):692–701. doi:10.1093/beheco/araa007.

Summers CH, Andrews TJ. 1996. Aggression, and the Acquisition and Function of Social Dominance in Female *Anolis Carolinensis*. Behaviour. 133(15–16):1265–1279. doi:10.1163/156853996X00396.

Sumpter DJT, Beekman M. 2003. From nonlinearity to optimality: pheromone trail foraging by ants. Animal Behaviour. 66(2):273–280. doi:10.1006/anbe.2003.2224.

Sumpter DJT, Krause J, James R, Couzin ID, Ward AJW. 2008. Consensus Decision Making by Fish. Current Biology. 18(22):1773–1777. doi:10.1016/j.cub.2008.09.064.

Surget-Groba Y, Heulin B, Guillaume C-P, Thorpe R, Kupriyanova L, Vogrin N, Maslak R, Mazzotti S, Venczel M, Ghira I, et al. 2001. Intraspecific Phylogeography of *Lacerta vivipara* and the Evolution of Viviparity. Molecular Phylogenetics and Evolution. 18:449–459. doi:10.1006/mpev.2000.0896.

Sutherland RJ, Hamilton DA. 2004. Rodent spatial navigation: at the crossroads of cognition and movement. Neuroscience & Biobehavioral Reviews. 28(7):687–697. doi:10.1016/j.neubiorev.2004.09.012.

Suzuki TN. 2011. Parental alarm calls warn nestlings about different predatory threats. Current Biology. 21(1):R15–R16. doi:10.1016/j.cub.2010.11.027.

Svensson, Wong. 2011. Carotenoid-based signals in behavioural ecology: a review. Behaviour. 148(2):131–189. doi:10.1163/000579510X548673.

Swaney W, Kendal J, Capon H, Brown C, Laland KN. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. Animal Behaviour. 62(3):591–598. doi:10.1006/anbe.2001.1788.

Szulkin M, Sheldon BC. 2008. Dispersal as a means of inbreeding avoidance in a wild bird population. Proceedings of the Royal Society B: Biological Sciences. 275(1635):703–711. doi:10.1098/rspb.2007.0989.

Szymkowiak J. 2013. Facing Uncertainty: How Small Songbirds Acquire and Use Social Information in Habitat Selection Process? Springer Science Reviews. 1(1):115–131. doi:10.1007/s40362-013-0012-9.

Szymkowiak J, Thomson RL, Kuczyński L. 2016. Wood warblers copy settlement decisions of poor quality conspecifics: support for the tradeoff between the benefit of social information use and competition avoidance. Oikos. 125(11):1561–1569. doi:10.1111/oik.03052.

Szymkowiak J, Thomson RL, Kuczyński L. 2017. Interspecific social information use in habitat selection decisions among migrant songbirds. Behav Ecol. 28(3):767–775. doi:10.1093/beheco/arx029.

Szymkowiak J, Thomson RL. 2019. Nest predator avoidance during habitat selection of a songbird varies with mast peaks and troughs. Behav Ecol Sociobiol. 73(7):91. doi:10.1007/s00265-019-2702-z.

T

Taborsky B, Oliveira RF. 2012. Social competence: an evolutionary approach. Trends in Ecology & Evolution. 27(12):679–688. doi:10.1016/j.tree.2012.09.003.

Tait C, Naug D. 2022 Jan 26. Interindividual variation in the use of social information during learning in honeybees. Proceedings of the Royal Society B. doi:10.1098/rspb.2021.2501.

Tan H, Hirst AG, Atkinson D, Kratina P. 2021. Body size and shape responses to warming and resource competition. Functional Ecology. 35(7):1460–1469. doi:10.1111/1365-2435.13789.

Tannerfeldt M, Elmhagen B, Angerbjörn A. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. Oecologia. 132(2):213–220. doi:10.1007/s00442-002-0967-8.

Tavolga WN, Popper AN, Fay RR. 2012. Hearing and Sound Communication in Fishes. Springer Science & Business Media.

Taylor TB, Buckling A. 2010. Competition and Dispersal in *Pseudomonas aeruginosa*. The American Naturalist. 176(1):83–89. doi:10.1086/652995.

Teitelbaum CS, Mueller T. 2019. Beyond Migration: Causes and Consequences of Nomadic Animal Movements. Trends in Ecology & Evolution. 34(6):569–581. doi:10.1016/j.tree.2019.02.005.

Templeton JJ, Kamil AC, Balda RP. 1999. Sociality and social learning in two species of corvids: The pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). Journal of Comparative Psychology. 113(4):450–455. doi:10.1037/0735-7036.113.4.450.

Terleph TA. 2004. The function of agonistic display behaviours in *Gnathonemus petersii*. Journal of Fish Biology. 64(5):1373–1385. doi:10.1111/j.0022-1112.2004.00401.x.

Teyssier A, Bestion E, Richard M, Cote J. 2014. Partners' personality types and mate preferences: predation risk matters. Behav Ecol. 25(4):723–733. doi:10.1093/beheco/aru049.

Thoen C, Bauwens D, Verheyen RF. 1986. Chemoreceptive and behavioural responses of the common lizard *Lacerta vivipara* to snake chemical deposits. Animal Behaviour. 34(6):1805–1813. doi:10.1016/S0003-3472(86)80266-4.

Thomson RL, Sirkiä PM, Villers A, Laaksonen T. 2013. Temporal peaks in social information: prospectors investigate conspecific nests after a simulated predator visit. Behav Ecol Sociobiol. 67(6):905–911. doi:10.1007/s00265-013-1513-x.

Thorlacius M, Hellström G, Brodin T. 2015. Behavioral dependent dispersal in the invasive round goby *Neogobius melanostomus* depends on population age. Curr Zool. 61(3):529–542. doi:10.1093/czoolo/61.3.529.

Thorogood R, Davies NB. 2016. Combining personal with social information facilitates host defences and explains why cuckoos should be secretive. Scientific Reports. 6:19872. doi:10.1038/srep19872.

Tibbetts EA. 2008. Resource value and the context dependence of receiver behaviour. Proceedings of the Royal Society B: Biological Sciences. 275(1648):2201–2206. doi:10.1098/rspb.2008.0477.

Tibbetts EA, Izzo A. 2010. Social Punishment of Dishonest Signalers Caused by Mismatch between Signal and Behavior. Current Biology. 20(18):1637–1640. doi:10.1016/j.cub.2010.07.042.

Tibbetts EA. 2014. The Evolution of Honest Communication: Integrating Social and Physiological Costs of Ornamentation. Integr Comp Biol. 54(4):578–590. doi:10.1093/icb/icu083.

Tinbergen N. 1952. ‘Derived’ Activities; Their Causation, Biological Significance, Origin, and Emancipation During Evolution. The Quarterly Review of Biology. 27(1):1–32. doi:10.1086/398642.

Tolvanen J, Forsman JT, Thomson RL. 2017. Reducing cuckoo parasitism risk via informed habitat choices. Auk. 134(3):553–563. doi:10.1642/AUK-17-30.1.

Tolvanen J, Kivelä SM, Doligez B, Morinay J, Gustafsson L, Bijma P, Pakanen V-M, Forsman JT. 2020. Quantitative genetics of the use of conspecific and heterospecific social cues for breeding site choice. Evolution. 74(10):2332–2347. doi:10.1111/evo.14071.

Tóth Z, Tuliozi B, Baldan D, Hoi H, Griggio M. 2017. The effect of social connections on the discovery of multiple hidden food patches in a bird species. Sci Rep. 7(1):816. doi:10.1038/s41598-017-00929-8.

Tóth Z, Jaloveczki B, Tarján G. 2020. Diffusion of Social Information in Non-grouping Animals. Frontiers in Ecology and Evolution. 8. doi:10.3389/fevo.2020.586058.

Trapp RM, Bell AM. 2017. The Effect of Familiarity with Demonstrators on Social Learning in Three-Spined Sticklebacks (*Gasterosteus aculeatus*). Ethology. 123(3):213–220. doi:10.1111/eth.12590.

Trochet A, Legrand D, Larranaga N, Ducatez S, Calvez O, Cote J, Clobert J, Baguette M. 2013. Population sex ratio and dispersal in experimental, two-patch metapopulations of butterflies. Journal of Animal Ecology. 82(5):946–955. doi:10.1111/1365-2656.12082.

Trochet A, Dupoué A, Souchet J, Bertrand R, Deluen M, Murarasu S, Calvez O, Martinez-Silvestre A, Verdaguer-Foz I, Darnet E, et al. 2018. Variation of preferred body temperatures along an altitudinal gradient: A multi-species study. Journal of Thermal Biology. 77:38–44. doi:10.1016/j.jtherbio.2018.08.002.

Trombulak SC. 1985. The Influence of Interspecific Competition on Home Range Size in Chipmunks (Eutamias).

J Mammal. 66(2):329–337. doi:10.2307/1381245.

Trompf L, Brown C. 2014. Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. Animal Behaviour. 88:99–106. doi:10.1016/j.anbehav.2013.11.022.

U/V

Uller T, Olsson M. 2004. Ectoparasite susceptibility in lizards from populations sympatric and allopatric with ticks. Écoscience. 11(4):428–432. doi:10.1080/11956860.2004.11682852.

Uller T, Olsson M. 2005. Trade-offs between offspring size and number in the lizard *Lacerta vivipara*: a comparison between field and laboratory conditions. Journal of Zoology. 265(3):295–299. doi:https://doi.org/10.1017/S0952836904006326.

Van Moorleghem C, Bauwens D, Claus K, Martín J, Van Damme R. 2020. Cracking the chemical code: European common lizards (*Zootoca vivipara*) respond to an hexane soluble predator kairomone. Biochemical Systematics and Ecology. 93:104161. doi:10.1016/j.bse.2020.104161.

Vanpé C, Gaillard J, Kjellander P, Mysterud A, Magnien P, Delorme D, Laere GV, Klein F, Liberg O, Mark Hewison AJ. 2007. Antler Size Provides an Honest Signal of Male Phenotypic Quality in Roe Deer. The American Naturalist. 169(4):481–493. doi:10.1086/512046.

Varela SAM, Teles MC, Oliveira RF. 2019. The correlated evolution of social competence and social cognition. Functional Ecology. 0(0). doi:10.1111/1365-2435.13416.

Vásquez RA, Ebensperger LA, Bozinovic F. 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. Behav Ecol. 13(2):182–187. doi:10.1093/beheco/13.2.182.

Vercken E, de Fraipont M, Dufty AM, Clobert J. 2007. Mother's timing and duration of corticosterone exposure modulate offspring size and natal dispersal in the common lizard (*Lacerta vivipara*). Hormones and Behavior. 51(3):379–386. doi:10.1016/j.yhbeh.2006.12.006.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. Journal of Evolutionary Biology. 20(1):221–232. doi:10.1111/j.1420-9101.2006.01208.x.

Vercken E, Clobert J. 2008. Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*). Écoscience. 15(3):320–326. doi:10.2980/15-3-3135.

Vercken E, Sinervo B, Clobert J. 2008. Colour variation in female common lizards: why we should speak of morphs, a reply to Cote et al. Journal of Evolutionary Biology. 21(4):1160–1164. doi:10.1111/j.1420-9101.2008.01535.x.

Vercken E, Sinervo B, Clobert J. 2012. The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment. Behav Ecol. 23(5):1059–1067. doi:10.1093/beheco/ars075.

Vilella-Pacheco Z, Mitchem LD, Formica VA, Brodie III ED. 2021. Male competition reverses female preference for male chemical cues. Ecology and Evolution. 11(9):4532–4541. doi:10.1002/ece3.7348.

Voelkl B, Huber L. 2007. Common marmosets (*Callithrix jacchus*) do not utilize social information in three simultaneous social foraging tasks. Anim Cogn. 10(2):149–158. doi:10.1007/s10071-006-0053-4.

Vogel D, Dussutour A. 2016. Direct transfer of learned behaviour via cell fusion in non-neural organisms. Proceedings of the Royal Society B: Biological Sciences. 283(1845):20162382. doi:10.1098/rspb.2016.2382.

Voituron Y, Hérold J, Grenot C. 2000. Metabolic Adaptations of Overwintering European Common Lizards (*Lacerta vivipara*). Physiological and Biochemical Zoology. 73(3):264–270. doi:10.1086/316742.

Voituron Y, Verdier B, Grenot C. 2002. The respiratory metabolism of a lizard (*Lacerta vivipara*) in supercooled and frozen states. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology. 283(1):R181–R186. doi:10.1152/ajpregu.00378.2001.

W

Wadhams GH, Armitage JP. 2004. Making sense of it all: bacterial chemotaxis. Nat Rev Mol Cell Biol. 5(12):1024–1037. doi:10.1038/nrm1524.

Wagner RH, Danchin É. 2010. A taxonomy of biological information. Oikos. 119(2):203–209. doi:10.1111/j.1600-0706.2009.17315.x.

Wang S, Haegeman B, Loreau M. 2015. Dispersal and metapopulation stability. PeerJ. 3:e1295. doi:10.7717/peerj.1295.

Wang W. 2016. Population dispersal and Allee effect. Ricerche mat. 65(2):535–548. doi:10.1007/s11587-016-0273-0.

Ward AJW, Mehner T. 2010. Multimodal mixed messages: the use of multiple cues allows greater accuracy in social recognition and predator detection decisions in the mosquitofish, *Gambusia holbrooki*. Behav Ecol. 21(6):1315–1320. doi:10.1093/beheco/arq152.

Webster M, Laland K. 2008. Social learning strategies and predation risk: minnows copy only when using private information would be costly. Proceedings of the Royal Society B: Biological Sciences. 275(1653):2869–2876. doi:10.1098/rspb.2008.0817.

Webster MM, Hart PJB. 2006. Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. Behav Ecol Sociobiol. 60(1):77–86. doi:10.1007/s00265-005-0143-3.

Webster MM, Laland KN. 2017. Social information use and social learning in non-grouping fishes. Behav Ecol. 28(6):1547–1552. doi:10.1093/beheco/arx121.

Webster MS, Ligon RA, Leighton GM. 2018. Social costs are an underappreciated force for honest signalling in animal aggregations. Animal Behaviour. 143:167–176. doi:10.1016/j.anbehav.2017.12.006.

Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E. 2010. Use of Social Information in Seabirds: Compass Rafts Indicate the Heading of Food Patches. PLOS ONE. 5(3):e9928. doi:10.1371/journal.pone.0009928.

Wey TW, Spiegel O, Montiglio P-O, Mabry KE. 2015. Natal dispersal in a social landscape: Considering individual behavioral phenotypes and social environment in dispersal ecology. Curr Zool. 61(3):543–556. doi:10.1093/czoolo/61.3.543.

Whitham TG. 1980. The theory of habitat selection: Examined and extended using Pemphigus aphids. American Naturalist. 115(4):449–466.

Wiklund CG. 1996. Determinants of Dispersal in Breeding Merlins (*Falco Columbarius*). Ecology. 77(6):1920–1927. doi:10.2307/2265795.

Wilkinson A, Huber L. 2012 Feb 13. Cold-Blooded Cognition: Reptilian Cognitive Abilities. The Oxford Handbook of Comparative Evolutionary Psychology. doi:10.1093/oxfordhb/9780199738182.013.0008.

Williams RJ, Dunn AM, Hanke G, Dixon JW, Hassall C. 2020. Response behaviour of native lizards and invading wall lizard to interspecific scent: implications for invasion success. Animal Behaviour. 166:109–117. doi:10.1016/j.anbehav.2020.05.016.

Williams HJ, Safi K. 2021. Certainty and integration of options in animal movement. Trends in Ecology & Evolution. 36(11):990–999. doi:10.1016/j.tree.2021.06.013.

Wilson RS, Husak JF, Halsey LG, Clemente CJ. 2015. Predicting the Movement Speeds of Animals in Natural Environments. Integr Comp Biol. 55(6):1125–1141. doi:10.1093/icb/icv106.

Winandy L, Di Gesu L, Lemoine M, Jacob S, Martin J, Ducamp C, Huet M, Legrand D, Cote J. 2021. Maternal and personal information mediates the use of social cues about predation risk. Behavioral Ecology.(araa151). doi:10.1093/beheco/araa151.

Winters AE, Green NF, Wilson NG, How MJ, Garson MJ, Marshall NJ, Cheney KL. 2017. Stabilizing selection on individual pattern elements of aposematic signals. Proceedings of the Royal Society B: Biological Sciences. 284(1861):20170926. doi:10.1098/rspb.2017.0926.

Wolff JO. 1993. What Is the Role of Adults in Mammalian Juvenile Dispersal? Oikos. 68(1):173–176. doi:10.2307/3545324.

Wray MK, Klein BA, Seeley TD. 2012. Honey bees use social information in waggle dances more fully when foraging errors are more costly. Behav Ecol. 23(1):125–131. doi:10.1093/beheco/arr165.

Wu NC, Seebacher F. 2022. Physiology can predict animal activity, exploration, and dispersal. Commun Biol. 5(1):1–11. doi:10.1038/s42003-022-03055-y.

Wurtz MC, Cussen V, Cornelius JM. 2021. The effects of food limitation on behavior, corticosterone, and the use of social information in the red crossbill (*Loxia curvirostra*). Anim Cogn. 24(6):1305–1317. doi:10.1007/s10071-021-01520-5.

Wyatt TD. 2014. Pheromones and Animal Behavior: Chemical Signals and Signatures. 2nd ed. Cambridge: Cambridge University Press.

Y/Z

Yip EC, Rao D, Smith DR, Lubin Y. 2019. Interacting maternal and spatial cues influence natal – dispersal out of social groups. Oikos. 128(12):1793–1804. doi:10.1111/oik.06531.

Yossen MB, Buteler M, Lozada M. 2021 Nov 28. Context-dependent use of olfactory cues by foragers of Vespula germanica social wasps. Anim Cogn. doi:10.1007/s10071-021-01583-4.

Zajitschek SR, Zajitschek F, Clobert J. 2012. The importance of habitat resistance for movement decisions in the common lizard, *Lacerta vivipara*. BMC Ecology. 12:13. doi:10.1186/1472-6785-12-13.

Zedrosser A, Støen O-G, Sæbø S, Swenson JE. 2007. Should I stay or should I go? Natal dispersal in the brown bear. Animal Behaviour. 74(3):369–376. doi:10.1016/j.anbehav.2006.09.015.

Zuk M. 1991. Sexual ornaments as animal signals. Trends in Ecology & Evolution. 6(7):228–231. doi:10.1016/0169-5347(91)90028-V.

Zuri I, Bull CM. 2011 Feb 15. The use of visual cues for spatial orientation in the sleepy lizard (*Tiliqua rugosa*). Canadian Journal of Zoology. doi:10.1139/z99-243.

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media.