J. Zool., Lond. (2003) **260**, 123–128 © 2003 The Zoological Society of London Printed in the United Kingdom DOI:10.1017/S0952836903003455

To run or hide? Age-dependent escape behaviour in the common flat lizard (*Platysaurus intermedius wilhelmi*)

Martin J. Whiting*, Simon P. Lailvaux, Leeann T. Reaney and Monica Wymann

Communication and Behaviour Research Group, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

(Accepted 10 September 2002)

Abstract

Flat lizards *Platysaurus intermedius wilhelmi* occur on small discrete rock outcrops in Mpumalanga Province, South Africa. These rock outcrops are structurally simple and this, combined with the lizard's behaviour (ambush foraging in the open), make them ideal for field studies of anti-predatory behaviour. Lizards were approached in the field and how escape behaviour was influenced by habitat and age-sex class was recorded. Juveniles (*c*. 4 months of age) responded quite differently to an approaching human 'predator' compared with adult males and females (which responded similarly). Compared to adults, juveniles allowed a closer approach by the investigator; took longer to find a refuge and therefore fled further; were more likely to remain visible in the open and maintain visual contact with the investigator; and more likely to flee into vegetation when given the opportunity to take refuge in a crevice. We suggest that because a greater suite of predators (including arthropods living in rock crevices) feed on small juvenile lizards, this may affect their choice of refuge and result in the avoidance of crevices when chased. Finally, because juveniles were frequently found on small rock outcrops, the influence of rock outcrop area on anti-predatory behaviour was tested. Escape behaviour (time to refuge) was independent of rock outcrop area.

Key words: anti-predatory tactics, refuge, behavioural compensation, predation, reptile, *Platysaurus intermedius wilhelmi*

INTRODUCTION

Predator–prey interactions in lizards have received much recent attention. Lizards are often ideal candidates for such studies because many taxa autotomize their tails, are easily observed and, because of strong site fidelity, easily relocated; they also signal to predators, and can be easily captured by an investigator. Recent work on predation risk and anti-predatory behaviour in lizards has focused on prey–predator honest signalling (Leal & Rodríguez-Robles, 1997; Leal, 1999), influence of conspicuousness on predation risk (Cooper & Vitt, 1991; Olsson, 1993; Cooper, 1998*a*; Martín & López, 2000), refuge selection in relation to predation risk (Cooper, 1997*a*, 1998*a*, 1999*a*; Cooper, van Wyk & Mouton, 1999), costs of refuge use (Martín & López, 1999), perception of predation risk (Bulova, 1994; Cooper, 1997*a*,*b*, 1998*b*,*c*), influence of habitat structure and incline on anti-predatory behaviour (e.g. Bulova, 1994; Martín & López, 1995*a*,*b*; Losos & Irschick, 1996; Jayne & Ellis, 1998; Irschick & Jayne, 1999; Cuadrado, Martín & López, 2001), age-dependent escape behaviour (Martín & López, 1995*b*), trade-offs in social and anti-predatory behaviour (Cooper, 1999*b*), reactive and anticipatory deflection of predatory attack (Cooper, 1998*d*,*e*), costs associated with tail autotomy (e.g. Fox & Rostker, 1982; Althoff & Thompson, 1994; Martín & Salvador, 1997; Fox & McCoy, 2000), thermal dependence of escape behaviour (Hertz, Huey & Nevo, 1982; Cooper, 2000), and combinations of some of the above variables (Bulova, 1994; Smith, 1997).

Little attention has been devoted to differences in escape tactics between juvenile and adult lizards (reviewed in Greene, 1988). Smith (1997) compared reactions of juveniles and adults to approaching predator models and found one difference: juveniles fled more frequently in the absence of a cover object than adults. Cuadrado *et al*. (2001) reported that hatchling chameleons *Chamaeleo chamaeleon* were more likely to 'free-fall' from vegetation when threatened and less likely to respond with 'mouth opening' than juveniles and adults. The results of other studies show no consistent pattern. In some instances juveniles are warier than adults, while in other species the converse is true (Greene, 1988). Other studies involving juvenile lizards have focused on autotomy of conspicuous tails (e.g. Clark & Hall, 1970; Cooper & Vitt, 1985; Vitt & Cooper, 1986; Niewiarowski *et al*., 1997). Juveniles, because of their small size, are vulnerable to a greater array

*All correspondence to: M. J. Whiting.
E-mail: martin@gecko.biol.wits.ac.za

of predators than adults (Greene, 1978, 1988; Arnold, 1988; Whiting, Godwin & Coldren, 1991) and in general have low first year survivorship (Dunham, 1981; Andrews, 1991; James, 1991), presumably as a result of higher predation. Furthermore, by virtue of their age, juveniles are likely to be less experienced with predator avoidance, having had fewer encounters with predators than adults. As such, juvenile lizards often have morphological features that increase their probability of survival (e.g. coloured tails; Cooper & Vitt, 1985, 1991), behave differently, or a combination of the two (Huey & Pianka, 1977). Lack of experience and susceptibility to a wider range of predators in juveniles compared to adults should result in different escape strategies in the two groups.

Platysaurus intermedius wilhelmi (common flat lizard) is a small cordylid lizard (maximum SVL = 83 mm) restricted to rocky outcrops in Mpumalanga and Kwazulu-Natal Provinces, South Africa, and with a limited distribution in Mozambique and Swaziland (Broadley, 1978; Branch, 1998). Males and females are sexually dimorphic for coloration (Branch, 1998) and body size (pers. obs.). Little is known about their ecology or behaviour, although dissection of museum specimens suggests an omnivorous diet (Broadley, 1978). A recent laboratory study reported on digestive physiology (McKinon & Alexander, 1999). Hatchlings appear in December–January (Branch, 1998) and are readily visible on rock outcrops; they use the same habitat as adults, but may also occur on small open outcrops devoid of adults (pers. obs.).

Several factors probably interact to determine how an animal perceives and reacts to the threat of predation. In lizards, such factors include temperature (Hertz *et al*., 1982; reviewed in Greene, 1988; Cooper, 2000), predator type/stimulus (Middendorf & Sherbrooke, 1992), the approach path and field of view of the predator (Cooper, 1997*b*), predator distance (Bulova, 1994; Cooper, 1997*a*), proximity and type of refuge (Cooper, 1997*a*, 1998*a*, 1999*a*), habitat structure (Martín & López, 1995*a*), locomotor performance (Huey, 1982; Garland, 1985), age (reviewed in Greene, 1988), predation pressure (Smith, 1997), habituation, learning and social transmission (Greene, 1988) and reproductive condition (Cooper, 1999*b*).

The focus of our study was to examine response to risk factors and differences in escape tactics among juvenile and adult *Platysaurus i. wilhelmi*. We predicted that relative to adults, juveniles would behaviourally compensate for their greater risk of predation. Furthermore, the role habitat plays in influencing escape 'decisions' by flat lizards in relation to age and sex was explored.

MATERIALS AND METHODS

Study area

Field work was conducted on Pullen Farm (24°35′S, 31°11′E), 35 km east of Nelspruit, Mpumalanga Province, South Africa. The area is hilly and consists of numerous granite exfoliation domes in moist savanna. Due to vegetation encroachment, rocky outcrops vary in size from a longest axis of < 10 m to in excess of several hundred metres. These outcrops are also structurally simple and generally consist of loose, free-standing rocks or exfoliating sheets of granite. During the rainy season (October–April), each outcrop is generally ringed with dense grass clumps and thick surrounding vegetation. Field work was conducted during April 2000. Flat lizards breed in spring, which allowed for the exclusion of reproductive behaviour (e.g. territoriality and female presence) that could confound measures of adult escape behaviour.

Field experiment 1: time to cover and refuge selection

We conducted two sets of trials in which lizards were approached from a distance exceeding that at which they react (normally *c*. 6 m). In the first set of trials ($n = 92$), we recorded the following: (1) the time (s) a lizard took to find cover; (2) the refuge type in which the lizard took cover (rock crevice, vegetation, rock–vegetation complex); (3) if a lizard had a choice between rock and vegetation. All approaches were conducted by the same individual (MJW); approach speed was slow (*c*. 0.8 m/s). Lizards were approached until they took refuge. All individuals were classed as either juveniles (*c*. 18–30 mm snout–vent length (SVL); *c*. 4 months of age), males, or females/sub-adult males. Because sub-adult males sometimes retain a female-like appearance, we conservatively grouped them with females.

Field experiment 2: approach distance, flight distance and final destination

The second set of trials ($n = 32$) were conducted by the same individual (SPL). The purpose of these trials was to quantify approach and flight distances for all age–sex classes and to give lizards a choice between taking refuge and remaining in the open. Approach distance was the distance between the lizard and the observer when the lizard first moved. Flight distance was the distance the lizard fled from its initial stationary position to when it stopped moving. The protocol for each trial consisted of the following: when a lizard moved a minimum of 10 cm as a result of SPL's approach, a marker was dropped; SPL stopped his approach at the lizard's initial location and dropped a second marker; after 5 s the lizard's final destination was scored (visible in open or concealed in a crevice or vegetation) and indicated with a third marker; finally, if a lizard was still in the open, SPL then approached it a second time until the lizard took refuge. The type of refuge was scored and whether the lizard had a choice of refuge type (rock *vs* vegetation) was noted. Approach distance was measured as the distance between marker 1 and 2. Flight distance was measured as the distance between marker 2 and 3. Approach and flight distance were measured with a 3 m tape to the nearest

10 cm. Data on final refuge selected were combined with that of the first experiment.

Because of the small size of the rock outcrops, all lizards had the opportunity to flee into vegetation, but were not always near adequate rock crevices. If a rock measuring at least 30 cm along its longest axis was within 2 m of the escape route of the lizard, we scored it as having a choice. Our arbitrary choice of minimum rock size was conservative as lizards sometimes chose smaller rocks.

Influence of habitat area on escape behaviour

We measured rock outcrop area using a 25 m tape. A series of measurements were taken (nearest 10 cm) such that each outcrop could be broken into geometric shapes for calculation of area (m^2). We tested whether juvenile escape behaviour (time to refuge) was related to rock outcrop size. If > 1 juvenile was approached on the same outcrop, the mean was taken. Adults generally did not occur on the smaller outcrops and were therefore not included in this analysis.

Statistical analysis

Differences among age–sex classes in approach and flight distance and time-to-cover, were evaluated using Kruskal–Wallis single-factor analysis of variance followed by a post hoc comparison of mean ranks (Analytical Software, 1996). Where necessary, adults were combined and compared to juveniles using Mann–Whitney tests, where the normal approximation for continuity correction was applied (Analytical Software, 1996). Categorical data were handled with χ^2 tests, while the relationship between rock outcrop size and juvenile escape behaviour was assessed with a Pearson correlation test. Differences were considered significant at alpha < 0.05. Means are reported ± 1 SE. All tests were 2-tailed.

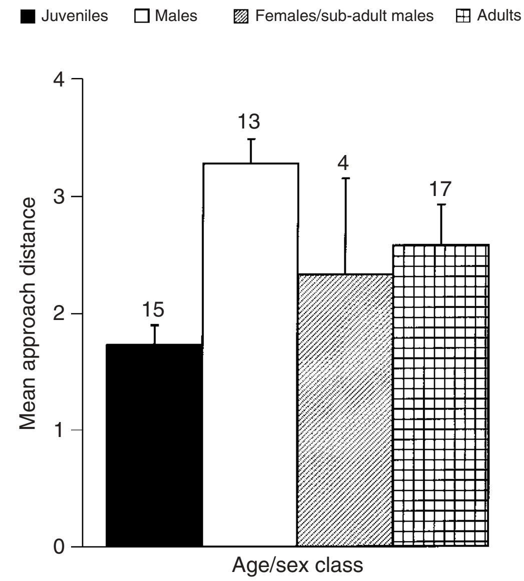

Fig. 1. Mean approach distance, m (± 1 SE), defined as the distance between the approaching investigator and the location from which *Platysaurus intermedius wilhelmi* fled, by age–sex class (see text for details). Sample sizes above each bar.

Fig. 2. Mean time to cover (± 1 SE), defined as the time *Platysaurus intermedius wilhelmi* took to take refuge after first detecting the investigator, by age–sex class (see text for details). Sample sizes are above each bar.

RESULTS

Approach distance

The minimum approach distance at which a lizard reacted to an approaching human was dependent on age–sex class ($H = 14.4$, $n = 32$, $P = 0.0008$; Fig. 1). Juveniles allowed closer approach than males ($P < 0.05$), but a small number of females/sub-adult males ($n = 4$) precluded significant differences when compared with juveniles or adult males. When adults were combined, a strong significant difference in favour of closer approach to juveniles still persisted (Mann–Whitney, $Z = 3.5$, $n = 32$, $P = 0.0005$).

Time to cover

The amount of time a lizard was visible following initial reaction (those lizards that went directly to refuge) was strongly dependent on age–sex class ($H = 31.89$, $n = 67$, $P < 0.0001$; Fig. 2). Adults (males and females/sub-adult males) took a similar amount of time to seek refuge ($P >$ 0.05), while juveniles took much longer ($P < 0.05$). When the same analysis was repeated for only those lizards which had a choice in refuge (rock *vs* vegetation), the analysis held at the same level of significance.

Flight distance

Flight distance was also strongly dependent on age–sex class ($H = 18.1$, $n = 32$, $P = 0.0001$; Fig. 3). Juveniles

Fig. 3. Mean flight distance (± 1 SE), defined as the distance *Platysaurus intermedius wilhelmi* fled from an initial stationary position, because of an approaching investigator, to the point at which it stopped moving, by age–sex class (see text for details). Sample sizes are above each bar.

ran further from an approaching human than either adult group ($P < 0.05$).

Final destination and refuge selection

For trials in which lizards were approached, but not forced to seek a refuge, all adults sought refuges in which they were completely concealed (13 males, four females). By contrast, most juveniles (66%) remained in the open ($n = 15$); although this was significant when compared with adults, there was no difference between the number of juveniles seeking refuge compared with those remaining in the open ($\chi^2{}_1 = 1.7$, $P > 0.1$). When pursued and forced to take refuge, adults ($n = 61$) showed a strong preference for cover in rock crevices (94% of males chose rock refuges: $\chi^2{}_1 = 15$, $n = 16$, $P < 0.001$; 84% of females chose rock refuges: $\chi^2{}_1 = 27.5$, $n = 45$, $P < 0.0001$; sexes combined: $\chi^2{}_1 = 42.1$, $n = 61$, $P < 0.0001$; 88% chose rock crevices), while juveniles ($n = 27$) frequently sought cover in vegetation (78%; $\chi^2{}_1 = 4.92$, $n = 21$, $P < 0.05$). Also, one juvenile and four adults sought refuge in rock–vegetation complexes.

Influence of habitat area on escape behaviour

Mean rock outcrop area was 174.5 ± 47 m^2 (range 7.8–726.7; $n = 19$). There was no correlation between rock outcrop size and how much time a juvenile spent seeking refuge ($r = 0.09$, $n = 19$, $P = 0.72$).

DISCUSSION

Our results indicate clear differences in the escape tactics used by adult and juvenile flat lizards. Compared to adults, juveniles allowed closer approach, fled further, took longer to seek refuge, often remained in view of the approaching investigator, and were more likely to take refuge in vegetation than adults. Predation is a pervasive selection pressure and is especially high during an animal's first year. For example, hatchling sea turtles run a gauntlet of predators that include large vertebrates such as birds and relatively small invertebrates such as crabs. As a consequence, juvenile animals tend to compensate for this increased vulnerability in some way. Juvenile *P. i. wilhelmi* were *c.* 4–5 months of age and still small (*c.* 18–30 mm SVL). Juveniles were therefore susceptible to a greater array of predators than adults (Greene, 1978, 1988; Arnold, 1988; Whiting *et al.*, 1991). Increased predation risk should result in adaptations that improve survival probability and result in adaptations that are lost or in some way altered as lizards approach maturity and selective pressures change. Evidence in support of this prediction comes from a diversity of lizard taxa. For example, several North American skinks have bright blue tails as juveniles, only to be lost at maturity (Cooper & Vitt, 1985). This strategy has evolved independently in numerous taxa and also occurs in African *Mabuya quinquetaeniata* and *Scelotes capensis* (Branch, 1988). Bright tails are also frequently accompanied by tail waving to deflect predators away from the body (Cooper & Vitt, 1985; Cooper, 1998*d*,*e*). In the lacertid *Heliobolus lugubris*, juveniles mimic the colour, locomotion and activity schedules of noxious carabid beetles. Once the lizard exceeds the body size of the beetle, they undergo a colour change and no longer mimic the beetle (Huey & Pianka, 1977). Although effects of morphological features are often amplified by behaviour (e.g. tail waving), behavioural modification alone may also occur as an anti-predatory strategy. For example, gravid female water skinks shift their anti-predatory tactics towards crypsis to compensate for reduced agility (Schwarzkopf & Shine, 1992). Juvenile escape behaviour in *P. i. wilhelmi* presumably represents an adaptation maximizing predator avoidance from a different suite of predators than those that attack adults.

It is probable that differences in scaling, and therefore performance, could account for some of the variation in escape behaviour between adults and juveniles (Martín & López, 1995*b*). Smaller lizards simply do not have the same performance capabilities in terms of maximum sprint speed and endurance (e.g. Garland, 1985). However, body size is expected to scale allometrically to performance. This relationship was not measured, but the highly significant differences in certain escape variables (e.g. approach and flight distances) suggest that other factors contributed to this variation. For example, Martín & López (1995*b*) found that age-/size-dependent escape responses persisted when the effect of body size was removed in the lacertid *Psammodromus algirus*. In the laboratory, juvenile *P. algirus* were slower to escape predation attempts and did so in less time and over shorter distances.

We approached lizards sufficiently slowly to allow them time to select an appropriate refuge. Adults consistently took refuge in a crevice, while juveniles escaped into dense surrounding vegetation, although some did go into crevices (19%). One juvenile went into a crevice only to immediately leave and go into a second one. Under most circumstances, juveniles did not have sufficient time to evaluate a crevice and make sure that it was predator-free before entering. Scorpions, spiders and centipedes are all potential predators of small lizards (Greene, 1988) and all occurred on rock outcrops in our study area (pers. obs.). We suggest that the presence of invertebrate predators in crevices may deter entry. Experimental study is required to test this idea.

Acknowledgements

This study was funded by a University Research Committee grant to MJW from the University of the Witwatersrand. We are grateful to Bill Cooper and two anonymous reviewers for useful comments on an earlier draft.

REFERENCES

Althoff, D. M. & Thompson, J. N. (1994). The effects of tail autotomy on survivorship and body growth of *Uta stansburiana* under conditions of high mortality. *Oecologia (Berl.)* **100**: 250–255.

Analytical Software. (1996). *Statistix for windows.* Tallahassee, FL: Analytical Software.

Andrews, R. M. (1991). Population stability of a tropical lizard. *Ecology* **72**: 1204–1217.

Arnold, E. N. (1988). Caudal autotomy as a defense. In *Biology of the Reptilia*: 235–273. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss.

Branch, B. (1998). *A field guide to the snakes and other reptiles of southern Africa.* Cape Town, South Africa: Struik.

Broadley, D. G. (1978). A revision of the genus *Platysaurus* A. Smith (Sauria: Cordylidae). *Occas. Pap. Natl Mus. Rhod. Ser. B Nat. Sci.* **6**: 129–185.

Bulova, S. J. (1994). Ecological correlates of population and individual variation in antipredator behaviour of two species of desert lizards. *Copeia* **1994**: 980–992.

Clark, D. R. Jr & Hall, R. J. (1970). Function of the blue tail-coloration of the five-lined skink (*Eumeces fasciatus*). *Herpetologica* **26**: 271–274.

Cooper, W. E. Jr (1997*a*). Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool.* **75**: 943–947.

Cooper, W. E. Jr (1997*b*). Threat factors affecting antipredatory behaviour in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. *Copeia* **1997**: 613–619.

Cooper, W. E. Jr (1998*a*). Effects of refuge and conspicuousness on escape behaviour by the broad-headed skink (*Eumeces laticeps*). *Amphib.-Reptilia* **19**: 103–108.

Cooper, W. E. Jr (1998*b*). Direction of predator turning, a neglected cue to predation risk. *Behaviour* **135**: 55–64.

Cooper, W. E. Jr (1998*c*). Risk factors and emergence from refuge in the lizard *Eumeces laticeps*. *Behaviour* **135**: 1065–1076.

Cooper, W. E. Jr (1998*d*). Reactive and anticipatory display to deflect predatory attack to an autotomous lizard tail. *Can. J. Zool.* **76**: 1507–1510.

Cooper, W. E. Jr (1998*e*). Conditions favoring anticipatory and reactive displays deflecting predatory attack. *Behav. Ecol.* **9**: 598–604.

Cooper, W. E. Jr (1999*a*). Escape behaviour by prey blocked from entering the nearest refuge. *Can. J. Zool.* **77**: 671–674.

Cooper, W. E. Jr (1999*b*). Tradeoffs between courtship, fighting, and antipredatory behaviour by a lizard, *Eumeces laticeps*. *Behav. Ecol. Sociobiol*. **47**: 54–59.

Cooper, W. E. Jr (2000). Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour* **137**: 1299–1315.

Cooper, W. E. Jr, Van Wyk, J. H. & Mouton, P. Le F. N. (1999). Incompletely protective refuges: selection and associated defences by a lizard, *Cordylus cordylus* (Squamata: Cordylidae). *Ethology* **105**: 687–700.

Cooper, W. E. Jr & Vitt, L. J. (1985). Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. *Zeitschr. Tierpsychol.* **70**: 265–276.

Cooper, W. E. Jr & Vitt, L. J. (1991). Influence of detectability and ability to escape on natural selection of conspicuous autotomous defenses. *Can. J. Zool.* **69**: 757–764.

Cuadrado, M., Martín, J. & López, P. (2001). Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon. Biol. J. Linn. Soc.* **72**: 547–554.

Dunham, A. E. (1981). Populations in a fluctuating environment: the comparative population ecology of the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus. Misc. Publ. Mus. Zool., Univ. Mich.* **158**: 1–62.

Fox, S. F. & McCoy, J. K. (2000). The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. *Oecologia (Berl.)* **122**: 327–334.

Fox, S. F. & Rostker, M. A. (1982). Social cost of tail loss in *Uta stansburiana. Science* **218**: 692–693.

Garland, T. Jr (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis. J. Zool. (Lond.)* **207**: 425–439.

Greene, H. W. (1978). Predation and the defensive behaviour of green iguanas (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* **12**: 169–176.

Greene, H. W. (1988). Antipredator mechanisms in reptiles. In *Biology of the Reptilia*: 1–152. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss.

Hertz, P. E., Huey, R. B. & Nevo, E. (1982). Fight *versus* flight: body temperature influences defensive responses of lizards. *Anim. Behav.* **30**: 676–679.

Huey, R. B. (1982). Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe* **25**: 43–48.

Huey, R. B. & Pianka, E. R. (1977). Natural selection for juvenile lizards mimicking noxious beetles. *Science* **195**: 201–203.

Irschick, D. J. & Jayne, B. C. (1999). A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides. Physiol. Biochem. Zool.* **72**: 44–56.

James, C. D. (1991). Population dynamics, demography, and life history of sympatric scincid lizards (*Ctenotus*) in central Australia. *Herpetologica* **47**: 194–210.

Jayne, B. C. & Ellis, R. V. (1998). How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia. Anim. Behav.* **55**: 1115–1130.

Leal, M. (1999). Honest signalling during prey–predator interactions in the lizard *Anolis cristatellus. Anim. Behav.* **58**: 521–526.

Leal, M. & Rodríguez-Robles, J. A. (1997). Signalling displays during predator–prey interactions in a Puerto Rican anole, *Anolis cristatellus. Anim. Behav.* **54**: 1147–1154.

Losos, J. B. & Irschick, D. J. (1996). The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim. Behav.* **51**: 593–602.

Martín, J. & López, P. (1995*a*). Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus. Can. J. Zool.* **73**: 129–132.

Martín, J. & López, P. (1995*b*). Escape behaviour of juvenile *Psammodromus algirus* lizards: constraint of or compensation for limitations in body size? *Behaviour* **132**: 181–192.

Martín, J. & López, P. (1999). An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos* **84**: 499–505.

Martín, J. & López, P. (2000). Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammodromus algirus*. *Can. J. Zool.* **78**: 265–270.

Martín, J. & Salvador, A. (1997). Effects of tail loss on the time-budgets, movements and spacing patterns of Iberian rock lizards, *Lacerta monticola*. *Herpetologica* **53**: 117–125.

McKinon, W. & Alexander, G. J. (1999). Is temperature independence of digestive efficiency an experimental artifact in lizards? A test using the common flat lizard (*Platysaurus intermedius*). *Copeia* **1999**: 299–303.

Middendorf, G. A. & Sherbrooke, W. C. (1992). Canid elicitation of blood-squirting in a horned lizard (*Phrynosoma cornutum*). *Copeia* **1992**: 519–527.

Niewiarowski, P. H., Congdon, J. D., Dunham, A. E., Vitt, L. J. & Tinkle, D. W. (1997). Tales of lizard tails: effects of tail autotomy on subsequent survival and growth of free-ranging hatchling *Uta stansburiana*. *Can. J. Zool.* **75**: 542–548.

Olsson, M. (1993). Nuptial coloration and predation risk in model sand lizards, *Lacerta agilis*. *Anim. Behav.* **46**: 410–412.

Smith, D. G. (1997). Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. *Behav. Ecol.* **8**: 622–629.

Vitt, L. J. & Cooper, W. E. Jr (1986). Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age-specific differences in costs and benefits. *Can. J. Zool.* **64**: 583–592.

Whiting, M. J., Godwin, J. & Coldren, M. K. (1991). *Cnemidophorus sexlineatus* (six-lined racerunner lizard) and *Cophosaurus texanus* spider predation. *Herpetol. Rev.* **22**: 58.