



Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards

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Abstract

Relationships between predator avoidance behaviour and predation pressure were investigated in the wall lizard, *Podarcis muralis*. The wariness of lizards belonging to high (1185 m) and low elevation (308 m) populations under two different predation pressure levels was compared. Wall lizards belonging to the lowland population experienced greater predation pressure than those belonging to the highland population. Lizards belonging to the population under higher predation pressure had higher frequency of refuge use, and had longer flight initiation distances (i.e. the distance lizards allowed the observer to approach before fleeing). In contrast, neither the distance fled (i.e. the total distance they fled in one continuous movement from the lizard's initial position until hiding or stopping at a safe distance) nor the distance to the nearest refuge were significantly different between populations. Escape responses were independent of ambient temperature in the lowland population, but animals belonging to the highland population had longer flight initiation distances when the ambient temperatures were higher. These findings suggest that predator avoidance behaviour may vary with predation pressure.

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1. Introduction

Rapid flight toward refuges is usually the option of choice when lizards have been detected by a predator (Greene, 1988). Prey should not necessarily flee toward refuges as soon as a predator is detected, because fleeing has costs in energy and time taken away from other important activities (Lima and Dill, 1990; Cooper, 1999; Martín and López, 2000). Risk of capture should be traded off against the cost of fleeing, and animals should flee only when predators are a serious threat (Burger and Gochfeld, 1990; Martín and López, 1996; Cooper, 1997a; Kramer and Bonen-

fant, 1997; Recarte et al., 1998; Martín and López, 1999a). Hence, predator avoidance behaviour should vary with predation pressure, and increasing harassment by predators may lead to increasing wariness of lizards (Stone et al., 1994; Blázquez et al., 1997). Most available information suggests that the ability to assess the level of predation risk and the presence of flexibility in the decision-making process are adaptive characteristics of escape behaviour, regardless of their genetic basis (Delibes and Blázquez, 1998).

In lizards, predator–prey interactions can be influenced by habitat selection (Bulova, 1994; Martín and López, 1995; Downes and Shine, 1998). However, as Smith and Ballinger (2001) suggested, few studies have actually estimated predation risk or differences in predation risk in different habitats (but see Brown

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and Ruby, 1977; Parker, 1994; Smith, 1996). Therefore, predation pressure in two populations of the wall lizard *Podarcis muralis* occupying different habitats was studied and the prediction that predator avoidance behaviour should vary with predation pressure was also tested. We specifically tested: (1) predation pressure experienced by lizards belonging to both populations, (2) whether lizards under higher predation pressure react to and flee from an approaching observer at greater distances, (3) whether lizards from both study sites showed different escape tactics, (4) the relationships of flight initiation distance and distance fled with ambient temperatures and distance to a refuge.

2. Materials and methods

2.1. Subjects and study sites

The study species, *P. muralis* (snout-to-vent length of adult individuals ranges between 48 and 69 mm) is a small lacertid lizard that occurs over a wide range in Southern Europe. It is distributed in the north of the Iberian Peninsula, this area being the southern edge of its range. A complete description of this species, its geographical distribution, and more detailed aspects of its ecology are given by Pérez-Mellado (1998).

The study was conducted during the summer (10–17 August) of 2001 in Cantabria, northern Spain. A study area (43°13'46"N, 4°09'38"W; elevation 308 m) in the Cieza Mountains, and a study site (43°10'44"N, 3°40'36"W; elevation 1185 m) in the Valnera Mountains were selected. Cieza Mountains are included in the Natural Park of Saja-Besaya, where the vegetation mainly consists of thick forest of *Quercus robur*, as well as less abundant and dispersed bushes of *Ilex aquifolium*, *Laurus nobilis*, *Prunus spinosa*, *Cornus sanguinea*, *Frangula alnus* and *Corylus avellana*. *Deschampsia flexuosa*, *Brachypodium sylvaticum*, *Holcus mollis* and ferns (*Dryopteris affinis*, *D. aemula*, *D. dilatata*, *Polystichum setiferum* and *Blechnum spicant*) dominated grassy areas. Lizards selected sunny patches within the oak wood, occupying ground talus in humid slopes where vegetation included *Erica vagans*, *E. cinerea*, *E. mackaiana*, *Daboecia cantabrica*, *Calluna vulgaris* and *Ulex gallii*.

The habitat at the Valnera Mountain site was open, a mountainous grassland with sparse rocky areas. Lizards mainly occupied vertical rocky surfaces and grassy microhabitats. The dominant vegetation consists of *Nardus stricta*, accompanied by *Agrostis tenuis*, *Ajuga pyramidalis*, *Anthoxanthum odoratum*, *Festuca rubra*, *F. eskia*, *Luzula nutans*, *Pedicularis pyrenaica*, *Trifolium alpinum*, *Ranunculus bulbosus* and *R. amplexicaulis*.

2.2. Procedure

2.2.1. Predation pressure

Tail break frequency in lizards has been used as a rough estimate of relative predation pressure (Jacksic and Fuentes, 1980; Schall and Pianka, 1980; Turner et al., 1982). Thus, I noted the presence of broken or regenerated tails in the lizards. However, tail break frequencies indicate predator efficiency as well as frequency of predation attempts (Schoener, 1979; Jacksic and Greene, 1984; Medel et al., 1988). An alternative approach to evaluate the effect of predation consists of recording predatory attacks on soft replicas of the prey species of interest (Brodie, 1993; Brodie and Janzen, 1995; Castilla and Labra, 1998). Thus, soft replicas were used to determine the predation pressure on both study sites. Lizard replicas were constructed using pre-coloured non-toxic plasticine. A plaster mould was used to obtain replicas similar in size and body shape to adult *P. muralis*. Different plasticine colours were mixed to mimic the main colouration of animals. An implicit assumption of this approach is that the resemblance between replicas and lizards, which was apparent to a human observer, was also perceived as such by visually hunting predators (Castilla et al., 1999). Lizard replicas were equally conspicuous in both habitats since they were placed on rocky surfaces where basking lizards had been observed previously, and that mimicked the main colouration of model.

Within each area, 25 replicas were positioned every 5 m along a transect line. All replicas were placed on sites that appeared to be good basking sites for animals, and were located in a position that simulated an immobile basking lizard. Subsequently, replicas were surveyed on two consecutive days. I recorded whether a replica was intact or exhibited imprints, their position on the replica (head, body, tail), the number and the shape of the markings, and the suspected predator.

Only data obtained when a presumed lizard predator first attacked a replica were retained. A replica was considered as being attacked by a lizard predator when it showed bill marks of birds, tooth marks of mammals (e.g. square-shape tooth), or when the replica disappeared (Castilla et al., 1999). Replicas showing marks of rodents were considered as non-attacked.

2.2.2. Escape behaviour

I walked slowly through the area on a linear path bypassing the zone in which I was looking for lizards between 10:00 and 13:00 (GMT) until an adult lizard was sighted with binoculars. I used binoculars with a minimum focus distance of 3.5 m. Thus, at both sites, animals were spotted from a distance approximately 4 m. Upon spotting a lizard, I attempted to approach the animal by walking directly towards it at the same medium speed (approximately 40 m/min), simulating a predatory attack (Martín and López, 1999b). To avoid confounding effects that may affect the risk perception of lizards, the same person performed all approaches, in a similar way and wearing the same clothing (Burger and Gochfeld, 1993), while another person recorded the lizard's behaviour. I observed two types of escape tactics: (1) some lizards made a short flight to a hiding place, and (2) other animals made a short flight without hiding in any refuge. I gathered quantitative data on two components of the lizard's escape behaviour: (1) flight initiation distance, the distance from the lizard that the lizard allowed the observer to approach before fleeing, and (2) distance fled, the total distance fled in one continuous movement from the lizard's initial position until hiding or stopping at a safety distance (Bulova, 1994; Cooper, 1997b).

The distance to the nearest potential refuge available in the direction of the escape trajectory (i.e. bushes or rock crevices) was measured in order to analyse whether the escape behaviour of lizards was determined by the availability of refuges (Cooper, 1997b; Martín and López, 1995).

In some species of lizards, the escape response has been related to temperature (Hertz et al., 1982; Rocha and Bergallo, 1990; Smith, 1997; Cooper, 2000). Animals could not be captured immediately after each trial in order to measure their body temperature. Hence, immediately after each escape sequence, the air (shaded bulb, 1 cm above the sighting

point), and the substrate temperatures were measured to the nearest 0.1 °C with a digital thermometer. Air and substrate temperatures are relevant variables for thermoregulation in *P. muralis* (Braña, 1991).

Escape behaviour by gravid females of *P. muralis* involves crypsis (Braña, 1993). However, this study took place in mid August, when lizards had finished the mating season and *P. muralis* females did not show external signs of pregnancy. Hence, it is improbable that reproductive status could influence this experiment.

2.2.3. Statistical analyses

Given the large size of the examined areas, repeated measurements of the same individual were avoided sampling each area only once. Therefore, data have been treated as independent. We used standard statistical methods (Pearson correlation coefficient, *t*-test, and chi-square test) to evaluate relationships or differences among variables at $\alpha = 0.05$. Yates Corrected Chi-square was applied when some expected frequencies became less than 10 (Siegel, 1956). Parametric statistics were used when the assumptions of the models could be reasonably met (Sokal and Rohlf, 1981). To ensure normality, data were logarithmically transformed when required (Sokal and Rohlf, 1981). Means are given \pm one standard error.

A multivariate analysis of variance (MANOVA) was performed on air and substrate temperatures at the sighting point. We previously tested the assumptions associated with this analysis: multivariate normality, homogeneity of covariance matrices and independence. Thus, we checked whether the air and substrate temperatures at the sighting point differed between study sites.

3. Results

3.1. Predation pressure

The percentage of lizards with broken or regenerated tails was higher in Cieza Mountains (87.88%, $n = 66$) than in Valnera Mountains (33.33%, $n = 21$) (chi-square test; $\chi^2 = 25.09$, d.f. = 1, $P = 0.000001$). Frequency of predation on lizard replicas was again higher in Cieza Mountains (chi-square test; $\chi^2 = 5.33$, d.f. = 1, $P = 0.02$; Fig. 1).

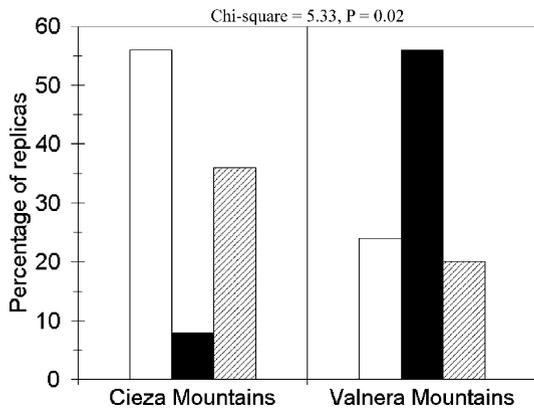


Fig. 1. Percentage of lizard replicas that had been attacked (white), that did not show any mark (black), and that showed marks of rodents (lines) in both study areas. Result of inter-area comparison is shown as well.

I observed the snake *Coronella austriaca*, one of the main predators of *P. muralis* in the Cantabrian region (Pérez-Mellado, 1998), eating an adult specimen of *P. muralis* in Cieza Mountains. In this site, other predators of lizards have been detected, such as *Buteo buteo*, *Vipera seoanei*, and *Martes martes*. The only lizard predator observed in Valnera Mountains was *Falco tinnunculus*.

3.2. Escape behaviour

Lizards on Cieza Mountains and those on Valnera Mountains differed in escape tactics. The former responded to the approach of the simulated predator by making a short flight to the nearest available refuge and hiding entirely from the observer (100%, $n = 66$). The latter usually reacted by making a short flight

without hiding in any refuge, but keeping the simulated predator under surveillance (80.95%, $n = 21$). The difference in frequency of refuge use was significant (Yates Corrected Chi-square test; $\chi^2 = 61.36$, d.f. = 1, $P < 0.00001$).

Flight initiation distances, but not distances fled, differed between study areas (Table 1). Thus, lizards from the Cieza Mountains exhibited significantly greater flight initiation distances than lizards on Valnera Mountains ($t = 4.30$, d.f. = 85, $P = 0.00005$). Distances fled were not significantly different between the two sampling places ($t = 1.70$, d.f. = 58,78, $P = 0.10$).

Air and substrate temperatures differed significantly between study sites (MANOVA; Wilks' Lambda = 0.76, Rao's $R = 13.36$, d.f. = 2,84, $P = 0.000009$). Air temperatures ($F = 25.40$, d.f. = 1,85, $P = 0.000003$) and substrate temperatures ($F = 22.45$, d.f. = 1,85, $P = 0.000009$) were higher in the Cieza Mountains than in the Valnera Mountains (Table 1). However, air and substrate temperatures were not significantly correlated with flight initiation distances gathered at Cieza Mountains (Table 2). On the contrary, air and substrate temperatures were positively correlated with flight initiation distances registered at Valnera Mountains (Table 2). Also, air and substrate temperatures were not significantly correlated with distances fled obtained at either study site (Table 2).

The distance to the nearest potential refuge available in the direction of the escape trajectory did not differ significantly between both sampling places ($t = 1.90$, d.f. = 85, $P = 0.06$) (Table 1). Flight initiation distance increased with distance to the refuge in Valnera Mountains ($r = 0.70$, $P < 0.001$), but not for animals in the Cieza Mountains ($r = 0.21$, $P = 0.09$). The difference in relationship between flight initiation

Table 1

Characteristics (mean \pm S.E.M.) of the ambient temperatures at sighting point, magnitude of the escape responses of two *P. muralis* lizard populations, and results of inter-area comparisons

Variable	Study site		
	Cieza Mountains ($n = 66$)	Valnera Mountains ($n = 21$)	P
Flight initiation distance (cm)	125.86 \pm 9.67	47.48 \pm 10.72	0.00005
Distance fled (cm)	51.58 \pm 6.61	28.14 \pm 5.29	0.10
Distance to refuge (cm)	24.09 \pm 1.64	18.62 \pm 4.56	0.06
Air temperature ($^{\circ}$ C)	23.25 \pm 0.16	21.70 \pm 0.25	0.000003
Substrate temperature ($^{\circ}$ C)	28.09 \pm 0.33	25.11 \pm 0.44	0.000009

Table 2

Results of the Pearson product–moment correlation between air and substrate temperatures, and flight initiation distances and distances fled in two *P. muralis* lizard populations

Variable	Study site			
	Cieza Mountains (<i>n</i> = 66)		Valnera Mountains (<i>n</i> = 21)	
	Flight initiation distance	Distance fled	Flight initiation distance	Distance fled
Air temperature	$r = -0.08$, ns	$r = -0.17$, ns	$r = 0.44^*$	$r = 0.27$, ns
Substrate temperature	$r = -0.10$, ns	$r = -0.20$, ns	$r = 0.53^*$	$r = 0.33$, ns

Note. ns: $P > 0.05$.

* $P < 0.05$.

distance and distance to refuge between populations was significant ($P = 0.02$).

4. Discussion

This study suggests that differences in wariness between two populations of *P. muralis* lizards may arise through differences in predation pressure between populations. Data from tail break frequency and those from predatory attacks on soft replicas of the lizards suggested that lizards belonging to the lowland population (Cieza Mountains) experienced greater predation pressure than those belonging to the highland population (Valnera Mountains). Thus, the data are consistent with the hypothesis that predation pressure can contribute to intraspecific variation in antipredator behaviour (Blázquez et al., 1997). However, the habitats differed in numerous ways in addition to predation, precluding a firm conclusion that predation pressure causes the observed differences in antipredator behaviour.

The distance to a safe refuge can be used as a measure of the risk that lizards take, because the risk of capture is higher for prey that are farther from the refuge (Bulova, 1994; Blázquez et al., 1997; Cooper, 1997b). Lizards from the two populations showed similar distances to the nearest potential refuge, but lizards from the low elevation population were more wary than the high elevation ones. Presumably, lizards could learn to be wary after being attacked by a predator (Marcellini and Jensen, 1991). Since diversity of escape behaviour seems to be low at both sites, these results fit the previous findings of Schall and Pianka (1980). They suggested that escape diversity should be maximal at intermediate levels of predation, whereas

at sites where few lizards have been attacked and most are docile, escape diversity would be low. Likewise, at sites where most individuals have been attacked most would be wary, and escape diversity would again be low with primarily wary tactics.

Response to a predator may depend on the body temperature of the potential prey, because reptiles with low body temperatures show lower escape performance (Christian and Tracy, 1981; Hertz et al., 1982; Huey, 1982). When the ambient temperature is low several species flee at greater distances when the predator approach than when the ambient temperature is high (Rand, 1964; Rocha and Bergallo, 1990; Smith, 1997). Other species become more aggressive or show a cryptic escape strategy at lower temperatures whereas they immediately flight at higher body temperatures (Hertz et al., 1982; Layne and Ford, 1984; Shine et al., 2000). Our results indicate that lizards on Valnera Mountains had longer flight initiation distances when the ambient temperatures were higher. Perhaps, costs of refuge use can also affect escape decisions, and lizards may be considering the loss of heating opportunities in deciding when to escape (Bulova, 1994; Cooper, 2000; Martín and López, 2000). On the contrary, in the low altitude population located in Cieza Mountains, ambient temperatures were not significantly correlated with flight initiation distances. Similar results have been found in the escape responses of a lizard (Martín and López, 1995), and a water snake (Weatherhead and Robertson, 1992). Also, escape behaviour was not influenced by distance to cover in specimens on Cieza Mountains. Thus, Braña (1991) found less dependence of body temperature of *P. muralis* during the summer in northern Spain upon ambient temperature in the lowland than in the highland populations examined.

Some studies have suggested that vegetation coverage level could influence the escape behaviour of lizards, as specimens which were in very well-covered places showed a closer flight initiation distance than those which were in more open sites (Bulova, 1994; Martín and López, 1995; Snell et al., 1988). However, our results differed from these suggestions. Thus, lizards on Valnera Mountains, occupying the less vegetatively complex habitat (i.e. with less vegetation cover), had shorter flight initiation distances than lizards on Cieza Mountains. This might be related to the differences in predation pressure between both sites.

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References

- Blázquez, M.C., Rodríguez-Estrella, R., Delibes, M., 1997. Escape behaviour and predation risk of mainland and island spiny-tailed iguanas (*Ctenosaura hemilopha*). *Ethology* 103, 990–998.
- Braña, F., 1991. Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. *Herpetol. J.* 1, 544–549.
- Braña, F., 1993. Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* 66, 216–222.
- Brodie III, E.D., 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* 47, 227–235.
- Brodie III, E.D., Janzen, F.J., 1995. Experimental studies of Coral snake mimicry: generalized avoidance of ringed snake pattern by free-ranging avian predators. *Funct. Ecol.* 9, 186–190.
- Brown, C.K., Ruby, D.E., 1977. Sex-associated variation in the frequencies of tail autotomy in *Sceloporus jarrovi* (Sauria: Iguanidae) at different elevations. *Herpetologica* 33, 380–387.
- Bulova, S.J., 1994. Ecological correlates of population and individual variation in antipredator behaviour of two species of desert lizards. *Copeia* 1994, 980–992.
- Burger, J., Gochfeld, M., 1990. Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. *J. Comp. Psychol.* 104, 388–394.
- Burger, J., Gochfeld, M., 1993. The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. *J. Herpetol.* 27, 426–430.
- Castilla, A.M., Gosá, A., Galán, P., Pérez-Mellado, V., 1999. Green tails in lizards of the genus *Podarcis*: Do they influence the intensity of predation? *Herpetologica* 55, 530–537.
- Castilla, A.M., Labra, A., 1998. Predation and spatial distribution of the lizard *Podarcis hispanica atrata*: an experimental approach. *Acta Oecol.* 19, 107–114.
- Christian, K.A., Tracy, C.R., 1981. The effect of the thermal environment on the ability of Galápagos land iguanas to avoid predation during dispersal. *Oecologia* 49, 218–223.
- Cooper Jr., W.E., 1997a. Threat factors affecting antipredator behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. *Copeia* 1997, 613–619.
- Cooper Jr., W.E., 1997b. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool.* 75, 943–947.
- Cooper Jr., W.E., 1999. Tradeoffs between courtship, fighting, and antipredatory behaviour by a lizard, *Eumeces laticeps*. *Behav. Ecol. Sociobiol.* 47, 54–59.
- Cooper Jr., W.E., 2000. Effect of temperature on escape behavior by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour* 137, 1299–1315.
- Delibes, M., Blázquez, M.C., 1998. Tamelessness of insular lizards and loss of biological diversity. *Conserv. Biol.* 12, 1142–1143.
- Downes, S., Shine, R., 1998. safety or solitude?. Using habitat selection experiments to identify a lizard's priorities. *Anim. Behav.* 55, 1387–1396.
- Greene, H.W., 1988. Antipredator mechanisms in reptiles. In: Gans, C., Huey, R.B. (Eds.), *Biology of the Reptilia*, vol. 16. Wiley, New York, pp. 1–152.
- 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. Temperature, physiology and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*, vol. 12. Academic Press, London, pp. 25–91.
- Jacksic, F.M., Fuentes, E.R., 1980. Correlates of tail losses in twelve species of *Liolaemus* lizards. *J. Herpetol.* 14, 137–141.
- Jacksic, F.M., Greene, H.W., 1984. Empirical evidence of non-correlation between tail loss frequency and predation intensity on lizards. *Oikos* 42, 407–411.
- Kramer, D.L., Bonenfant, M., 1997. Direction of predator approach and the decision to flee to a refuge. *Anim. Behav.* 54, 289–295.
- Layne, J.R., Ford, N.B., 1984. Flight distance of the queen snake *Regina septemvittata*. *J. Herpetol.* 18, 496–498.
- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640.
- Marcellini, D.L., Jensen, T.A., 1991. Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersi*: Implications for anti-predator behavior. *J. Herpetol.* 25, 238–241.
- Martín, J., López, P., 1995. Influence of habitat structure on the escape tactics of the lizard *Psammotromus algirus*. *Can. J. Zool.* 73, 129–132.
- Martín, J., López, P., 1996. The escape response of juvenile *Psammotromus algirus* lizards. *J. Comp. Psychol.* 110, 187–192.

- Martín, J., López, P., 1999a. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos* 65, 328–333.
- Martín, J., López, P., 1999b. Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammotromus algirus*. *Ethology* 105, 439–447.
- Martín, J., López, P., 2000. Costs of refuge use affect escape decisions of Iberian rock lizards *Lacerta monticola*. *Ethology* 106, 483–492.
- Medel, R.G., Jiménez, J.E., Fox, S.E., Jacksic, F.M., 1988. Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos* 53, 321–324.
- Parker, W.S., 1994. Demography of the fence lizard, *Sceloporus undulatus*, in northern Mississippi. *Copeia* 1994, 136–152.
- Pérez-Mellado, V., 1998. *Podarcis muralis* (Laurenti, 1768). In: Salvador, A. (Coord.), Ramos, M.A., et al. (Eds.), *Reptiles*, vol. 10. Fauna Ibérica, Museo Nacional de Ciencias Naturales, CSIC, Madrid, pp. 283–294.
- Rand, A.S., 1964. Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* 45, 863–864.
- Recarte, J.M., Vincent, J.P., Hewison, A.J.M., 1998. Flight responses of park fallow deer to the human observer. *Behav. Process.* 44 (1), 65–72.
- Rocha, C.F., Bergallo, H.G., 1990. Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. *Ethol. Ecol. E* 2, 263–268.
- Schall, J.J., Pianka, E.R., 1980. Evolution of escape behavior diversity. *Am. Nat.* 115, 551–566.
- Schoener, T.W., 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology* 60, 1110–1115.
- Shine, R., Olsson, M.M., Lemaster, M.P., Moore, I.T., Mason, R.T., 2000. Effects of sex, body size, temperature, and location on the antipredator tactics of free-ranging gartersnakes (*Thamnophis sirtalis*, Colubridae). *Behav. Ecol.* 11, 239–245.
- Siegel, S., 1956. *Nonparametric Statistics for the Behavioral Sciences*. MacGraw-Hill, New York, 342 pp.
- Smith, G.R., 1996. Tail loss in the striped plateau lizard, *Sceloporus virgatus*. *J. Herpetol.* 30, 552–555.
- Smith, D.G., 1997. Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. *Behav. Ecol.* 8, 622–629.
- Smith, G.R., Ballinger, R.E., 2001. The ecological consequences of habitat and microhabitat use in lizards: a review. *Contemporary Herpetology*, vol. 3. Retrieved January 12, 2002 from <http://research.calacademy.org/herpetology/herpdocs/ch/2001/3/index.htm>.
- Snell, H.L., Jennings, R.D., Snell, H.M., Harcourt, S., 1988. Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evol. Ecol.* 2, 353–369.
- Sokal, R., Rohlf, F.J., 1981. *Biometry*. Freeman, San Francisco, 859 pp.
- Stone, P.A., Snell, H.L., Snell, H.M., 1994. Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. *Conserv. Biol.* 8, 569–573.
- Turner, F.B., Medica, P.A., Jennrich, R.I., Maza, B.G., 1982. Frequencies of broken tails among *Uta stansburiana* in southern Nevada and a test of the predation hypothesis. *Copeia* 1982, 835–840.
- Weatherhead, P.J., Robertson, I.C., 1992. Thermal constraints on swimming performance and escape response of northern water snakes (*Nerodia sipedon*). *Can. J. Zool.* 70, 94–98.