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Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards

B. VANHOOYDONCK* and R. VAN DAMME
University of Antwerp (UIA), Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium

Summary

1. Microhabitat use and antipredator behaviour (i.e. behavioural response to a bird model and refuge microhabitat) was measured in an experimental set-up for 11 lacertid lizard species. Additionally, locomotor performance (sprint speed, climbing and clambering speed, manoeuvrability and endurance) of the same species was quantified.
2. The results showed considerable interspecific variation in microhabitat use, behavioural response and choice of refuge microhabitat. Part of that variation could be linked to differences in locomotor capacity.
3. Species that frequently made use of open microhabitats tended to be fast sprinters, but had limited endurance. The behavioural data suggest these species will not start running before the predator is close at hand, and thus having high sprint capacities might be more beneficial than great endurance.
4. Species that spent most of their time on vertical elements appeared to be fast climbers. As such microhabitats tend to be quite exposed, lizards living there are conspicuous to predators and being able to escape fast seems relevant.
5. Contrary to our expectations, species mostly observed in the vegetated microhabitats did not excel in clambering capacity or manoeuvrability. Possibly, dense vegetation constitutes a safe harbour and species may no longer be under selection for locomotor speed.
6. Behavioural response when confronted with an aerial predator was context-dependent in most species: most lizards fled more when in open or vertical microhabitats than when in densely vegetated ones. Moreover, when fleeing most species sought refuge in the vegetation. These findings support our idea that vegetated patches may constitute a safe harbour for lacertids.

Key-words: Adaptation, ecomorphology, interspecific comparison, locomotion

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Introduction

The congruence between animal body form and habitat use is generally considered one of the most illustrative outcomes of adaptive evolution. Still, remarkably few studies have investigated the process in sufficient detail to reveal the selective pressures and trade-offs that cause the morphological differentiation. Earlier studies often contented themselves with demonstrating statistical relationships between aspects of body form and habitat use, subsequently lapsing into 'adaptive story telling' (Gould & Lewontin 1979) to explain them. In an attempt to avoid that mistake, and following recommendations by Arnold (1983) and Emerson & Arnold (1989), contemporary students of ecomorphology typically break up the relationship between morphology and ecology into a morphology → performance and a performance → ecology component. In studies of habitat use, 'performance' is usually assessed in terms of locomotor capacities. Although much recent work has centred on the mechanical and physiological causes of variation in locomotor capacity (see Garland & Losos 1994; Van Damme & Vanhooydonck 2001), far fewer studies have investigated whether and how this performance variation affects the probability of survival in different habitats.

If performance variation among species from different habitats is adaptive, then it can be predicted that species will excel in those performance aspects that they require in nature (Losos & Sinervo 1989; Sinervo & Losos 1991; Irschick & Losos 1998, 1999). For

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*Author to whom correspondence should be addressed. E-mail: vhooyd@uia.ua.ac.be

instance, an animal from an open habitat would be expected to have a relatively high running capacity, whereas a related arboreal species would be predicted to have good climbing skills. The existence of evolutionary trade-offs between different performance aspects (e.g. running *vs* climbing) will promote differences in performance (and morphology) between animals of different habitats. This shows the importance of measuring different appropriate aspects of performance when studying ecomorphological relationships.

Deciding which performance aspect measure is appropriate for a particular species may be more troublesome than expected. Rough descriptions of general habitat characteristics will not do. Especially for species that are relatively small compared with the habitat elements surrounding them, it is important to know which particular microhabitats the animals are exploiting. For instance, a lizard living on the forest floor is likely to experience different challenges than a lizard living on tree trunks in the same forest. Since most species will use several microhabitats during their daily activities, one should also have an idea of the time spent in each of these microhabitats. Also, it is often unclear whether, in the field, lizards occur in a specific microhabitat because they prefer it or because predators or competitors drive them into it. This way, species can be forced into microhabitats to which they are not adapted (e.g. Losos & Spiller 1999). In addition to data on habitat use, information on the behaviour of the species may be essential. For instance, stamina may be a relevant performance measure for a species of open areas that flees over long distances when approached by a predator. However, for a second species, inhabiting a similar habitat but fleeing only over short distances, measures of maximal speed or acceleration may be more appropriate. For a third species, one that does not flee but relies on its cryptic coloration, measures of locomotor abilities may be irrelevant all together.

With these ideas in mind, we here examine relationships between microhabitat use, antipredator behaviour and different aspects of locomotor performance in a set of 11 lacertid lizard species. Members of the Lacertidae occupy a wide variety of habitats and microhabitats (Arnold 1989). They are all relatively small, agile, actively foraging and heliothermic lizards, and casual field observations suggest that all, at least to some degree, use bouts of rapid locomotion to escape predators, to catch prey, and during social interactions. In earlier papers, we have shown an evolutionary trade-off between stamina and speed (Vanhooydonck, Van Damme & Aerts 2001) but not between level-running capacity and climbing skills (Van Damme, Aerts & Vanhooydonck 1997; Vanhooydonck & Van Damme 2001) in these lizards. We present quantitative data on microhabitat use in semi-natural conditions. We test the following putative links between microhabitat use and locomotor capacities. (1) Depending on their behaviour, lizards that frequently use open microhabitats will be either fast or have great endurance. (2) Species that often use vertical structures (walls, rocks, trunks) will display good climbing skills. (3) Species of cluttered habitats will show good clambering skills and/or high manoeuvrability. To examine possible confounding effects due to differences in behaviour, we also observed lizards during simulated attacks by a predator. We noted the antipredator behaviour of the lizards (flight *vs* immobility) and examined both its context (microhabitat) specificity and its relations with locomotor capacities. The prediction here is that animals are more likely to flee in microhabitats in which they are able to locomote relatively well. Finally, we also investigated whether lizards ran to particular habitats, i.e. habitats that provide cover, or habitats in which the lizards perform well.

Table 1. Species (number of males, number of females), snout–vent length and manoeuvrability. Data are means and standard deviations per species. Data on sprint speed, climbing speed, clambering speed and endurance of the same species can be found in Vanhooydonck & Van Damme (2001) and Vanhooydonck *et al.* (2001)

Species (*N*)	Snout–vent length (mm)	Manoeuvrability (cm/s)
Gallotia galloti (6, 9)	98·53 ± 16·24	78·16 ± 44·07
Lacerta oxycephala (9, 7)	56·77 ± 2·80	101·23 ± 26·03
Lacerta bedriagae (10, 5)	71·73 ± 6·11	112·01 ± 31·25
Podarcis sicula (10, 5)	68·23 ± 2·29	84·66 ± 25·20
Podarcis muralis (10, 11)	52·08 ± 5·24	47·84 ± 19·43
Podarcis tiliguerta (10, 4)	56·87 ± 2·55	84·78 ± 35·78
Lacerta bilineata (4, 2)	92·69 ± 11·16	144·76 ± 35·10
Takydromus sexlineatus (6, 3)	51·79 ± 2·61	18·21 ± 8·58
Acanthodactylus pardalis (9, 3)	59·22 ± 2·52	100·22 ± 41·71
Acanthodactylus scutellatus (2, 2)	67·70 ± 8·11	163·69 ± 53·28
Latastia longicaudata (4, 5)	73·83 ± 5·77	77·22 ± 37·50

Materials and methods

STUDY ANIMALS

Adult individuals of eight species of lacertid lizards were caught by noose at different sites in Western Europe and the Canary Islands. Specimens of three additional species (*Acanthodactylus pardalis*, *A. scutellatus* and *Latastia longicaudata*) were obtained from the pet trade. For each species, Table 1 lists the scientific name, number of males and (non-gravid) females, snout–vent length and manoeuvrability. Data on sprint speed, climbing speed, clambering speed and endurance of the same species can be found in Vanhooydonck & Van Damme (2001) and Vanhooydonck *et al.* (2001). Table 2 lists the number of observations on microhabitat use, refuge microhabitat and behavioural response to a predator per species and per microhabitat type.

The animals were transported to our laboratory in the University of Antwerp, where they were housed in groups of four or five individuals of the same species, in glass terraria of 100 cm by 50 cm. Each terrarium

Table 2. Species (number of males, number of females), number of observations on microhabitat use, refuge microhabitat and fleeing tendency per species and per microhabitat type. Total number of observations on behavioural response (sum of fleeing and staying put) are given between brackets in 'fleeing tendency' column. Seven species spent more than 50% of their time in one particular microhabitat in undisturbed conditions (in bold)

	Microhabitat use			Refuge microhabitat			Fleeing tendency (total)		
Species (*N*)	Open	Vertical	Vegetated	Open	Vertical	Vegetated	Open	Vertical	Vegetated
Gallotia galloti (6, 4)	49	47	38	5	16	22	31 (41)	8 (32)	4 (25)
***Lacerta oxycephala* (3, 2)**	34	**84**	16	0	13	4	10 (16)	7 (46)	0 (8)
***Lacerta bedriagae* (7, 4)**	50	**173**	54	8	56	25	28 (32)	53 (110)	8 (30)
Podarcis sicula (7, 5)	81	30	86	0	17	25	32 (43)	8 (13)	2 (38)
***Podarcis muralis* (8, 8)**	**142**	81	30	28	19	28	63 (76)	11 (41)	1 (10)
Podarcis tiliguerta (9, 4)	134	115	51	24	45	101	94 (120)	72 (76)	4 (47)
Lacerta bilineata (4, 2)	56	19	48	0	3	17	17 (52)	2 (19)	1 (46)
***Takydromus sexlineatus* (4, 2)**	17	21	**65**	8	6	9	12 (17)	10 (21)	1 (65)
***Acanthodactylus pardalis* (8, 3)**	**220**	32	22	10	2	21	35 (147)	0 (26)	0 (11)
***Acanthodactylus scutellatus* (2, 1)**	**67**	1	9	1	0	1	2 (67)	0 (1)	0 (9)
***Latastia longicaudata* (5, 1)**	**148**	16	13	10	13	15	36 (76)	0 (9)	3 (5)

contained a sandy substrate, some stones and bits of vegetation. Two 100-W bulbs suspended 20 cm above the substrate provided heat and light for 10 h a day. The two larger species (*Gallotia galloti* and *Lacerta bilineata*) were housed individually in similar terraria. All animals were fed daily live crickets dusted with calcium. Water was always available.

The snout–vent length (SVL) of all individuals was measured from the tip of the snout to the posterior edge of the anal scale, using digital callipers (Mitutoyo CD-15DC, precision 0·01 mm; Mitutoyo (UK) Ltd, Tetford, UK).

All experiments were carried out within 6 weeks of the animals being captured.

PERFORMANCE TESTING

Maximal sprint speed, clambering speed (i.e. the ability to move up a wire mesh) and climbing speed (i.e. the ability to move up a smooth slate) were measured by means of an electronic racetrack; endurance was measured on a running belt (see Vanhooydonck & Van Damme 2001 and Vanhooydonck *et al.* 2001 for details on equipment and procedures). Manoeuvrability was defined as the speed with which the lizards could move through a pinboard that was positioned in the racetrack. The pinboard consisted of 53 equally spaced wooden pins with a diameter of 8 mm. The distance between the pins was adjusted to the size of the species being tested (*L. bilineata* and *G. galloti*, 45 mm; *Podarcis muralis* and *Takydromus sexlineatus*, 26 mm; all other species, 35 mm). Six pairs of photocells, positioned at 10-cm intervals, registered when a lizard passed. Each individual lizard was raced five times. Prior to experimentation and in between trials, the lizards were placed for at least 1 hour in an incubator set at the selected body temperatures of the different species (38 °C for *A. scutellatus*, *A. pardalis* and *L. longicaudata*; 35 °C for all other species; see review in Castilla, Van Damme & Bauwens 1999). Each run was scored as 'good' or 'poor' (cf. van Berkum & Tsuji 1987; Tsuji *et al.* 1989). 'Poor' trials were eliminated from the analyses. As an estimate of manoeuvrability, we used the highest speed over any 10 cm.

MICROHABITAT USE

Lizards were observed in a large (4 m × 4 m) terrarium, holding the following eight types of microhabitats:

1. A dense stand of purple moor grass (*Molinia caerulea*), *c.* 0·5 m high and with a total area of 3 m^2.
2. A strip of grass (*Poa annua*), *c.* 5 cm high and with an area of 3 m^2.
3. A patch of moss with a surface of 3 m^2.
4. A *c.* 3 m^2 surface closely planted with *c.* 20 cm high shrubs (*Lonicera* spp.).
5. A strip of sand, also 3 m^2 in surface.
6. A wall of piled stones, 0·5 m high and with a top surface of 0·5 m^2.
7. A series of logs, each 1 m long, and loosely stacked to a height of 0·3 m.
8. A tree trunk of 20 cm diameter, cut off at a height of 40 cm.

Eight 500-W lamps, one above each type of microhabitat, provided heat and light throughout the experiment. The distance between the bulbs and the substratum was adjusted to ensure that lizards would experience similar heat loads in each microhabitat patch.

The smaller species (SVL < 80 mm) were introduced into the test terrarium in groups of a maximum of eight individuals, the larger species in groups of a maximum of five individuals. Species were always kept apart. Each lizard was given an individual dot code on its back (non-toxic paint) for rapid identification. To avoid disturbance, all observations were made from behind a blind. After an initial habituation period of 1 hour, the microhabitat occupied by each individual lizard in the terrarium was recorded at 30-min intervals over a total time period of 7 h. All animals seemed normally active and moving frequently. Therefore, we believe that consecutive point observations can be considered independent of each other. The lizards remained in the test terrarium for two consecutive days. Water was present in all eight microhabitat patches. To facilitate interpretation, we decided to pool the above-mentioned types of patches into three classes of microhabitat that clearly differ in structural features: an 'open' microhabitat (combination of low grass (2), moss (3) and sandy (5) patches); a 'vegetated' microhabitat (combination of moor grass (1) and shrub (4) patches) and a 'vertical' microhabitat (stone wall (6), logs (7) and trunk (8)).

ANTIPREDATOR BEHAVIOUR

In a second set of observations, the set-up described above was used to quantify the behaviour of the 11 species when confronted with a model of an aerial predator. One hour after the lizards had been introduced into the terrarium, a wooden bird model was pulled from one side of the terrarium to the other, at a height of 1 m above the substrate. The model had the size, the shape and the colour of a corvid bird. Corvid birds consume many species of lacertid lizards (Strijbosch 1981; Cramp 1985). Antipredator behaviour was simply scored as 'fleeing' when the lizard fled in response to the model, or 'immobile' when it stayed put. In addition, when lizards fled, the microhabitat to which they ran was noted (hereafter referred to as the 'refuge microhabitat'). The predator stimulus was shown once an hour over a total time period of 7 h (per day). The lizards remained in the test terrarium for two consecutive days.

STATISTICAL ANALYSES

Three proportions were calculated for the observations on microhabitat preference for each individual lizard: (1) number of observations in open microhabitat against total number of observations; (2) number of observations in vertical microhabitat against total number of observations; and (3) number of observations in vegetated microhabitat against total number of observations. The same proportions were calculated for the observations on refuge microhabitat.

Two proportions were used for the observations on behavioural response when confronted with the predator model: (1) number of times each species fled against total number of observations on behaviour (hereafter referred to as fleeing tendency) and (2) number of times each species stayed put against total number of observations on behaviour.

Calculations were made of the mean per species of SVL, the performance measures and proportions. SVLs and performance measures were logarithmically transformed ($\log_{10}$), and proportions were arcsine transformed prior to statistical analyses (Sokal & Rohlf 1995).

Because species share parts of their evolutionary history, they cannot be regarded as independent data points in statistical analyses (Felsenstein 1985, 1988; Harvey & Pagel 1991; Garland *et al.* 1993). In recent years, various computer programs have been developed to take phylogenetic relationships among species into account in statistical analyses (see Harvey & Pagel 1991; Garland *et al.* 1993; Losos & Miles 1994). In this study, the independent contrasts approach was used (Felsenstein 1985, 1988).

The independent contrasts of the $\log_{10}$-transformed means per species of SVL, sprint speed, climbing speed, clambering speed, manoeuvrability and endurance were calculated (PDTREE, Garland, Midford & Ives 1999). The contrasts of the performance measures were then regressed against the contrasts of SVL (regression through the origin, see Garland, Harvey & Ives 1992) and calculated the residuals. The independent contrasts of the arcsine transformed proportions of the observations on microhabitat preference, behavioural response and refuge microhabitat were calculated, using the same program (PDTREE, Garland *et al.* 1999).

To test for correlations between the performance traits, on the one hand, and microhabitat or behavioural variables, on the other, bivariate Pearson product moment correlations were performed on the (residual, in case of the performance measures) contrasts of the parameters of interest. In fact, these correlations represent correlations between evolutionary changes in one trait and evolutionary changes in the other. However, we will refrain from stating this explicitly every time in the 'Results' and 'Discussion' sections to improve the readability of the paper. *P*-values $< 0{\cdot}1$ were used to determine statistical significance.

To test whether these correlations differed for males and females, the above-described analyses were redone for each sex separately. The results were comparable. For simplicity, we only report the results for the pooled (i.e. both sexes combined) data set.

The independent contrast method requires information on the topology and branch lengths of the phylogenetic tree. As the phylogenetic relationships within the lacertids are incompletely resolved, a combination of results was used from morphological (Arnold 1989, 1998) and mitochondrial DNA studies (Harris, Arnold & Thomas 1998; Harris & Arnold 1999) to compile a 'currently best' tree (Fig. 1). Some unresolved nodes remain. So far, all attempts of phylogeny reconstruction in lacertids, even the most recent ones using molecular techniques, have failed to unravel these relationships and the polytomies might in fact represent explosive speciation events (Arnold 1989; Harris *et al.* 1998; Harris & Arnold 1999; Fu 2000). Thus we considered the unresolved nodes 'hard' polytomies (see Purvis & Garland 1993). Also, few data are available on the divergence times within the lacertids. Therefore, all branch lengths were set to unity. In the

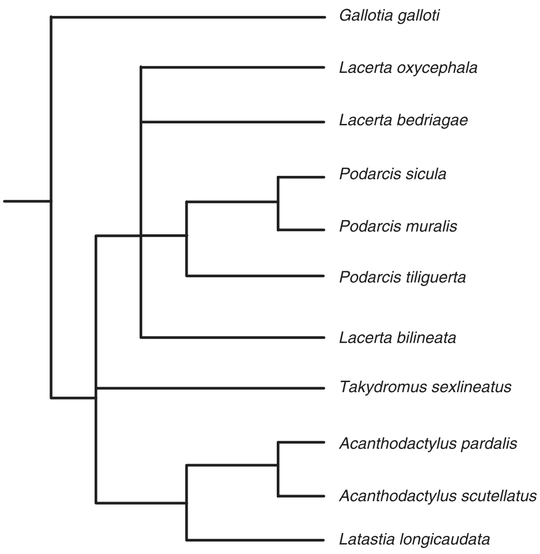

Fig. 1. Phylogenetic tree of the 11 lacertid lizard species used in the analyses. The tree is a currently best approximation, based on morphological characters and on mitochondrial DNA sequences (see text for references).

PDTREE program (Garland *et al.* 1999), we checked whether the absolute values of the standardized contrasts were significantly correlated with their standard deviations. None of the correlations was significant. Moreover, it has been shown previously that the actual lengths of the branches do not alter the outcome of phylogenetic analyses to a great extent (Martins & Garland 1991; Walton 1993; Irschick *et al.* 1996; Díaz-Uriarte & Garland 1998).

To test for inter- and intraspecific differences in microhabitat use, behavioural response and refuge microhabitat RXC contingency table analyses and log linear analyses were used. Because the number of individuals observed in the experimental set-up differed among species, individual variation (i.e. within species) may affect the outcome of the statistical analyses. This was explicitly tested for the microhabitat use data by introducing individual and the interaction between individual and microhabitat use as random factors (both nested within species) in a log linear analysis (GLIMMIX procedure in SAS 6·12; Littell *et al.* 1996). The variance components for both factors were estimated as 0, implying that individuals within species did not differ significantly in microhabitat use. Theoretically, we should have repeated this kind of analysis with the data on refuge microhabitat and behavioural response. However, the low number of observations per individual prevented us from doing so. For further analyses, all data per species were pooled.

Results

MICROHABITAT USE AND LOCOMOTOR PERFORMANCE

The 11 species of lacertid lizards clearly differed in their relative use of the three types of microhabitats available in the test-terrarium (RXC-test, $\chi^2_{20} = 695{\cdot}4$, $P < 0{\cdot}0001$, Table 2). Specimens of *A. scutellatus*, *A. pardalis* and *L. longicaudata* spent most of their time in the open microhabitat, individuals of *Lacerta bedriagae* and *L. oxycephala* were most often seen on the vertical elements, and individuals of *T. sexlineatus* in the vegetated patches. *Podarcis sicula* and *L. bilineata* frequented the open and the vegetated microhabitats, but seemed to avoid the vertical elements. *Podarcis muralis* and *P. tiliguerta* used the open and vertical microhabitats, but were seldomly observed in the vegetated patches. *Gallotia galloti* seemed the most catholic species, spending equal amounts of time in all three microhabitats.

Does the observed variation in microhabitat use among species correlate with variation in locomotor performance? In the Introduction, we presupposed a potential relationship between the tendency to use open habitats and either speed or endurance. We found a positive correlation between the proportion of time spent in the open microhabitat and maximal sprint speed ($r = 0{\cdot}75$, $t_9 = 3{\cdot}37$, $P = 0{\cdot}008$; Fig. 2a). The correlation between open habitat use and endurance capacity was negative ($r = -0{\cdot}55$, $t_9 = -1{\cdot}97$, $P = 0{\cdot}08$; Fig. 2b). Secondly, we expected that species that frequently make use of vertical elements would excel in climbing speed. There is a positive relationship between the proportion of time species spent on the vertical elements in the terrarium, and maximal climbing speed ($r = 0{\cdot}53$, $t_9 = 1{\cdot}89$, $P = 0{\cdot}09$; Fig. 3). Finally, we suggested that species of vegetated areas would have high clambering speed and manoeuvrability. However, the proportion of time spent in the vegetated areas showed negative, rather than positive relations with either performance measure (clambering speed: $r = -0{\cdot}81$, $t_9 = -4{\cdot}15$, $P = 0{\cdot}003$; manoeuvrability: $r = -0{\cdot}55$, $t_9 = -1{\cdot}97$, $P = 0{\cdot}08$).

FLEEING TENDENCY, MICROHABITAT USE AND LOCOMOTOR PERFORMANCE

The proportion of animals that fled when approached by the predator model varied dramatically among species (RXC-test, $\chi^2_{20} = 695{\cdot}4$, $P < 0{\cdot}0001$, Table 2). This variation showed no relationship with variation in speed ($r = -0{\cdot}15$, $t_9 = -0{\cdot}44$, $P = 0{\cdot}67$) or endurance capacity ($r = 0{\cdot}32$, $t_9 = 1{\cdot}01$, $P = 0{\cdot}34$).

However, interspecific differences in antipredator behaviour were confounded by species-specific effects of microhabitat occupation on fleeing tendency (log linear analysis, species × behaviour × microhabitat interaction: $\chi^2_{20} = 96{\cdot}5$, $P < 0{\cdot}0001$). With the exception of *A. scutellatus* ($\chi^2_2 = 0{\cdot}31$, $P = 0{\cdot}86$), all species showed a different fleeing tendency in different microhabitats (all $\chi^2_2 > 7{\cdot}95$, all $P < 0{\cdot}02$). Of the 10 species that shift their antipredator behaviour in response to the microhabitat in which they find themselves, 9 show a similar pattern. These lizards tend to run away most often when in the open microhabitat, and least often when in

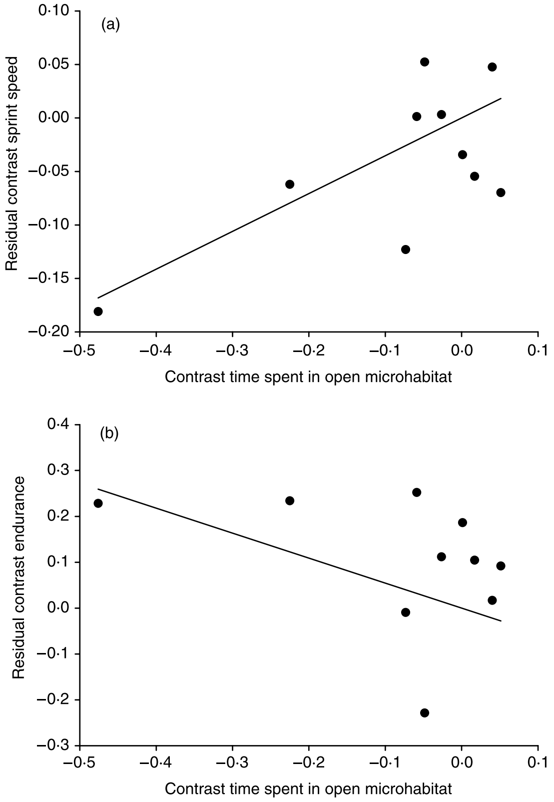

Fig. 2. The bivariate relationships between time spent in open microhabitat and locomotor performance among the 11 species: (a) the positive correlation between the phylogenetic independent contrasts of the proportion of time spent in open microhabitat (after arcsine transformation and per species) and residual phylogenetic independent contrasts of ($\log_{10}$-transformed means per species of) sprint speed (r through origin = 0.75); (b) the negative correlation between the phylogenetic independent contrasts of the proportion of time spent in open microhabitat (after arcsine transformation) and residual phylogenetic independent contrasts of ($\log_{10}$-transformed means of) endurance (r through origin = −0.55).

the vegetated microhabitat. The exception is *L. longicaudata*, who choose to run as often in the vegetated as in the open areas, but stay put when on vertical elements.

Does fleeing tendency correlate with habitat use under undisturbed conditions? That is, do lizards flee sooner (or, conversely, remain stationary) when they are confronted with a predator in their 'preferred' microhabitat? We tested this idea in the seven species that, in the undisturbed experiment, spent more than 50% of their time in a particular microhabitat (Table 2). *Takydromus sexlineatus*, which in undisturbed conditions 'preferred' vegetated areas, fled more often when attacked in open areas or on vertical elements than when in vegetated areas ($x_1^2 = 43{\cdot}91$, $P < 0{\cdot}0001$). *Lacerta oxycephala*, normally most often seen on vertical elements, had a similar reaction: they tended to stay put when attacked in their 'preferred' microhabitat, but fled more often when approached in open or vegetated areas ($x_1^2 = 6{\cdot}00$, $P = 0{\cdot}01$). *Latastia longicaudata*, *A. pardalis* and *P. muralis* showed the opposite response; they fled sooner in their 'preferred' (i.e. the open) microhabitat than when in other areas ($x_1^2 = 3{\cdot}24$, $P = 0{\cdot}07$, $x_1^2 = 10{\cdot}88$, $P = 0{\cdot}001$ and $x_1^2 = 44{\cdot}48$, $P < 0{\cdot}0001$, respectively). Finally, we found no differences in fleeing tendency between 'preferred' and 'non-preferred' microhabitats in *L. bedriagae* ($x_1^2 = 1{\cdot}55$, $P = 0{\cdot}21$) and *A. scutellatus* ($x_1^2 = 0{\cdot}31$, $P = 0{\cdot}58$).

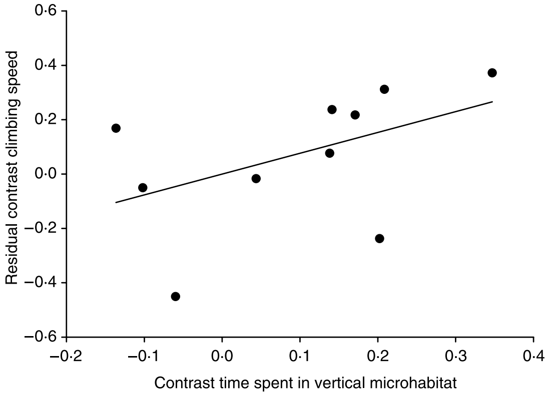

Fig. 3. The positive correlation between the phylogenetic independent contrasts of the proportion of time spent in vertical microhabitat (after arcsine transformation and per species) and residual phylogenetic independent contrasts of ($\log_{10}$-transformed means per species of) climbing speed (r through origin = 0.53).

The apparent context-dependency of the antipredator behaviour induced us to refine our predictions on possible correlations between fleeing tendency and locomotor performance. We now tested whether (1) the tendency to flee in open areas is correlated with sprint speed or endurance; (2) the tendency to flee on vertical elements is correlated with climbing speed; and (3) the tendency to flee in vegetated patches is correlated with clambering speed or manoeuvrability. There is a positive relationship between the tendency to flee in open areas and endurance capacity ($r = 0{\cdot}53$, $t_9 = 1{\cdot}88$, $P = 0{\cdot}09$). All other correlations proved non-significant (all $P > 0{\cdot}27$).

REFUGE MICROHABITAT, MICROHABITAT USE AND LOCOMOTOR PERFORMANCE

Refuge microhabitat choice varied among the 11 species (Table 2, RXC-test, $x_{20}^2 = 115{\cdot}2$, $P < 0{\cdot}0001$). When running from the predator, *L. oxycephala* and *L. bedriagae* most often went for the vertical elements, while *P. sicula*, *P. tiliguerta* and *L. bilineata* went for the vegetated areas. *Gallotia galloti* ran either towards vegetated areas or towards vertical elements. The two *Acanthodactylus* species chose vegetated or open microhabitats to flee to. The three remaining species (*L. longicaudata*, *T. sexlineatus* and *P. muralis*) seemed more catholic in refuge choice. The microhabitat from which they departed did not influence the refuge choice of the species (log linear analysis, $x_{40}^2 = 39{\cdot}80$, $P = 0{\cdot}48$).

Do species flee towards 'preferred' habitats? If so, we expect a positive correlation between tendency to

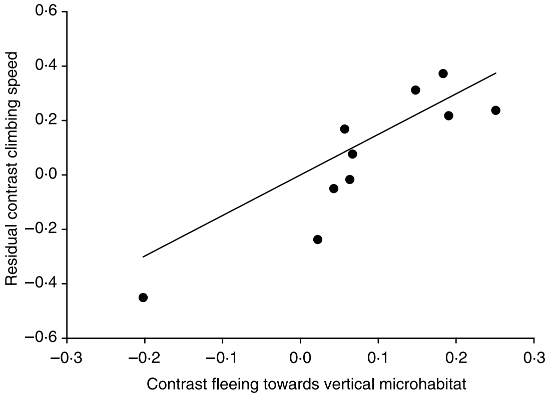

Fig. 4. The positive correlation between the phylogenetic independent contrasts of fleeing tendency towards vertical microhabitat (after arcsine transformation and per species) and residual phylogenetic independent contrasts of ($\log_{10}$-transformed means per species of) climbing speed (r through origin = 0.86).

flee towards a particular habitat and microhabitat use in undisturbed conditions. This seemed to be the case for the vertical and vegetated microhabitat. Lizards that occurred most often on the vertical elements in the microhabitat use experiment, also more frequently chose these elements as a refuge microhabitat during predatory encounters ($r = 0·70$, $t_9 = 2·98$, $P = 0·015$), while species mostly occurring in the vegetated areas also took refuge more frequently in the vegetation when confronted with the predator model ($r = 0·64$, $t_9 = 2·51$, $P = 0·033$). A similar correlation for the open microhabitat proved non-significant ($r = 0·10$, $t_9 = 0·29$, $P = 0·77$).

Finally, we tested whether refuge choice correlated with locomotor performance. Tendency to run towards open areas did not correlate with running speed ($r = 0·14$, $t_9 = 0·43$, $P = 0·68$) or with endurance ($r = 0·02$, $t_9 = 0·05$, $P = 0·96$). Species that ran towards vegetated areas were not particularly manoeuvrable ($r = -0·13$, $t_9 = -0·39$, $P = 0·7$) and do not have exceptional clambering skills ($r = -0·42$, $t_9 = -1·37$, $P = 0·20$). However, species that fled towards the vertical elements in the terrarium tended to have good climbing capacities ($r = 0·86$, $t_9 = 4·97$, $P = 0·0008$; Fig. 4).

Discussion

Our observations on microhabitat use in experimental conditions correspond remarkably well to qualitative field data available in the literature. Both *Acanthodactylus* species and *L. longicaudata* are ground-dwelling lizards from open, dry places with sparse vegetation (Arnold 1998). Although *P. muralis* is a typically climbing species, it often occurs in dry and less grassy habitats (Arnold & Burton 1978). *Lacerta oxycephala* typically occurs on very steep slopes such as walls, cliffs and rocks (Bischoff 1984; Arnold 1998). *Lacerta bedriagae* is mostly confined to large boulders and rocky outcrops (Castilla *et al.* 1989; Delaugerre & Cheylan 1992; Vanhooydonck, Van Damme & Aerts 2000). *Takydromus sexlineatus* is always found among dense vegetation (Karsen, Wai-neng Lau & Bogadek 1986; Arnold 1998). Both *P. sicula* and *L. bilineata* occur among shrubs, but are often seen dashing across relatively open strips of land (Delaugerre & Cheylan 1992; Arnold 1998; Vanhooydonck *et al.* 2000). *Podarcis tiliguerta* is a typical wall lizard that also spends considerable time foraging in the surrounding vegetation (Delaugerre & Cheylan 1992; Van Damme *et al.* 1990; Arnold 1998). Finally, *G. galloti* is highly catholic with respect to microhabitat use (Thorpe & Baez 1987). The close agreement between habitat use in the laboratory and under natural conditions suggests that species in the field occupy their 'preferred' habitat, i.e. that microhabitat choice is not constrained by external factors such as competition or predation risk. Alternatively, since our experiments were conducted on mature animals, microhabitat use in the experimental set-up may reflect prior experiences rather than innate 'preferences'. Observations on naive individuals could settle this case.

Our prediction that microhabitat use should correlate with relevant aspects of locomotor performance was only partially met. Species that make more frequent use of open areas tend to be the faster sprinters but have relatively limited stamina. Our behavioural observations help to explain this finding. Species from open areas (*A. scutellatus*, *A. pardalis* and *L. longicaudata*) often remained motionless throughout the experiments with the predator model. This suggests that in encounters with real predators, they rely on their cryptic coloration and will not start running before the predator is close at hand. Lizards using this kind of antipredator tactic are aided by high sprinting abilities, rather than by great endurance capacities. The negative relation between time spent in open areas and endurance capacity could result from selection on stamina in the other microhabitats (i.e. densely vegetated or vertical elements) or may merely reflect the evolutionary trade-off between sprinting speed and endurance in these lizards (Vanhooydonck *et al.* 2001). Similar correlations between sprint capacity and the use of open microhabitats have been reported for other lizard species and populations (Sinervo & Losos 1991; Garland & Losos 1994).

Unexpectedly, we did not find a positive correlation between time spent in densely vegetated microhabitats and clambering capacity. This contrasts with studies on *Sceloporus* and *Anolis* lizards that demonstrated a correlation between climbing locomotor abilities (i.e. surefootedness, clinging or grasping ability) and degree of arboreality (Losos & Sinervo 1989; Sinervo & Losos 1991; Losos & Irschick 1996). A plausible explanation for this disparity is the difference in locomotor behaviour between lacertid and *Sceloporus* or *Anolis* lizards. Whereas the latter lizards frequently move on stems and branches, lacertids in our experimental set-up seldom clambered into the vegetation, but moved around on the substrate in between and below the shrubs and plants. If our observations are representative of the lizards' behaviour in the field, selection may not be acting on clambering speed. However, following this line of thought, one would expect to find a positive correlation between time spent in the vegetated microhabitats and manoeuvrability, and this idea is not supported by our data. Possibly, dense clumps of vegetation constitute a safe harbour, in which fast locomotion is no longer required. If so, species living in such areas may no longer be under selection for locomotor abilities. Clearly, we need more information on locomotor movement patterns, speed and behaviour in the field, especially in cluttered areas.

Our final prediction that species that make use of vertical elements would excel in climbing ability was confirmed. This suggests that moving on near vertical slopes requires specific locomotor skills (and possibly design features; see Van Damme *et al.* 1997; Vanhooydonck & Van Damme 2001) and that species living on such microhabitats are selected for climbing speed. Speed does seem relevant to animals living on walls, rocks and boulders, because these habitats tend to be quite exposed and therefore the risk of (aerial) attacks is high.

Based on our data, we did not find evidence for sexual differences in the relationships between locomotor performance, habitat use and antipredator behaviour. This, however, might be due to the low number of individuals of each sex per species. To quantitatively assess the prevalence of sexual dimorphism in these traits, further studies are planned.

Our results show considerable interspecific variation in tendency to flee from the predator model. Moreover, the choice to stay put or to flee is context-dependent in most species: most lizards flee more readily when in open or vertical microhabitats than when in dense vegetation. This accords with the idea that patches of dense vegetation constitute a safe harbour to lacertids (see above), at least during encounters with an aerial predator (see also Snell *et al.* 1988; Bulova 1994). Future experiments will have to test whether this response depends on the type of predator. Remaining in densely vegetated patches may not be an appropriate response when confronted with terrestrial predators (e.g. snakes, small mammals). Our prediction that lizards would stay put more frequently when attacked in their 'preferred' microhabitat, was only confirmed in two species (*T. sexlineatus* and *L. oxycephala*). The relative immobility of *T. sexlineatus* in its 'home' microhabitat (densely vegetated areas) accords with the above-mentioned 'safe harbour' idea. However, the fact that *L. oxycephala* also chooses to stay put more frequently when it is in its 'home' microhabitat (vertical elements), seems to suggest that this species feels more confident in its 'home' microhabitat. This may relate to its excellence in the aspects of locomotion relevant in this particular microhabitat (i.e. climbing speed). Still, the generality of this idea is limited, since in two other species with a marked 'preference' for a particular microhabitat, fleeing tendency was unaffected by microhabitat. Three species (*A. pardalis*, *L. longicaudata* and *P. muralis*) even showed the opposite response: they fled more readily when attacked in their 'home' microhabitat (open areas). The reason for this interspecific variation in the context-dependency of antipredator behaviour remains unclear.

Our results on refuge-seeking behaviour show that most species considered often flee towards patches of dense vegetation when attacked by an aerial predator. This gives further support to our idea that such patches are considered 'safe' by the lizards. Similarly, the one species with a marked preference for the vegetated microhabitat (i.e. *T. sexlineatus*) flees towards this microhabitat 35% of the time when confronted with the predator model in the other microhabitats. This finding is analogous to the antipredator response of *Uma scoparia* and *Callisaurus draconoides* lizards: both species most frequently hid in burrows or ran towards vegetative cover when approached by human 'predators' (Jayne & Ellis 1998; Irschick & Jayne 1999). Only 6 out of 52 escapes in *U. scoparia* ended at exposed locations (Jayne & Ellis 1998). Still, within our data set, considerable interspecific variation remains. Saxicolous species (*L. oxycephala*, *L. bedriagae*) tend to flee more often towards the vertical elements. The same holds true when they are confronted with the predator model in their non-preferred microhabitat: 53% and 23% of the time, respectively, they flee from their non-preferred to their preferred microhabitat. Moreover, seeking refuge in vertical microhabitat is correlated with climbing ability. Possibly, vertical structures such as stone walls, piles of logs and tree trunks also offer good refuge opportunities, but their exploitation may require special (locomotor) skills. Species from vegetated microhabitats, on the other hand, frequently flee towards densely vegetated patches but do not excel in clambering capacity or manoeuvrability. Again, fast locomotion might not be selected for in this kind of microhabitat (see above).

In conclusion, our experiments have revealed considerable variation in microhabitat use, antipredator behaviour and refuge choice among a set of lacertid lizards. We have been able to link only part of this variation to variation in different aspects of locomotor capacity. Our results show that the presumed relationships between microhabitat use, performance and animal design (which are at the heart of ecomorphological theory) need validation, and that detailed knowledge on behaviour is primordial in such analyses.

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