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Historical influence of predation pressure on escape by *Podarcis* lizards in the Balearic Islands

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Island tameness (reduced escape behaviour on islands where prey have experienced prolonged relaxation of predation pressure) is known in several taxa, although the relationships between recent predation pressure and escape on islands are poorly known. We investigated escape by numerous populations exposed to differing predation pressure of two sister species of *Podarcis* lizards in the Balearic Islands. Our main findings are that flight initiation distance was greater in *Podarcis pityusensis* than *Podarcis lilfordi* and increased as predation pressure increased in *P. pityusensis*. Island tameness led to extinction of *P. lilfordi* on Menorca and Mallorca following anthropogenic introduction of predators; this species is extant only on nearby islets. The lack of relationship between recent predation pressure and flight initiation distance in *P. lilfordi* indicates that the historically acquired deficit in the ability to adjust escape behaviour to predation pressure still exists. *Podarcis pityusensis*, which was exposed to greater natural predation pressure before human introduction of predators, survives on Ibiza and Formentera, as well as on islets. Retention of the ability to respond to predation pressure is consistent with our finding that flight initiation distance increases as predation pressure increases among current populations. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **107**, 254–268.

ADDITIONAL KEYWORDS: antipredatory behaviour – flight initiation distance – predation risk – refuge use – Squamata.

INTRODUCTION

Escape behaviour has been studied extensively (Stankowich & Blumstein, 2005), primarily to test theories that predict how closely a prey permits a predator to approach before fleeing (flight initiation distance; FID) and how long a prey hides in refuge from costs and benefits of these behaviours (Ydenberg & Dill, 1986; Martín & López, 1999; Blumstein, 2003; Stankowich & Coss, 2006; Cooper & Frederick, 2007a, b, 2010). The emphasis has been on testing effects of factors affecting predation risk and costs of escaping or remaining in refuge within single populations (Martín, Marcos & López, 2005; Stankowich & Blumstein, 2005; Stankowich & Coss, 2007; Cooper & Wilson, 2008). Far less is known about variation of escape behaviour among populations, relationships among escape variables, and factors that may influence variation in escape behaviour among populations.

Interspecific differences in FID occur in birds (Blumstein, 2003; Møller, 2008a, b, 2010), ungulates (Stankowich, 2008), and lizards (Cooper, 2006a; Cooper & Avalos, 2010a). Although FID and other escape variables have been studied more in lizards than other taxa, little is known about their intraspecific variation among populations (Shallenberger, 1970; Stone, Snell & Snell, 1994; Stankowich & Blumstein, 2005). Even studies of multiple lizard species often have focused on effects of risk factors within species (Cooper, 2006a; Cooper & Whiting, 2007a, b).

Because risk of being captured is greater for lizards farther from refuge, FID often increases as the distance to refuge increases (Bulova, 1994; Cooper,

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1997a, 2000a; Martín & López, 2000). Therefore, FID is predicted to be longer in populations and individuals having longer distance to refuge. The distance fled may also increase as risk increases (Martín & López, 1996; Cooper, 2000a, 2003a, 2007, 2009a; Cooper, Hawlena & Pérez-Mellado 2009a), although, when lizards flee directly to refuge, the distance fled is more strongly affected by the distance to refuge than predation risk (Cooper, 1997a). We predict that, at both individual and population levels, the distance fled is positively correlated with FID in species that infrequently enter refuges, although it may be unrelated to FID in species that frequently enter refuges when approached. Prey adjacent to refuge are likely to enter refuge when fleeing, although prey farther from refuge often flee toward refuge but stop without entering it. Because of the influence of distance from refuge, the proportion of lizards that enter refuge is predicted to increase as the distance fled decreases.

FID is predicted to be shorter in populations exposed to weaker predation pressure, as exemplified by island tameness (diminution of wariness on islands where predators are rare or absent; Darwin, 1839). If chronically exposed to predators, prey may be forced to accept greater risk to meet other needs, such as foraging, favouring shorter FID (Lima & Bednekoff, 1999). Therefore, the prediction that FID increases as predation pressure increases is clouded in studies of multiple populations when predators that attack prey are present during prolonged intervals in some but not all populations. The prediction that FID increases as predation pressure increases is theoretically sound when predators are present for brief intervals.

Island tameness, implying a very short FID, has been reported on remote islands lacking terrestrial predators, and is assumed to reflect an evolutionary decrease in escape response (Darwin, 1839; Lack, 1947; Curio, 1976). Empirical studies demonstrate island tameness in wallabies (Blumstein & Daniel, 2002), birds in the Falkland Islands (Humphrey, Livezy & Siegel-Causey, 1987), and lizards (Rödl *et al.*, 2007), and show that the introduction of predators often leads to the extinction of birds on islands where escape capacity had been lost during the prolonged absence of predators (Olson & James, 1982; Steadman, 1995; Holdaway, 1999; Holdaway & Jacomb, 2000; Grayson, 2001). Island tameness appears to exist in several lacertid lizard species (Pérez-Mellado, Corti & Lo Cascio, 1997; Vervust, Grab & van Damme, 2007; Cooper, Hawlena & Pérez-Mellado, 2009a). In the Balearic lizard (*Podarcis lilfordi*, Lacertidae) FID, distance fled, and hiding time in refuge were shorter and the probability of entering refuge was lower on an islet where lizards experience a lower predation pressure than on one where the predation pressure is higher (Cooper, Hawlena & Pérez-Mellado, 2009a). In the same species, tail autotomy, which increases the probability of escape by distracting a predator, is harder to induce and severed tails move less vigorously on an islet where predation pressure is lower than on one where it is higher (Cooper, Pérez-Mellado & Vitt, 2004), as well as on both islets than in a mainland congener (Cooper *et al.*, 2004). Another lacertid, *Podarcis sicula*, was introduced in 1971 to an island with low avian predation pressure; after just over 30 years, lizards exhibited a shorter FID, distance fled, and legs, as well as a reduced sprint speed, than on the source island (Vervust *et al.*, 2007). FID by the lacertid *Podarcis muralis* was longer in a lowland population that experiences higher predation pressure than in a high-elevation population with a lower predation pressure (Diego-Rasilla, 2003).

These findings are consistent with the diminution of escape and escape-related morphology and physiology under aq prolonged reduction of predation pressure, although comparisons of two or three populations cannot establish the general occurrence of island tameness. Indeed, no relationship was found between postautotomic tail activity and predation pressure in six Mediterranean lacertid species (Pafilis, Valakos & Foufopoulos, 2005). In a more extensive study of Mediterranean lacertids, autotomy occurred more easily in populations exposed to higher predation pressure (Pérez-Mellado *et al.*, 1997). Furthermore, some antipredatory responses may be lost rapidly (Blumstein, Daniel & Springett, 2004), whereas others may be retained for many generations in the absence of particular predators (Coss, 1991; Van Damme & Castilla, 1996; Stankowich & Coss, 2007).

Habituation to human presence affects escape by lizards and other prey (Stankowich & Blumstein, 2005). When people are frequently present but do not attack, lizards exhibit a shorter FID than at sites where people are less frequently present (Stankowich & Blumstein, 2005; Cooper & Whiting, 2007a; Cooper, 2009a, 2010; Cooper & Avalos, 2010b). Therefore, interpopulational differences in habituation might obscure the effects of predation pressure. If reduced escape behaviour were to occur where decreased predation pressure is accompanied by habituation, an independent effect of predation pressure could not be inferred without accounting for effects of habituation.

Podarcis lilfordi and its sister species *Podarcis pityusensis* are endemic in the Balearic Islands (Spain) (Fig. 1), with the former occurring only on islets surrounding Menorca and Mallorca, and the latter on both the main islands Ibiza and Formentera and their associated islets (collectively the Pityusics). We examined the hypothesis that island tameness may have led to extinction of *P. lilfordi* on Menorca

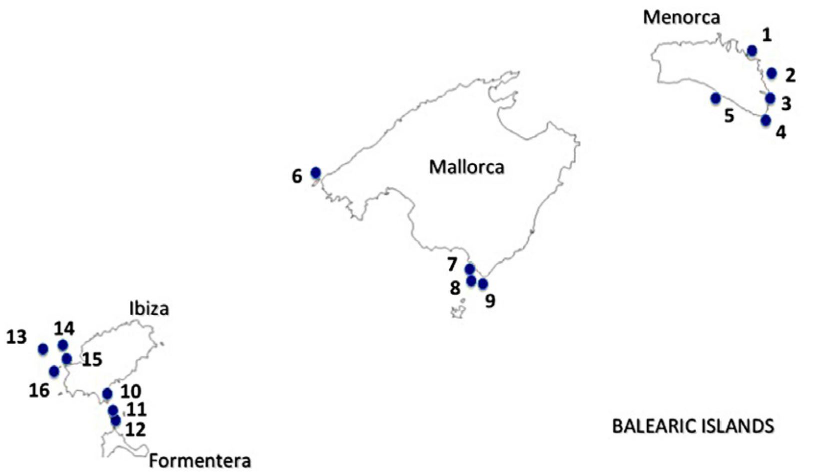

Figure 1. Study sites for *Podarcis lilfordi* and *Podarcis pityusensis* in the Balearic Islands. Populations of *P. lilfordi* occur only on islets associated with Menorca, and not on the main islands. *Podarcis pityusensis* occurs on the main islands Ibiza and Formentera and nearby islets. Sites sampled are indicated by numerals (1, Addaia gran; 2, Colom; 3, Rey; 4, Aire; 5, Binicodrell; 6, Dragonera; 7, Guardia; 8, Moltona; 9, Pelada; 10, Sa Canal; 11, Porcs; 12, Trucadors; 13, Bleda Plana; 14, Conillera; 15, Bosc; 16, Espartar).

and Mallorca after the people introduced predators, whereas *P. pityusensis* persisted in the main Pityusic Islands by retaining its escape capacities. We studied aspects of escape behaviour in these species on numerous islets and two sites on main islands aiming to assess relationships among escape variables across populations and species, differences in escape variables among populations and species, and relationships of escape variables to predation pressure and habituation. Because natural predators, even where endemic, are encountered infrequently and briefly at the study sties, risk allocation cannot account for differences in escape among populations. Although habituation and risk allocation as a result of human presence are both expected to be associated with reduced escape responses, risk allocation is unlikely to account for reduced escape responses because people do not attack lizards. Relationships among escape variables are important as a result of their potential effects on relationships between escape and predation pressure. For example, FID and the distance fled might increase and the probability of entering refuge might decrease as the distance to refuge increases; the probability of entering refuge may increase as the distance fled increases. We examined differences in escape behaviour between two major island groups and between species to assess possible influences on the relationship between escape and predation pressure. From the hypothesis that island tameness led to the extinction of *P. lilfordi* on Menorca and Mallorca, we predicted that escape behaviour would be unrelated to predation pressure in populations associated with these islands. Because *P. pityusensis* survives on the main Pityusic Islands, we predicted that wariness is greater in populations exposed to a higher predation pressure.

MATERIAL AND METHODS

STUDY SITES AND POPULATIONS

We collected data from 16 populations in the Balearic Islands of Spain. *Podarcis lilfordi* and *P. pityusensis* exhibit variation in colour patterns among populations. Populations at some sites (including Aire) are melanistic; others have brown and green patterns. Lizards in all populations were easily detected in their relatively open habitats, reducing the potential importance of such variation. *Podarcis pityusensis* [96 mm maximum male snout–vent length (SVL)] is slightly larger than *P. lilfordi*, which exhibits variable length among populations with a mean male SVL of approximately 81 mm (Pérez-Mellado, 1998a, b). Effects of body size on FID in adult lizards are not known. Sex differences occur in some species but not others in which males are larger than females (Stankowich & Blumstein, 2005), as in our studied species.

Data for adult lizards were collected on 11–29 June 2010, with the exceptions of those for Aire and Rei collected in late April and early May 2005. We restricted data collection to warm, sunny days when lizards were fully active, and therefore close to preferred body temperature. Data were collected from populations of *P. lilfordi* on islets surrounding Menorca and Mallorca (Fig. 1). Study sites for *P. pityusensis* included one each for the large islands of Ibiza (Sa Canal) and Formentera (Trucadors), as well as several islets nearby (Fig. 1).

Sites varied in ways that might affect escape behaviour, including predation pressure, exposure to people, density of vegetation, and abundance of refuges. They varied in island size and distance from a main island, which might affect accessibility to predators. We assessed predation pressure independent of these factors. Microhabitat differences were limited; all sites were semi-arid and experienced similar climatic conditions, and included vegetation, patches of bare ground, and rocks with crevices suitable as refuges.

Sites were ranked using two criteria: estimates of predation pressure on populations and of degree of human disturbance. In some cases, human presence and predation pressure coexist because predators, particularly feral cats, were introduced by people. In others, islands without frequent human presence receive frequent visits by avian predators. We ranked predation pressure using published information on presence of predators and our observations made over 30 years.

Ranks of predation pressure (Table 1) were determined primarily by assigning points to presence of predators (3 points for breeding kestrels (*Falco tinnunculus*), 2 points each for visiting predators that frequently consume lizards [kestrels, cats, and genets (*Genetta genetta*)]; and 1 point each for predators that less frequently kill lizards [weasels (*Mustela nivalis*), dogs, rats (*Rattus rattus*), snakes (*Rhinechis scalaris*), seagulls (*Larus* spp.), migrant birds, shrikes (*Lanius* spp.), owls (*Tyto alba*), Eleonor's falcons (*Falco eleonorae*), and human rabbit hunters]. Two groups of three islets had equal points. For Moltona, Guardia, and Pelada, which are are almost equidistant from a main island, rankings were decided based on island size because predators are more likely to visit larger islands. In the other tied group, the lowest rank was assigned to Porcs because it is far offshore, the middle rank was assigned to Binicodrell as a result of intermediate distance from the shore and the presence of people on a nearby beach that may deter predator visits, and the highest rank was assigned to Bosc as a result of its proximity to shore.

To rank habituation to human presence (Table 1), one point each was awarded for continuous current human presence, historical presence, prehistoric presence, presence of a lighthouse with occupants, presence of an automated lighthouse, a beach, hunters, fishermen, a jetty facilitating landing, extraction of products (rocks, minerals, vegetation), visits by tourists, and organized group visits. Based on ease of access, each site was assigned between 1 and 4 points (4, accessible by foot or car; 3, accesible by swimmers; 2, accesible by rowboat and kayak; 1, accessible only by motorboat). One group of three sites and another of four sites had tied points. In the former group, Pelada

Table 1. Rankings of predation pressure and habituation to human presence for 16 study sites

Species	Site	Rank predation pressure		Rank habituation	
		Overall	Within species	Overall	Within species
Podarcis lilfordi					
	Addaia Gran	7	4	10	7
	Aire	8	5	11	8
	Binicodrell	14	9	15	9
	Colom	4	2	5	3
	Dragonera	5	3	4	2
	Guardia	11	7	8	5
	Moltona	10	6	7	4
	Pelada	12	8	9	6
	Rei	3	1	3	1
Podarcis pityusensis					
	Bosc	13	5	12	4
	Conillera	6	3	6	3
	Bleda Plana	16	7	16	7
	Espartar	9	4	14	6
	Porcs	15	6	13	5
	Sa Canal	1	1	2	2
	Trucadors	2	2	1	1

(off Mallorca) was ranked highest; off Menorca, Aire was ranked lower than Addaia Gran as a result of the distance from the shore and the impression of human visitation. In the other group, the highest rank was assigned to Bosc as a result of the proximity to a large beach frequented by people, and the lowest rank was assigned to Binicodrell because its cliffs hinder human access. Espartar and Porcs are far from shore; habituation was ranked higher for Porcs than Espartar because Porcs has a lighthouse, an adjacent house, and a jetty that facilitates landing.

SIMULATION OF ATTACKS

Simulation of approach by a researcher elicits escape by diverse prey, including invertebrates (e.g. insects: Cooper, 2006b; crabs: Hemmi, 2005a, b) and vertebrates (Stankowich & Blumstein, 2005; fish: Grant & Noakes, 1987; frogs: Martín, Luque-Larena & López, 2005; Cooper, Caldwell & Vitt, 2008, 2009; Cooper, 2011; mammals: Kramer & Bonenfant, 1997; Blumstein & Pelletier, 2005; birds: Koivula, Rytkonen & Orell, 1995; Blumstein, 2003; Blumstein & Pelletier, 2005; and, in particular, lizards: Cooper, 1997a, 2009a, 2010; Martín & López, 1999; Cooper, Hawlena & Pérez-Mellado, 2009b). Simulated attack has the advantages of not actually exposing prey to predators, and of permitting approach on rough terrain. Escape by lizards in response to approaching human investigators is adjusted to degree of risk as predicted by escape theory (Ydenberg & Dill, 1986; Cooper & Frederick, 2007a, 2010). FID increases as the risk increases for a numerous risk factors, including predator approach speed and directness (Cooper, 1997a, b), distance from refuge (Cooper, 1997a, 2000a), and predator size (Cooper & Stankowich, 2010). It decreases as the cost of fleeing, such as a lost opportunity to forage or engage in social behaviour (Cooper, 1999, 2000b, 2003b, 2009c; Cooper, Pérez-Mellado & Hawlena, 2006), increases.

Predator-specific escape responses (Stuart-Fox, Whiting & Mousalli, 2006) are not detected in studies using human simulated predators but striped plateau lizards (*Sceloporus virgatus*) that escape by running, as do lacertids, exhibited similar escape responses to models of birds and snakes (Cooper, 2008). We attempted to eliminate experimenter bias as a result of knowledge of experimental design and predictions by standardizing approach behaviour, including speed and directness, gait, and posture, and by approaching each lizard only once.

DATA COLLECTION

Upon detecting an adult lizard when walking, the investigator approached it very slowly and stopped moving for several seconds when standing at a distance of 5.4–7.5 m. The range of starting distance, the distance between predator and prey when the approach begins, was limited because FID increases as the starting distance increases in some prey (Blumstein, 2003; Cooper, 2005), including *P. lilfordi* (Cooper, Hawlena & Pérez-Mellado, 2009c). The investigator's position when standing was marked with a small stone or a convenient landmark.

Because FID increases in lizards as approach speed increases (Cooper, 1997a, 2003a, b; 2009a) and standing distance and approach speed interactively affect FID in *P. lilfordi* (Cooper, Hawlena & Pérez-Mellado, 2009c), we used a consistent approach speed. After remaining motionless facing the lizard, the researcher approached directly at a mean ± SE speed of $0.8 \pm 0.0\ \mathrm{m\ s^{-1}}$ ($N = 10$). This speed was practiced periodical each day. The investigator approached until the lizard fled and then stopped moving immediately. Data recorded were starting distance, FID, distance fled before stopping for at least 1 s, the lizard's distance from the nearest suitable refuge before fleeing (i.e. rock crevices or dense vegetation), and whether the lizard entered a refuge or not. For individuals that did not enter a refuge, we recorded the distance to the nearest potential refuge that did not require a lizard to approach the investigator. We prevented pseudoreplication by moving between trials to new positions lacking previously observed lizards whenever possible. At most sites, lizards were sufficiently abundant that the probability of pseudoreplication was very low. It was necessary to traverse a few small islets multiple times when searching for lizards. In these cases, occasional pseudoreplication is possible but was minimized by noting lizard body size, markings, and locations.

STATISTICAL ANALYSIS

Relationships among escape variables (FID, distance fled, distance to refuge, and proportion of lizards that entered refuge) were examined by regression analysis using means at the 16 sites. Because data on distance fled, distance to refuge, and refuge entry were lacking for Aire and Rei, sample sizes for analyses involving these variables were 14. Separate linear regressions were conducted using data for individuals, with the exception that generalized linear models for a binomial variable with logit link functions were used to relate refuge entry to other variables. Because of heteroscedasticity of distance to refuge and distance fled, rank transformations of these variables were used in individual-based analyses.

Nested analysis of variance (ANOVA) and analysis of covariance (ANCOVA) (using distance to refuge as covariate as a result of its effects on escape behaviours) were conducted to assess differences in escape among island groups (Menorca, Mallorca, and the Pityusic Islands Ibiza and Formentera), sites nested within island groups, and between species and sites nested within species. When variances were heterogeneous as indicated by Levene's tests, analyses were conducted using rank-transformed data. Generalized linear models with a binomial distribution of refuge entry and a logit link function were used to assess effects on proportion of individuals that entered refuge. Chi-squared tests were used to evaluate differences among study sites with respect to the probability of entering refuge. For the proportion of individuals that entered refuges, an ANCOVA was conducted for sites with the distance fled as covariate. Newman–Keuls tests and, in two cases, Duncan's multiple range tests, were used to examine differences among pairs of island groups and sites for all variables except the proportion of lizards that entered refuge. Effect sizes for ANOVAs and ANCOVAs were reported as η^2 (Cohen, 1992). A generalized linear model using binomial distribution and logit link function was conducted to assess differences in the proportion of lizards that entered a refuge among sites in a non-nested ANCOVA with the distance fled as covariate.

Effects of predation risk and habituation on FID and the proportion of lizards that entered refuge were assessed using Spearman's rho correlation. These tests were conducted separately for each species.

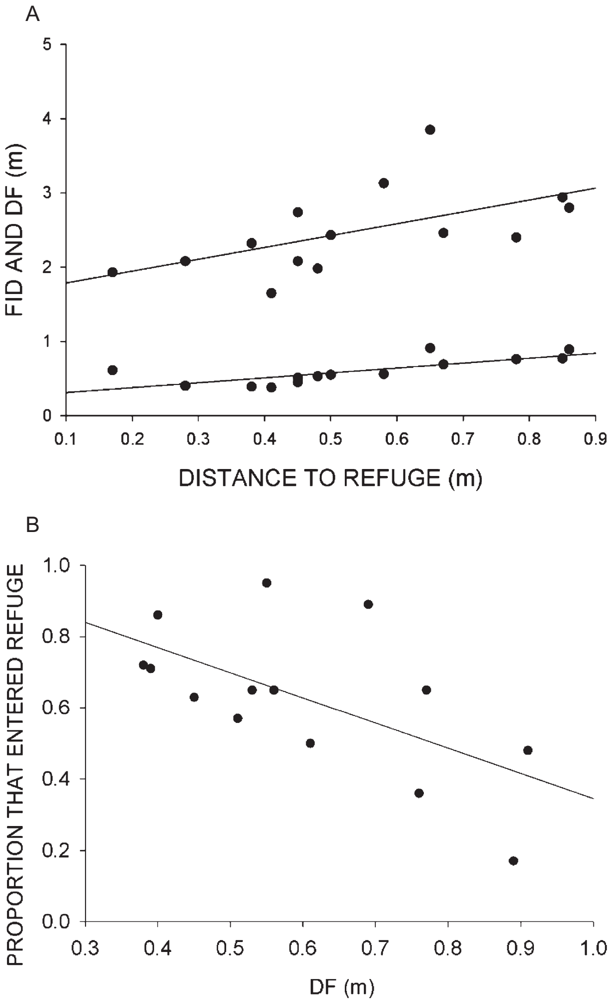

Figure 2. A, influence of distance to nearest refuge on flight initiation distance (FID; upper line and points) and distance fled (DF; lower line and points. B, relationship between distance fled and proportion of lizards that entered refuge.

RESULTS

Relationships among variables

FID increased as the distance to refuge increased ($F_{1,12} = 5.93$, $P = 0.03$ $R^2 = 0.34$) according to the equation FID = 1.60, DR + 1.63 m, where DR is the distance to the nearest refuge (m) (Fig. 2A; Table 2). The intercept was significantly greater than zero ($t_{12} = 4.34$, $P < 0.001$). Lizards with longer FIDs also fled further ($F_{1,14} = 5.51$, $P = 0.034$, $R^2 = 0.28$): DF = 0.38, FID – 0.25 m, where DF is the distance fled. The intercept was not significantly greater than zero ($t_{14} = 0.61$, $P = 0.55$). The distance fled also increased significantly as the distance to refuge increased ($F_{1,12} = 16.77$, $P = 0.0015$, $R^2 = 0.58$; DF = 0.66, DR + 0.25 m; Fig. 2A). The intercept was significantly greater than zero ($t_{12} = 2.66$, $P = 0.021$). In a multiple regression, the effect of distance to refuge remained significant ($t_{11} = 2.62$, $P = 0.024$) but that of FID did not ($t_{11} = 11.80$, $P = 0.10$; $F_{2,11} = 11.55$, $P = 0.0020$, $R^2 = 0.68$; DF = 0.12, FID + 0.47, DR + 0.06). The intercept did not differ significantly from zero ($t_{11} = 0.41$, $P = 0.69$). Conclusions using individual-based rather than site-based statistics were identical for the relationship between FID and DF. In individual-based analysis, the distance fled increased significantly as both FID and DR increased (multiple regression: $F_{2,247} = 75.67$, $P < 1.0 \times 10^{-6}$, $R^2 = 0.38$) but was more strongly associated with DR ($t_{247} = 10.71$, $P < 1.0 \times 10^{-6}$) than FID ($t_{247} = 4.54$, $P = 9.0 \times 10^{-6}$).

Individual-based analyses provided information about parallelism of slopes. Slopes of FID on rank DR did not differ significantly among sites ($F_{13,226} = 0.96$, $P = 0.50$) but the slope was significantly greater for *P. lilfordi* than for *P. pityusensis* ($F_{1,238} = 7.88$, $P = 0.0054$). However, the effect size was very small ($\eta^2 = 0.03$). FID increased as the rank distance to refuge increased in *P. lilfordi* ($F_{1,119} = 9.76$, $P = 0.0022$, $R^2 = 0.08$) but not in *P. pityusensis* ($F_{1,131} = 0.43$,

Table 2. Flight initiation distance (FID), distance fled (DF), distance to nearest refuge (DR), and proportion of individual lizards that entered refuge for sixteen study sites

	FID			DF			DR			Entered refuge	
Site	Mean	SE	*n*	Mean	SE	*n*	Mean	SE	*n*	Proportion	*n*
Colom	3.85	0.25	21	0.91	0.17	21	0.65	0.14	21	0.48	21
Binicodrell	2.46	0.15	9	0.69	0.15	9	0.67	0.16	9	0.89	9
Addaia Gran	2.32	0.22	21	0.39	0.04	21	0.38	0.04	21	0.71	21
Guardia	3.13	0.19	20	0.56	0.09	20	0.58	0.12	20	0.65	20
Moltona	2.43	0.22	20	0.55	0.13	20	0.50	0.13	20	0.95	20
Pelada	2.74	0.20	19	0.51	0.12	20	0.45	0.08	20	0.57	21
Dragonera	1.93	0.17	10	0.61	0.22	10	0.17	0.03	10	0.50	10
Trucadors	2.94	0.29	20	0.77	0.12	20	0.85	0.18	20	0.65	20
Bosc	2.08	0.20	14	0.40	0.07	14	0.28	0.05	14	0.86	14
Espartar	1.98	0.16	20	0.53	0.05	20	0.48	0.06	20	0.65	20
Bleda Plana	1.65	0.16	25	0.38	0.05	25	0.41	0.08	25	0.72	25
Conillera	2.40	0.19	28	0.76	0.11	28	0.78	0.13	28	0.36	28
Sa Canal	2.80	0.26	6	0.89	0.16	5	0.86	0.20	6	0.17	6
Porcs	2.08	0.22	20	0.45	0.11	17	0.45	0.11	20	0.63	19
Aire	1.79	0.13	38	0.59	0.18	7					
Rei	3.17	0.26	12	2.16	0.43	7					

$P = 0.51$). Slopes of rank distance fled on FID did not differ significantly between sites ($F_{13,222} = 1.76$, $P = 0.051$) or species ($F_{1,234} = 1.48$, $P = 0.22$). Slopes of rank distance fled on the rank distance to refuge did not differ significantly among sites ($F_{13,235} = 1.63$, $P = 0.08$) but differed significantly between species ($F_{1,234} = 4.22$, $P = 0.04$) with a very small effect size ($\eta^2 = 0.02$). For all data, rank DF increased significantly as FID ($t_{247} = 4.94$, $P = 1.0 \times 10^{-6}$) and rank DR ($t_{247} = 9.34$, $P < 1.0 \times 10^{-6}$) increased.

The proportion that entered refuge was not significantly related to the distance from refuge ($F_{1,12} = 2.50$, $P = 0.14$) or FID ($F_{1,12} = 1.17$, $P = 0.30$) but increased significantly as the distance fled decreased ($F_{1,12} = 4.79$, $P = 0.049$; $R^2 = 0.29$; $\mathrm{ER} = -0.71$, $\mathrm{DF} + 1.05$, where ER is the proportion that entered refuge; Fig. 2B). The intercept was significant ($t_{12} = 6.27$, $P < 1 \times 10^{-4}$). In an individual-based multiple regression using a generalized linear model for a binomial variable with a logit link function, the proportion that entered refuge increased as the distance fled decreased (Wald statistic = 6.79, $P = 0.0094$) but was not significantly related to the distance to refuge (Wald statistic = 3.58, $P = 0.058$).

Differences in escape variables among sites and between species

Aspects of escape differed among sites, major island groups, and species. The rank distance to refuge differed among island groups ($F_{2,240} = 5.68$, $P = 0.0039$; distances to refuge: Menorca, 0.54 ± 0.07 m, $N = 51$; Mallorca, 0.46 ± 0.06 m, $N = 70$; Pityusics, 0.58 ± 0.05, $N = 132$) but its effect size was very small ($\eta^2 = 0.04$). The distance to refuge was significantly greater for Menorcan than Mallorcan sites ($P = 0.022$), marginally greater for sites in the Ibiza-Formentera group than for Mallorcan sites ($P = 0.071$), and did not differ significantly between Menorcan and Pityusic sites ($P = 0.39$; Newman–Keuls tests). Sites nested within island groups differed significantly ($F_{11,240} = 2.77$, $P = 0.0021$; Fig. 3A; $\eta^2 = 0.13$). The distance to refuge was significantly shorter on Dragonera than Colom, Binicodrell, Trucadors, Espartar, Conillera, and Sa Canal; and shorter on Bosc than Sa Canal ($P < 0.05$ each). No other differences were significant. In a nested ANOVA, species did not differ in the rank distance to refuge ($F_{1,240} = 2.0$, $P = 0.16$; distances to refuge: *P. lilfordi*, 0.50 ± 0.04 m, $N = 121$; *P. pityusensis*, 0.58 ± 0.05 m, $N = 132$).

In a nested ANOVA, FID differed significantly among island groups ($F_{2,264} = 8.29$, $P = 0.0032$; $\eta^2 = 0.04$) and sites within island groups ($F_{13,264} = 6.83$, $P < 1.0 \times 10^{-6}$; Fig. 3B; $\eta^2 = 0.24$). FID was significantly shorter for the Pityusic group (2.21 ± 0.09 m, $N = 133$) than the Menorcan ($P = 0.000093$; 2.80 ± 0.13 m, $N = 77$) and Mallorcan ($P = 0.0018$; 2.65 ± 0.11, $N = 70$) groups. It was significantly longer on Colom and Rei than on Binicodrell, Addaia Gran, Aire, Moltona, Dragonera, Bosc, Espartar, Bleda Plana, Conillera, and Porcs; on Colom than Pelada, Trucadors, and Sa Canal; on Guardia than Dragonera, Espartar, and Bleda Plana; and on Trucadors and

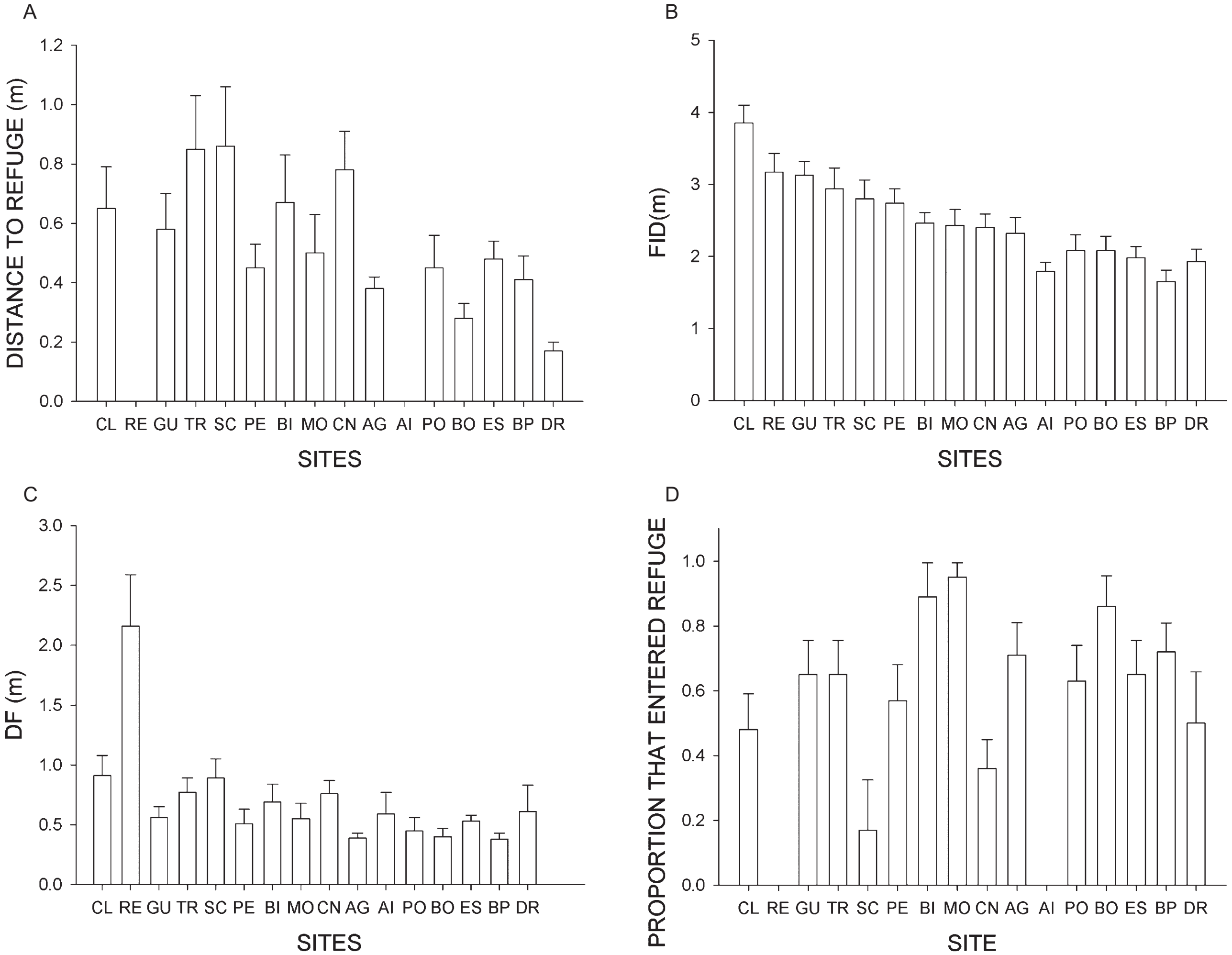

Figure 3. Variation among populations of distance to refuge (A), flight initiation distance (B), distance fled (DF) (C), and proportion of individuals that entered refuge (D). Bars show the mean ± SE. AG, Addaia Gran; AI, Aire; BI, Binicodrell; BO, Bosc; BP, Bleda Plana; CL, Colom; CN, Conillera; DR, Dragonera; ES, Espartar; GU, Guardia; MO, Moltona; PE, Pelada; PO, Porcs; RE, Rei; SC, Sa Canal; TR, Trucadors.

Sa Canal than Bleda Plana ($P < 0.05$ each). In a nested ANCOVA with the distance to refuge as covariate, effects of island group ($F_{2,239} = 14.33$, $P = 1.0 \times 10^{-6}$; $\eta^2 = 0.08$) and sites within island groups ($F_{11,239} = 5.74$, $P < 1.0 \times 10^{-6}$; $\eta^2 = 0.19$) were significant.

FID differed significantly between species (ANOVA, $F_{1,263} = 14.23$, $P = 0.00020$; Fig. 4; $\eta^2 = 0.05$; *P. lilfordi*: 2.73 ± 0.09 m, $N = 147$; *P. pityusensis*: 2.21 ± 0.09, $N = 132$) and sites within species ($F_{14,263} = 6.382$, $P < 1.0 \times 10^{-6}$; $\eta^2 = 0.25$). The same sites differed significantly from Colom and Rei as in the previous analysis of island groups ($P < 0.05$ each). The only other significant differences between sites were the longer FIDs on Porcs and Sa Canal than Bleda Plana ($P < 0.05$ each). In an ANCOVA with the distance to refuge as covariate, effects of species ($F_{1,238} = 25.33$, $P = 1.0 \times 10^{-6}$; $\eta^2 = 0.08$) and site within species ($F_{12,238} = 5.49$, $P < 1.0 \times 10^{-6}$; $\eta^2 = 0.20$) were significant.

Distance fled did not differ significantly between island groups in an ANOVA using rank data ($F_{2,236} = 0.60$, $P = 0.55$; raw distances fled: Menorca, 0.65 ± 0.08 m, $N = 51$; Mallorca, 0.55 ± 0.06 m, $N = 70$; Pityusics, 0.60 ± 0.04, $N = 129$) but differed significantly among sites within island groups ($F_{11,236} = 2.68$, $P = 0.0029$; $\eta^2 = 0.05$; Fig. 3C). No differences between pairs of sites were significant using Newman–Keuls tests. Using slightly less stringent Duncan's multiple range tests, the distance fled was longer on Colom than on Addaia Gran, Bosc, Bleda Plana, and Porcs; and at Sa Canal than on Addaia Gran, Bleda Plana, and Porcs ($P < 0/05$ each). In an ANCOVA using the rank distance to refuge as covariate, the effect of island group was not significant

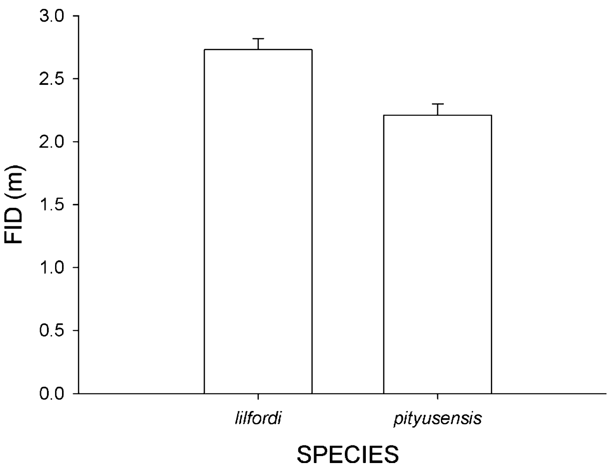

Figure 4. Mean flight initiation distances of *Podarcis lilfordi* and *Podarcis pityusensis*. Error bars show the SE. FID, flight initiation distance.

($F_{2,235} = 0.39$, $P = 0.68$) but the effect of site within island group remained significant ($F_{11,235} = 2.06$, $P = 0.024$; $\eta^2 = 0.07$).

Rank distance fled did not differ significantly between species in a nested ANOVA ($F_{1,235} = 0.00$, $P = 0.99$; raw distances fled: *P. lilfordi*, 0.59 ± 0.05 m, $N = 121$; *P. pityusensis*, 0.58 ± 0.04 m, $N = 129$) but differed significantly among sites within species ($F_{12,235} = 2.55$, $P = 0.0034$; $\eta^2 = 0.05$). The pattern of significance was identical to that in the ANOVA for island groups using Duncan's multiple range tests, except that the distance fled was significantly longer at Sa Canal than Bosc ($P < 0.05$). In a nested ANCOVA using the rank distance to refuge as covariate, the rank distance fled differed significantly among sites within species ($F_{12,234} = 1.87$, $P = 0.038$; $\eta^2 = 0.07$) but not between species ($F_{1,234} = 0.72$, $P = 0.40$).

The proportion of individuals that entered refuge did not differ significantly among island groups ($\chi^2_2 = 2.07$, $P = 0.36$; Menorca, 0.63 ± 0.07, $N = 51$; Mallorca, 0.70 ± 0.06, $N = 70$; Ibiza-Formentera, 0.60 ± 0.04, $N = 132$) in a generalized linear model with a binomial distribution of refuge entry and a logit link function but differed significantly among sites within island groups ($\chi^2 = 36.16$, d.f. = 11; $P = 0.00016$). In a similar analysis, the proportion that entered refuge did not differ between species ($\chi^2 = 1.48$, d.f. = 1; $P = 0.2$; *P. lilfordi*, 0.67 ± 0.04, $N = 121$; *P. pityusensis*, 0.60 ± 0.04, $N = 132$) but differed among sites within species ($\chi^2 = 36.71$, d.f. = 12; $P = 0.00025$). Paired comparisons were not conducted because they are not available in STATISTICA (StatSoft), although the proportion that entered refuge differed marginally among the 12 sites for which sample sizes were ≥ 10 ($\chi^2 = 19.49$, d.f. = 11; $P = 0.054$; Fig. 3D). After sequential Bonferroni adjustment for 65 possible paired comparisons (with raw P-values reported), significantly higher proportions of lizards entered refuges on Moltona than Conillera ($\chi^2 = 17.15$, d.f. = 1; $P = 4.0 \times 10^{-5}$) or Colom ($\chi^2 = 11.11$, d.f. = 1; $P = 0.0009$). The proportion that entered refuge was marginally greater on Bosc than Conillera ($\chi^2 = 9.35$, d.f. = 1; $P = 0.0022$). No other difference was significant. In a generalized linear model with the distance fled as covariate, the effect of site was significant ($\chi^2 = 31.10$, d.f. = 13; $P = 0.00334.0 \times 10^{-5}$).

INFLUENCE OF PREDATION RISK AND HABITUATION ON ESCAPE

Predation pressure (Mann–Whitney: $U = 29.0$; $N = 7.9$; $P = 0.83$) and habituation (Mann–Whitney: $U = 27.0$; $N = 7.9$; $P = 0.68$) did not differ between species. The species difference in FID required separate correlation for each species. Rank FID was significantly correlated with rank predation pressure in *P. pityusensis* ($\rho = 0.88$, $t_5 = 4.21$, $P = 0.0085$; Fig. 5A), as was the distance fled ($\rho = 0.96$, $t_5 = 8.14$, $P = 0.0045$; Fig. 5B). Also in *P. pityusensis*, rank FID and the distance fled were significantly correlated with rank habituation (FID: $\rho = 1.00$, $t = 5.03$ $P < 0.002$; Fig. 5C; distance fled: $\rho = 0.82$, $t_5 = 3.22$, $P = 0.023$; Fig. 5D). These correlations were not significant for *P. lilfordi* (predation pressure, FID: $\rho = 0.17$, $t_7 = 0.45$, $P = 0.67$; distance fled, $\rho = -0.57$, $t_7 = 1.36$, $P = 0.18$; habituation, FID: $\rho = 0.42$, $t_7 = 1.21$, $P = 0.26$; distance fled, $\rho = 0.40$, $t_7 = 1.154$, $P = 0.29$). Intraspecific correlations of predation pressure and habituation with proportion that entered refuge were not significant for either species. The perfect correlation between rank FID and rank habituation precluded partial correlation or multiple regression for *P. pityusensis* and the small sample size made it infeasible for distance fled.

DISCUSSION

RELATIONSHIPS AMONG VARIABLES

In population-based analyses, FID and the distance fled increased as the distance to refuge increased, although the distance to refuge was unrelated to refuge entry. The association between the distance fled and FID in a simple regression disappeared in a multiple regression of the distance fled on FID and the distance from refuge. Therefore, FID was not associated with the distance fled, although these variables increased as the distance from refuge increased. Individual-based analyses showed that relationships among escape variables were uniform across sites.

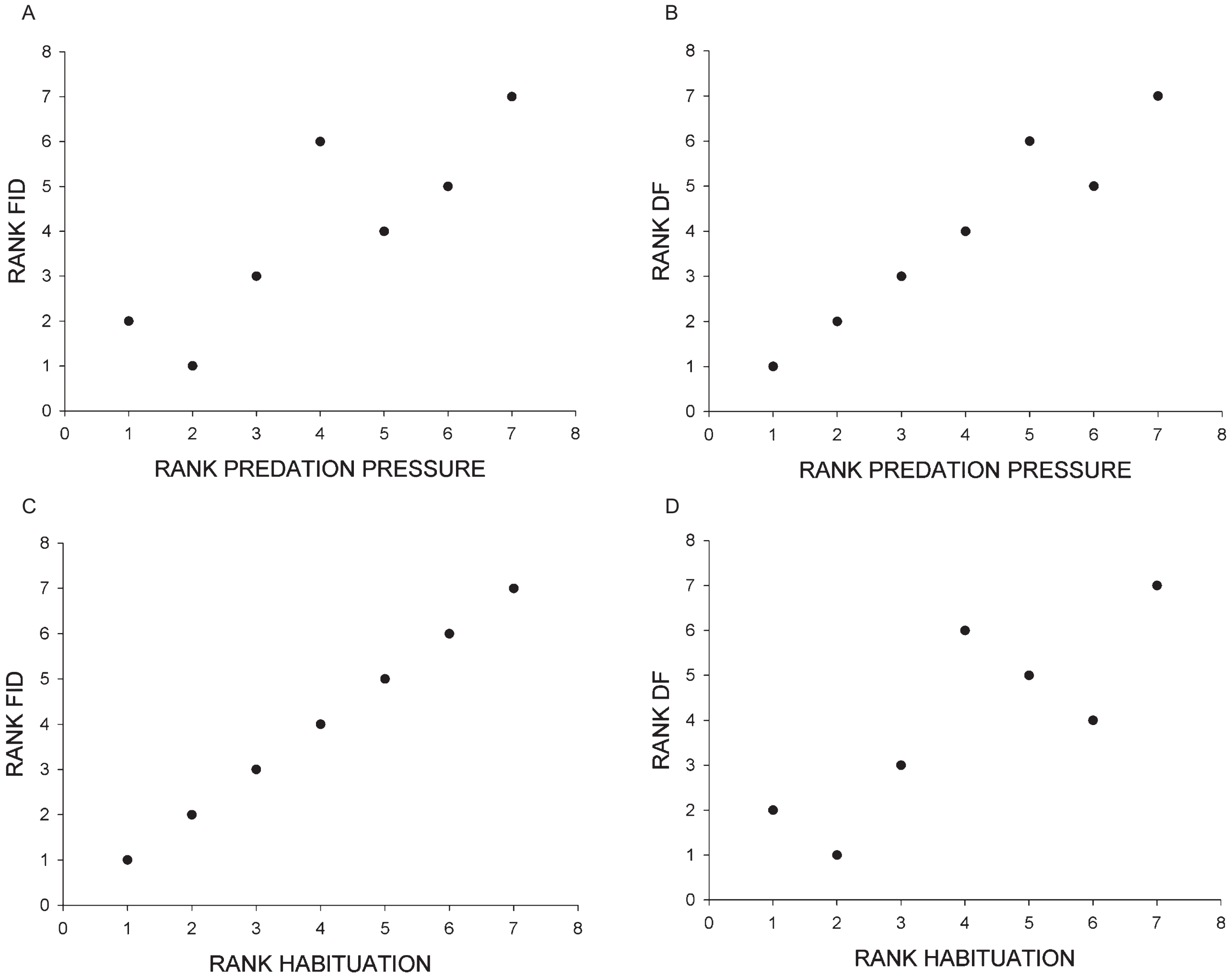

Figure 5. Ordinal level relationships for *Podarcis pityusensis* between predation pressure versus flight initiation distance (FID) (A) and (DF) distance fled (B), as well as between habituation to human presence versus flight initiation distance (C) and distance fled (D).

The individual-based analyses yielded similar findings, with the exception that both FID and the distance to refuge affected the distance fled, indicating that lizards fled further when the risk was greater. The distance to refuge affects the likelihood of being overtaken before reaching safety. Consequently, FID is greater when the distance from refuge is longer (Dill & Houtman, 1989; Cooper, 1997a, 2000a). Prey farther from the refuge may flee farther to be nearer the refuge when they stop fleeing (Cooper, 1997a, 2000a). Although the regressions do not establish causality, these considerations presumably account for the importance of the distance to refuge for FID and the distance fled (Stankowich & Blumstein, 2005). These relationships apply at the individuals and population levels. The increase of the distance fled as FID increases suggests that, when the risk is higher, lizards flee further, especially if they do not enter refuge.

The positive intercept of FID on the distance to refuge suggests that lizards may begin escape sufficiently early to maintain a margin of safety to reach refuge before the predator (Kramer & Bonenfant, 1997). The significance of the intercept of the distance fled on the distance to refuge would seem to indicate that prey do not flee when close enough to refuge, although they do flee. The true intercept must be zero for prey that enter refuge. It is positive because some individuals do not flee toward the nearest refuge and may flee a longer distance than the distance to refuge. Because escape begins at the FID, the intercept of distance fled on FID must occur at the origin, although it was significantly greater than zero only in individual-based tests.

The proportion that entered refuge, although unrelated to the distance from refuge and FID, was negatively correlated with the distance fled. It might have been predicted that lizards at sites where FID was longer would be more likely to flee longer distances and enter refuge. The lack of relationship between refuge entry and either FID or the distance from refuge occurred because many individuals fled adjacent to (but did not enter) refuges. Two factors may have contributed to the increase in refuge entry as the distance fled decreased: Lizards adjacent to refuge were more likely than others to enter, and lizards that did not enter sometimes fled farther than the nearest refuge. The likelihood of entering refuge increases under greater risk associated with rapid approach (Cooper & Whiting, 2007b; Cooper, 2009b).

Variation of escape behaviour among sites and species

FID, distance fled, and the probability of entering refuge all differed among populations. Although the distance to refuge varied among sites and was correlated with FID and the distance fled, both of these escape variables differed among sites independent of variation in the distance to refuge. The proportion of lizards that entered refuge varied across sites independently of the effect of the distance fled on refuge entry.

The findings are consistent with the existence of genetic variation upon which natural selection may act to alter escape behaviour in response to environmental factors such as predation pressure (Endler, 1986), although plasticity and variation in unstudied factors might have contributed to variation among sites. Factors might include differences in phylogeny, habitat features relevant to fleeing and refuge use, and predation pressure and habituation to people among sites. FID was 24% greater in *P. lilfordi* than *P. pityusensis*, although effect sizes for the differences between species and island groups were small as a result of substantial variability within species and island groups. The smaller size of *P. lilfordi* might have contributed to longer FID but, in previous studies, FID was longer in larger lizards or did not vary with body length (Stankowich & Blumstein, 2005). The only other differences between species were the greater slopes of FID and rank DF on rank DR for *P. lilfordi* than *P. pityusensis*, although the effect sizes of these differences were vey small. The escape behaviour or the two species was very similar but differed in minor ways that could be detected only using large sample sizes.

These results and correspondence between differences in FID between species and island groups suggest that an evolutionary change in FID may have occurred between the sister species *P. lilfordi* and *P. pityusensis*. Because predation pressure and habituation did not differ between species, it is unlikely that the difference in FID is a consequence of current difference in predation pressure or habituation. The longer FID of *P. lilfordi* does not appear to be associated with differences between island groups with respect to the distance to refuge and vegetation, or other obvious climatic or habitat differences.

Influences of predation pressure and habituation

FID and the distance fled were correlated with predation pressure in *P. pityusensis* but not *P. lilfordi*. Relationships between habituation and escape variables were strongly positive, whereas optimal escape theory predicts that FID and, in some circumstances, the distance fled decrease as habituation increases (Cooper & Frederick, 2007a, 2010; Cooper, 2009a). Empirical findings support these predictions for various prey (Stankowich & Blumstein, 2005), including lizards (Cooper *et al*., 2003; Cooper & Whiting, 2007a; Cooper, 2009a). Therefore, positive correlations of predation pressure with FID and the distance fled cannot be attributed to habituation. Rather, the effect of predation pressure overrides that of habituation.

Why is one species responsive to predation pressure but its sister species is not? The greatest predation pressure, flight initiation distance, and the distance fled for *P. pityusensis* occurred on large islands (Sa Can on Ibiza and Trucadors on Formentera. Predation pressure was lower and escape variables were diminished on small islets nearby. *Podarcis lilfordi* was extirpated by predators introduced by man (Pérez-Mellado, 2009) on the main islands of Menorca and Mallorca, and currently exists only on outlying islets. Therefore, differences in predation pressure have led to a divergence of escape behaviour among populations of *P. pityusensis* but not *P. lilfordi*.

Long isolation of *P. lilfordi* under relaxed predation pressure might have led to island tameness that did not permit sufficiently rapid evolution of escape behaviour to avoid extinction once domestic predators were introduced. The current lack of relationship between predation pressure and escape behaviour could indicate that island tameness persists and may be irreversible. Alternatively, variation in predation pressure among islets may be too small for natural selection to effect marked differences in escape behaviour. However, several aspects of tail autotomy are more effective on Colom than Aire (Cooper *et al*., 2004; Cooper & Pérez-Mellado, 2010) and lizards are warier on Rei than Aire (Cooper *et al*., 2009b; Cooper & Pérez-Mellado, 2010), as predicted by greater predation pressure on Colom and Rei than Aire. Our previous interpretations regarding effects of predation pressure in *P. lilfordi* may have been incorrect, as suggested by lack of a relationship between predation pressure and escape in the present study. Because we selected islets in earlier studies for their large differences in predation pressure, predation pressure might be an important factor. Uncontrolled differences among islets might have obscured relationships between predation pressure and escape.

The common ancestor of *P. lilfordi* and *P. pityusensis* had its origin around the time of the Messinian crisis of the Mediterranean, more than 5 Mya, when Plio-pleistocenic faunas of Balearic Islands were established (Brown *et al*., 2008; Alcover, 2010). The Gymnesic group of Mallorca and Menorca, and the Pityusic group of Ibiza and Formentera, were then very different. Two million years ago, the Pityusic Island, a common land mass of Ibiza and Formentera, was isolated from Great Balear, a large island including Mallorca and Menorca. Speciation of *P. lilfordi* and *P. pityusensis* started in two islands with very different predation environments. Ibiza, after almost complete extinction of its previous vertebrate fauna, was occupied only by several birds, some bats, and lizards, although it lacked terrestrial mammals (Alcover, 2010). The fauna of Menorca and Mallorca was significantly richer, including several endemic mammals, some reptiles, birds, and even amphibians (Alcover, 2010). The large number of bird species in the Pityusic Islands presumably subjected lizards to continuous predation pressure over many thousands of years, maintaining the antipredatory capacities of *P. pityusensis* almost intact, as indicated by autotomic capacity similar to that of continental species (Pérez-Mellado *et al*., 1997). In Menorca and Mallorca, the fossil record lacks mammalian predators and small avian predators (Alcover, Moyá-Solà & Pons-Moyá, 1981). During its prehuman evolution under greatly reduced predation pressure, *P. lilfordi* evolved a pronounced reduction of some antipredatory defences, including autotomic capacity (Pérez-Mellado *et al*., 1997; Cooper *et al*., 2004). When people arrived over 5000 years ago, the antipredatory defences of *P. lilfordi* presumably had reduced effectiveness. Both species subsequently were confronted with newly introduced predators, such as kestrels (*Falco tinnunculus*), weasels (*Mustela nivalis*), and/or cats (*Felis lybica*) (Sanders, 1984).

Podarcis pityusensis exhibits a strong relationship between current predation pressure and FID, whereas *P. lilfordi* does not. We hypothesize that, when confronted by predators introduced by human beings, *P. pityusensis* survived on the large islands of Ibiza and Formentera because intact antipredatory capacities permitted plastic and evolutionary adjustments of FID to new predators (and human disturbance). Although *P. lilfordi* retains the ability to adjust escape decisions to degree of predation risk (Cooper, Hawlena & Pérez-Mellado 2009a; Cooper *et al*., 2009b), these adjustments appear to have been insufficient to avoid predation by introduced predators. When the Balearic lizard was confronted by introduced predators similar to those introduced in the Pityusic Islands, it was rapidly extinguished on the main islands of Menorca and Mallorca during Roman times, surviving only on nearby islets. We hypothesize that this extinction occurred because the lizards had evolved island tameness with a loss of ability to rapidly evolve adequate escape behaviour.

If our interpretation is correct, why is FID longer in *P. lilfordi* than in *P. pityusensis*? Although FID differs between species, the effect size is very small, leaving little to explain. A small difference at the time of divergence might explain the current difference. Such a difference might have occurred randomly or have been based on unknown differences in predation regimes early in the evolutionary history of the species or, subsequently, because of temporal variation in predation pressure in prehistoric times unknown. Both species respond to predators at the individual level by fleeing, although only *P. pityusensis* varies its response between sites in relation to predation pressure.

The increase in FID by *P. pityusensis* as predation pressure increases is consistent with previous findings. Reduced FID on islands compared to mainland occurs in lizards (Shallenberger, 1970; Blázquez, Rodríguez-Estrella & Delibes, 1997; Cooper *et al*., 2004). FIDs of lizards in the Galapagos vary among islands and sites in relation to predation pressure (Stone *et al*., 1994; Rödl *et al*., 2007). FID by *P. sicula* was shortened within 30 years after introduction to an island where the lizards experienced a greatly reduced predation pressure (Vervust *et al*., 2007). These findings suggest that the escape behaviour of lizards is adjusted to levels of predation pressure to which their populations have been exposed historically and that responses to changes in predation pressure can sometimes take place rapidly. Our findings further suggest that island tameness can become fixed, which matches previous interpretations of extinctions of island taxa exposed to novel predators (Diamond, 1982; Steadman, 1995).

It remains possible that the lizards adjust unstudied aspects of antipredatory behaviour to predation risk. They might, for example, vary activity times, microhabitat use, predator-specific escape tactics, escape paths, running speed, effectiveness of autotomy, and time spent in refuge. In all populations that we studied, lizards are terrestrial; are active in the morning and afternoon; and use plants, holes, and crevices as refuges. In all populations lizards, fled away from investigators and usually toward refuges. We noted no obvious differences in running speed, although there were a lack data on speed or possible differences in escape tactics among different types of predators. Interpopulational variation exists with respect to reliance on and ease of autotomy (Cooper *et al*., 2004), as well as hiding time in refuge (Cooper, Hawlena & Pérez-Mellado, 2009a).

In summary, we propose that historical differences in exposure of the sister species to predation accounts for current difference in the relationship between predation pressure and FID. For *P. pityusensis*, adjustments to predation pressure appear to be stronger than those to habituation, although the responsiveness to both indicates a capacity to adjust FID within a lifetime (habituation) and perhaps across generations. Neither capacity is apparent in *P. lilfordi*, consistent with historical loss by evolution of island tameness. Whether adjustments to predation pressure reflect solely plastic responses during ontogeny, as suggested for the elapid snake *Notechis scutatus* (Aubret, Michniewicz & Shine, 2011), evolutionary processes, or both, remains unknown.

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