An Experimental Test of the Costs of Antipredatory Refuge Use in the Wall Lizard, Podarcis muralis

Author(s): José Martín and Pilar López

Source: *Oikos*, Mar., 1999, Vol. 84, No. 3 (Mar., 1999), pp. 499-505

Published by: Wiley on behalf of Nordic Society Oikos

Stable URL: https://www.jstor.org/stable/3546428

OIKOS 84: 499–505. Copenhagen 1999

An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*

José Martín and Pilar López

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

Prey often respond to predator presence by increasing their use of refuges. However, refuge use may have some costs such as lost opportunities for foraging, and also physiological costs, such as hypothermia. Many lizards escape from predators by fleeing into rock crevices, which because of shady and colder conditions decreases their body temperature below required optimal levels. By experimentally increasing the frequency of attacks by a simulated predator (human) toward a group of wall lizards, *Podarcis muralis*, we examined the hypothesis that lizards may respond to an increase in risk of predation with an increase in refuge use, but that this strategy entails costs to their body condition. At the end of the experimental period, experimental lizards increased the time spent in a refuge after an attack (recovery time), but they had significantly lower relative body mass than control individuals. We suggest that an increase in the time spent in refuges at unfavourable temperatures during the experiment led to a loss of time available for foraging and a diminution of the efficiency of physiological functions, which resulted in loss of mass.

J. Martín and P. López, Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, E-28006 Madrid, Spain (jose.martin@fresno.csic.es).

Prey often respond to predator presence by increasing their use of refuges (Werner et al. 1983, Kotler 1984, Sih 1986, Sih et al. 1992). However, refuges may have some costs that should be minimized, influencing the patterns of prey use of refuges, and this should have important effects on the predator-prey interaction (Sih 1987, Ruxton 1995). Costs of refuge use include, for example, the loss of time available for foraging (Godin and Sproul 1988, Koivula et al. 1995) or mate searching (Sih et al. 1990, Crowley et al. 1991). In addition, unfavourable conditions in refuges (e.g. suboptimal temperatures or oxygen levels) might entail physiological costs, such as hypothermia or hypoxia (Wolf and Kramer 1987, Weatherhead and Robertson 1992).

Many lizards escape from predators by fleeing into the nearest refuge (Greene 1988). However, this simple and safe strategy may have some costs, because available, or safer, refuges may be placed in microhabitats such as rock crevices with shady and colder conditions. In reptiles, the attainment and maintenance of an optimal body temperature are essential to maximize numerous physiological process, such as food digestion or gamete maturation (Huey 1982, Stevenson et al. 1985), and performance functions with important future fitness consequences such as sprint speed or foraging efficiency (Bennett 1980, Avery et al. 1982). Careful behavioural thermoregulation increases the time that lizards spend at physiologically favourable body temperatures (Grant and Dunham 1988, Bauwens et al. 1996). However, effective thermoregulation requires that appropriate sources of heat from solar radiation and/or warm substrates are available (Huey 1982). Refuge use may, thus, imply the loss of these sources of heat, and, consequently, the body temperature of a lizard retreated into a cool refuge will decrease below required preferred levels. This is specially important for small lizards, with low thermal inertia, because it could result in temperature impairment in only a few minutes.

Accepted 17 July 1998

ISSN 0030-1299
Printed in Ireland

In these circumstances, lizards should minimize time spent in a refuge, especially when refuge thermal conditions are unfavourable relative to external ones in solar irradiated patches.

Growth in ectotherms continues for very long periods, and is to a large extent indeterminate and set by environmental variables. Variation in reptilian growth rate is associated with differences in food availability, and time available for foraging and thermoregulation (Andrews 1982). Behavioural thermoregulation increases growth rate by increasing time available for voluntary food intake (Avery 1984, Autumm and De Nardo 1995). Besides, the selection of elevated body temperatures following feeding (Tossini et al. 1994) may increase both digestive rate and efficiency (Harlow et al. 1976, Harwood 1979). Therefore, when reptiles are prevented from attaining their selected body temperatures, the excess of energy stored as fat in the fat body and liver should decrease and they should display reduced growth rates (Sinervo 1990, Sinervo and Adolph 1994). This is important because the amount of stored fat, which can be estimated from individual body condition (i.e., mass relative to body length), affects survival and future reproductive success of lizards (Ballinger 1977, Pond 1981).

We hypothesized that lizards may respond to an increase in the presence of a predator (i.e. higher predation risk) with an increase in their refuge use. However, this strategy may entail some costs that might be reflected in the lizards' body condition. In this paper we test this hypothesis in a population of the common wall lizard, *Podarcis muralis*, by experimentally increasing the frequency of attacks by a simulated predator (human) toward a group of lizards during several days. We specifically examined how this increase in predation risk affected (1) the time spent by lizards in refuges after an attack (recovery time), and (2) the body condition of these individual lizards, in comparison with a control group that were not attacked.

Materials and methods

Species and study site

Podarcis muralis is a small lacertid lizard (60–76 mm adult snout-to-vent length, SVL) widespread in Central Europe, although in the Iberian Peninsula it is restricted to mountain areas of the northern half, where they occupy soil dwellings, talus and walls in shaded zones in forests (Martín-Vallejo et al. 1995). We chose this species because in the microhabitats selected shade greatly limits the time available to lizards for basking and foraging. Thus, even small restrictions of the time available, such as the time spent in a refuge to avoid a predator, should be important in this lizard species.

We performed the experiment in the Guadarrama Mountains, in a pine forest at Cercedilla (Madrid Prov., Central Spain) at an elevation of 1500 m. The dominant vegetation at this altitude consists of *Pinus sylvestris* forest, with shrubs such as *Juniperus communis* and *Cytisus scoparius*. We conducted the experiment at an artificial wall (120 m long × 5 m high) built with granite rocks to hold a sand bank. Active lizards were found basking or walking on the wall. Lizards used the numerous crevices between rocks as refuges. Shade produced by the nearby pine forest limited the activity of lizards on the wall to a maximum period of about 7 h daily, although during spring unfavourable weather conditions (i.e. rain and clouds) often limited the time available even more.

Experimental procedure

We conducted the experiment during April and May of 1997. In the first week of the experiment we searched for lizards by walking a track close to the wall between 0800 and 1400 h (G.M.T.). We approached individual lizards by simulating a predatory attack, thus we induced lizards to flee and hide in a refuge (crevices of the wall). Then, we measured their recovery time (see below) in the first attack as an estimation of the lizards' basal assessment of predation risk. Immediately thereafter we noosed these individual lizards to record SVL (to the nearest mm), tail length, body mass (measured to the nearest 0.1 g with a Pesola spring scale), sex and tail condition (only adult lizards with completed tails were used in the experiment). We randomly assigned individual lizards to the control ($N = 24$; 13 males and 11 females) or experimental group ($N = 20$; 11 males and 9 females). Although males were smaller in length but relatively heavier than females, lizards from the control and experimental group did not differ in either SVL (Two-way ANOVA, Sex, $F = 13.02$, $P = 0.0008$; Treatment, $F = 1.32$, $P = 0.26$; Interaction, $F = 0.95$, $P = 0.35$) or body mass residuals (Two-way ANOVA; Sex, $F = 8.45$, $P = 0.006$; Treatment, $F = 0.08$, $P = 0.78$; Interaction, $F = 0.09$, $P = 0.76$) (Fig. 2). Lizards were individually marked by toe clipping and with paint on the dorsum for temporary identification, and released at the capture site within less than two min.

In the next 15 d, we walked at a distance of 5–7 m from the wall several times between 0800 and 1400 h to locate and identify lizards with binoculars. We then applied the experimental treatment consisting of simulated predatory attacks to all the experimental individuals found, resulting in lizards retreating into refuges. We passed nearby control individuals without disturbing them. Each experimental individual was attacked an average of 2.7 ± 0.5 times per day, which resulted in about 38 simulated attacks per lizard during the experiment. Finally, in the last week of the experiment we approached every individual found by simulating a predatory attack to measure changes in recovery times after the experimental treatment, and then noosed them to record changes in SVL and body mass.

Recovery behaviour

We approached individual lizards by simulating a predatory attack by walking directly towards the lizard. To avoid confounding effects that may affect risk perception of lizards (Burger and Gochfeld 1993, Cooper 1997), the same person wearing the same clothing performed all approaches in a similar way, while another person recorded the lizard's behaviour. Lizards typically made a short flight to the nearest available refuge (rock crevices) and hid entirely from the observer. When the lizard hid we started a stopwatch and retreated to a distance of 5–7 m to observe from a hidden position with binoculars. We measured the time that the lizard spent in the refuge, which could be divided into two partial recovery times: time until the lizard's snout appeared from the refuge and the lizard looked outside (appearance time), and time until more than half of the lizard's body emerged from the refuge (emergence time). Because thermal conditions of the refuge did not affect the lizard once most of its body was outside of the refuge, thermal costs of refuge use were considered to be relevant only until this emergence time.

Recovery times of lizards may be dependent on the thermal costs of refuge use, which may be dependent on the thermal state of individuals when hiding (i.e. their body temperature), and/or the thermal conditions of the refuge (i.e. potential cooling rate) (unpublished data, see below). Thus, immediately after a lizard emerged from the refuge and resumed its activity, we measured the operative temperature at the point where the lizard was before the simulated attack and at the refuge using hollow copper models (Bakken et al. 1985, Bakken 1989). Models were 7 cm long by 1 cm diameter copper cylinders. The probe of a digital thermometer was suspended in the centre of the hollow model and both ends were sealed (Bakken 1989). Models were employed as a way to measure the integrated effect of solar radiation, thermal radiation, convection and conduction as they affected heat transfer at the surface of the animal (Bakken et al. 1985, Bakken 1989). Because the experimental design did not allow us to capture lizards to measure their body temperature immediately before they hid, potential body temperatures were estimated from operative temperatures.

Emergence times were significantly correlated with the operative temperatures of copper models placed in the exterior (Pearson correlation for all individuals pooled in their first attack: $r = 0.31$, $P = 0.047$), so they were also probably dependent on the body temperature of lizards before the attack. Nevertheless, emergence times were not correlated with the operative temperatures inside the refuges ($r = 0.06$, $P = 0.68$). Thus, lizards with potential higher initial body temperatures had longer recovery times, independently of refuge conditions. A similar result was obtained for appearance time (exterior: $r = 0.26$; interior: $r = 0.08$). Therefore, to correct recovery times taking into account the thermal state of lizards, we used the external operative temperature as a covariate in subsequent analyses.

Data analyses

We used repeated-measures three-way analyses of covariance (ANCOVAs) (Sokal and Rohlf 1995) to test for differences in each of the recovery times of the same individuals before and after the experimental treatment (within-subjects factor). External operative temperature was the covariate, and sex (male vs female) and group (experimental vs control) were the between-subjects factors. Sex was included to adjust for the size difference between males and females (see above), which might affect heating and cooling rates (Carrascal et al. 1992), and, hence, recovery times. The interactions between sex and treatment were included to determine whether the relationships between thermal conditions and recovery times were different in males and females. The interactions between group and treatment tested for effects of the experimental treatment on recovery times.

We also used a repeated-measures three-way ANCOVA to test for changes in relative body mass ($\log_e$ transformed) before and after the experimental treatment (within-subjects factor). We used SVL as a covariate, and sex and group as the between-subjects factors. Sex was included to adjust for the size difference between males and females (see above), which might affect body mass changes. The interaction between group and treatment tested for effects of the experimental treatment on relative body mass. Individual values of relative body mass were equivalent to the residuals from the regression equation of ln mass (g) on SVL (mm), which may represent an index of the relative amount of fat stored, and, hence, an estimation of individual physical condition or nutritional status (Bonnet and Naulleau 1994).

For each ANCOVA we first tested for slope heterogeneity; in each case it was not significant ($P > 0.20$ in all cases). Significance levels for the multiple tests of each ANCOVA were calculated by using the sequential Bonferroni adjustment of Rice (1989) for multiple comparisons (Chandler 1995).

Results

Recovery behaviour

The results of the ANCOVAs on recovery times of lizards indicated that at the beginning of the experiment lizards from the control and experimental group did not differ in recovery time, once corrected for different thermal conditions. However, after application of the treatment, experimental lizards had significantly longer recovery times than control lizards (Treatment × Group effect) (Fig. 1, Table 1). Therefore, experimental lizards seemed to increase their shyness to emerge from a refuge after they had suffered repeated attacks by a human observer. We did not find any effect of sex on recovery times.

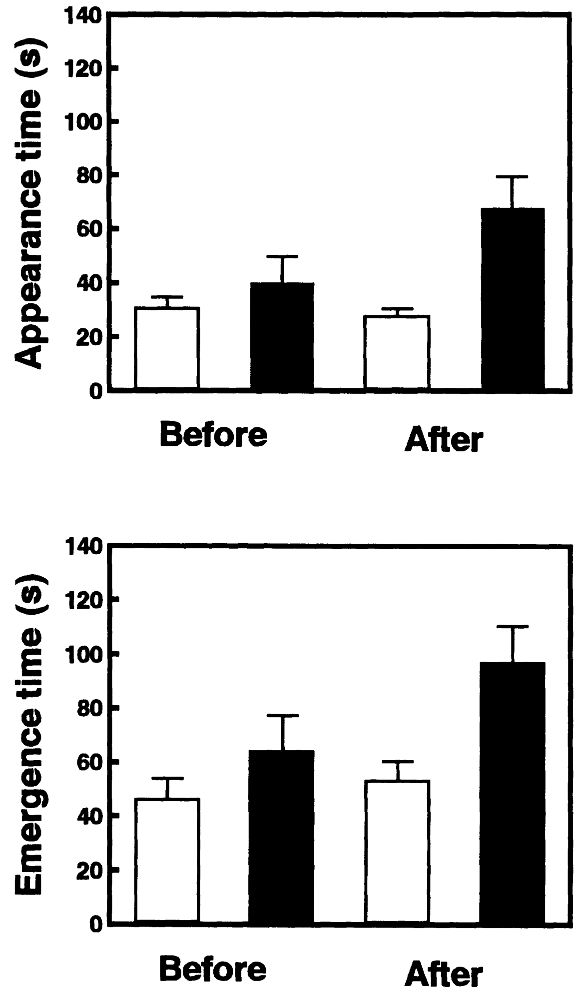

Fig. 1. Recovery times (mean + SE) of lizards after a simulated predator attack in the control (open bars) and experimental group (solid bars) before and after the experimental treatment.

Changes in body mass

Although, at the beginning of the experiment, lizards from the control and experimental group did not differ in either SVL or body mass residuals (see Materials and methods), the ANCOVA of body mass indicated that, at the end of the experiment, experimental lizards had significantly lower relative body mass than control lizards (Treatment × Group effect) (Fig. 2, Table 2).

Differences in body mass between groups were a consequence of control lizards increasing body mass during the experimental period, whereas experimental lizards lost mass, or increased mass only slightly, probably as a result of the experimental treatment (Two-way ANCOVA of differences between initial and final body mass with SVL as covariate; Sex, $F = 0.05$, $P = 0.82$; Group, $F = 12.78$, $P = 0.001$; Interaction, $F = 2.50$, $P = 0.12$) (Fig. 3). Thus, the regression equations between mass and SVL at the beginning of the experiment were similar in control and experimental lizards: Control: $\ln \text{mass} = 0.49 + 0.02\ \text{SVL}$, $r^2 = 0.49$, $P < 0.01$; Experimental: $\ln \text{mass} = 0.45 + 0.02\ \text{SVL}$, $r^2 = 0.68$, $P < 0.01$, whereas at the end of the experiment the regression equations were: Control: $\ln \text{mass} = 0.66 + 0.02\ \text{SVL}$, $r^2 = 0.50$, $P < 0.01$. Experimental: $\ln \text{mass} = 0.39 + 0.02\ \text{SVL}$, $r^2 = 0.36$, $P < 0.01$.

Discussion

The results of our experiment suggest that *P. muralis* lizards identified a higher probability of suffering attacks as an increase in predation risk, and that they were able to compensate for it by increasing the time spent in refuges. Modifications of microhabitat or refuge use according to perceived levels of predation risk seem to be widespread among animals (Gilliam and Fraser 1987, Lima and Dill 1990, Sih et al. 1992), and also among lizards (Carrascal et al. 1992, Martín and Salvador 1992, 1993a).

However, when changes in microhabitat or refuge use are costly, animals may face a trade-off when deciding the time spent in a refuge after a predator attack. The risk of predation is maximal at the moment of the attack, but it will decrease gradually as time spent in the refuge increases. This is because, at least when prey are abundant, most predators will probably leave the area and divert their attack to other exposed and unaware prey, after this particular one has disappeared into a refuge. Thus, the probability of the predator waiting for the prey outside the refuge (i.e. probability of a new attack) will decrease with time. On the other hand, the costs of refuge use will increase with time spent in the refuge (e.g. loss of time or decrease of body temperature in lizards). Prey should choose to get out of the refuge when the cost of refuge use is higher than the risk of predation. Therefore, this emergence

Table 1. Results of the repeated-measures three-way ANCOVAs examining group, sex, and treatment effects on each of the recovery times of lizards. In each ANCOVA, repeated factor was the recovery time before and after the experimental treatment, and external operative temperature was the covariate.

	Appearance			Emergence	
	df	*F*	*P*	*F*	*P*
Between subjects effects					
Group	1,38	15.36	0.00004*	20.05	0.00007*
Sex	1,38	0.01	0.91	0.36	0.55
Group × Sex	1,38	0.31	0.58	0.12	0.73
Within subjects effects					
Treatment	1,38	7.31	0.01	3.81	0.06
Treatment × Group	1,38	8.15	0.007*	7.84	0.0079*
Treatment × Sex	1,38	2.79	0.10	2.39	0.13
Treatment × Group × Sex	1,38	1.09	0.30	3.24	0.08

P values are unadjusted for multiple comparisons. Asterisks denote values significant at $\alpha = 0.05$ using the sequential Bonferroni method with 7 comparisons (Rice 1989).

time could be modified in two ways: by increasing the predation risk (then the diminution of predation risk should be slower and the time spent in the refuge should increase), or by increasing the cost of refuge use (then the time spent in the refuge should decrease). In our experiment, one of the costs of refuge use was probably the decrease of lizards' body temperature with time. In accordance with these predictions, lizards with higher initial body temperature stayed for longer periods inside the refuge. On the other hand, at the end of the experiment, experimental lizards increased the time spent inside the refuge. This may be because lizards that had suffered repeated attacks assessed that the probability of a new attack was higher (i.e. diminution of predation risk with time is slower).

The results of our experiment further indicate that an increase in the use of refuges may, however, entail some costs. Thus, at the end of the treatment experimental lizards had poorer body condition and, thus, probably less fat stored than control lizards. Variation in body condition has been explained by variation in food availability in natural populations of lizards (Ballinger 1977), and showed experimentally by manipulating food intake (Licht 1974). Thus, in our study the main cause that induced lower body mass in experimental lizards might be a decrease of the time available for foraging, which would lead to reduced food intake. This could result from an increase in time spent in the refuge, or outside the refuge but stationary looking for predators, instead of devoting time to forage. Similarly, lizards that have lost their tail compensate for a higher predation risk with changes in microhabitat use and time budgets (Martín and Salvador 1992, 1993a). However, these changes also affect their foraging success (e.g. by decreasing the diversity of prey in the diet; Martín and Salvador 1993b). This may partly explain why tailless lizards use up fat reserves more quickly (Dial and Fitzpatrick 1981).

Thermoregulation requirements may also be important to explain the low body condition of experimental lizards. Body temperature decreases inside the refuge, thus, lizards have to either spend more time basking to regain their preferred body temperature, or start to forage at suboptimal temperatures with a lower sprint speed and lower predatory efficiency (Bennett 1980, Avery et al. 1982). In addition, when the body temperature is lowered, the speed at which food is processed is also lowered and the energy available for storage decreases (Harlow et al. 1976, Harwood 1979). Other additional energetic costs for the experimental lizards might come from the frequent fleeing sequences needed to reach the refuge and escape from the predator. All of these costs of refuge use should influence notably the patterns of prey use of refuges (Sih et al. 1992), and also the escape decisions of prey (Ydenberg and Dill 1986). Thus, when the costs of refuge use are higher, prey should not only reduce their recovery time, but they should also delay their escape decisions, waiting for longer before retreating to the refuge.

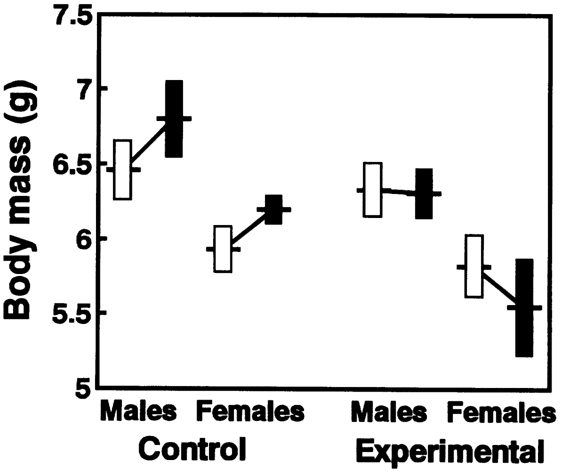

Fig. 2. Body mass (mean ± SE) of control and experimental lizards before (open bars) and after (solid bars) the experimental treatment.

Table 2. Repeated-measures three-way ANCOVA examining group, sex, and treatment effects on body mass of lizards ($\log_e$ transformed). Snout-to-vent length was the covariate. Repeated factor was the body mass before and after the experimental treatment.

	df	*F*	*P*
Between subjects effects			
Group	1,39	13.18	0.0008*
Sex	1,39	5.44	0.025
Group × Sex	1,39	0.18	0.68
Within subjects effects			
Treatment	1,39	1.88	0.18
Treatment × Group	1,39	9.18	0.004*
Treatment × Sex	1,39	1.68	0.20
Treatment × Group × Sex	1,39	0.20	0.66

P values are unadjusted for multiple comparisons. Asterisks denote values significant at $\alpha = 0.05$ using the sequential Bonferroni method with 7 comparisons (Rice 1989).

The addition of mass to an animal may influence its locomotory capabilities and, thus, increase the predation risk (Witter et al. 1994). The increment of mass associated with pregnancy (Schwarzkopf and Shine 1992) and recent feeding (Ford and Shuttlesworth 1986, Martín 1996) is known to reduce the locomotory capabilities of many reptiles. Experimental lizards in our study might compensate the cost of a lower relative body mass with the benefit of an increase in the manoeuvrability against predators' attacks, increasing their escape performance. Nevertheless, the reduction of fat stored may have important long-term consequences for reptiles. The amount of energy stored determines the time that an individual can stay alive during periods of low food availability, and thus affects survival (Pond 1981). For example, during the hibernation period, lizards that have lost their tail, and thus the fat stored there, have a lower survival (Bauwens 1981). Also, stored fat influences frequency of reproduction, and females with more fat have greater reproductive success (Ballinger 1977, Andren and Nilson 1983).

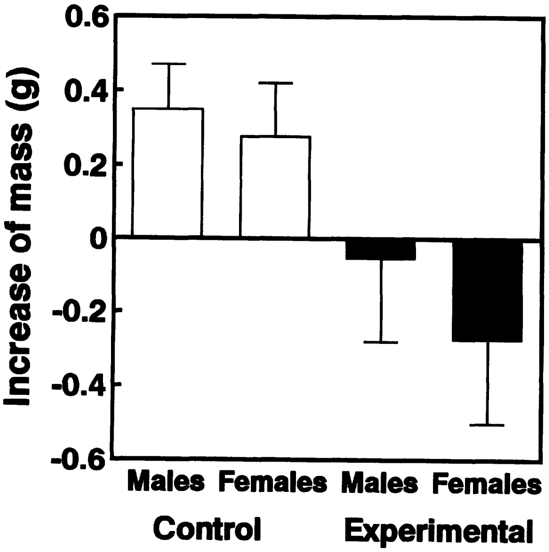

Fig. 3. Changes in body mass (mean ± SE) during the experiment of control (open bars) and experimental lizards (solid bars).

In conclusion, this experiment shows that *P. muralis* lizards are able to compensate for an increase in risk of predation by increasing the use of refuges, and by delaying the recovery time when predation risk is assessed to be higher. However, the use of refuges placed in microhabitats of low quality for foraging and for attaining preferred body temperatures entails costs that are reflected in the body condition of individuals. We suggest that restrictions in time available for foraging, and thermoregulatory costs (i.e. a higher proportion of time spent at unfavourable body temperatures) may have led to a loss of relative body mass of experimental lizards.

Acknowledgements – We thank L. M. Carrascal and M. Gomendio for helpful comments, Simon Lane for checking the English, and "El Ventorrillo" MNCN Field Station for use of their facilities. Financial support was provided by contracts from the DGICYT project PB-94-0067.

References

Andren, C. and Nilson, G. 1983. Reproductive tactics in an island population of adders, *Vipera berus* (L.), with a fluctuating food resource. – Amphibia-Reptilia 4: 63–79.

Andrews, R. M. 1982. Patterns of growth in reptiles. – In: Gans, C. and Pough, F. H. (eds), Biology of the Reptilia. Vol. 13. Academic Press, New York, pp. 273–320.

Autumm, K. and De Nardo, D. F. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. – J. Herpetol. 29: 157–162.

Avery, R. A. 1984. Physiological aspects of lizard growth: the role of thermoregulation. – Symp. Zool. Soc. Lond. 52: 407–424.

Avery, R. A., Bedford, J. D. and Newcombe, C. P. 1982. The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. – Behav. Ecol. Sociobiol. 11: 261–267.

Bakken, G. S. 1989. Arboreal perch properties and the operative temperature experienced by small animals. – Ecology 70: 922–930.

Bakken, G. S., Santee, W. R. and Erskine, D. J. 1985. Operative and standard operative temperature: tools for thermal energetics studies. – Am. Zool. 25: 933–943.

Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximate variation in a lizard. – Ecology 58: 628–635.

Bauwens, D. 1981. Survivorship during hibernation in the European common lizard, *Lacerta vivipara*. – Copeia 1981: 741–744.

Bauwens, D., Hertz, P. E. and Castilla, A. M. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. – Ecology 77: 1818–1830.

Bennett, A. F. 1980. The thermal dependence of lizard behaviour. – Anim. Behav. 28: 752–762.

Bonnet, X. and Naulleau, G. 1994. A body condition index (BCI) in snakes to study reproduction. – C. R. Acad. Sci. Ser. III Sci. Vie. 317: 34–41.

Burger, J. and Gochfeld, M. 1993. The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. – J. Herpetol. 27: 426–430.

Carrascal, L. M., López, P., Martín, J. and Salvador, A. 1992. Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. – Ethology 92: 143–154.

Chandler, C. R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. – Anim. Behav. 49: 524–527.

Cooper, W. E., Jr. 1997. 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.

Crowley, P. H., Travers, S. E., Linton, M. C., Cohn, S. L., Sih, A. and Sargent, R. C. 1991. Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game. – Am. Nat. 137: 567–596.

Dial, B. E. and Fitzpatrick, L. C. 1981. The energetic cost of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). – Oecologia 51: 310–317.

Ford, N. B. and Shuttlesworth, G. A. 1986. Effects of variation in food intake on locomotory performance of juvenile garter snakes. – Copeia 1986: 999–1001.

Gilliam, J. F. and Fraser, D. F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. – Ecology 68: 1856–1862.

Godin, J.-G. L. and Sproul, C. D. 1988. Risk taking in parasitized sticklebacks under threat of predation: effects of energetic need and food availability. – Can. J. Zool. 66: 2360–2367.

Grant, B. W. and Dunham, A. E. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. – Ecology 69: 167–176.

Greene, H. W. 1988. Antipredator mechanisms in reptiles. – In: Gans, C. and Huey, R. B. (eds), Biology of the Reptilia. Vol. 16. John Wiley and Sons, New York, pp. 1–152.

Harlow, E. A., Hillman, S. J. and Hoffman, M. 1976. The effect of temperature on the digestive efficiency of the herbivorous lizard *Dipsosaurus dorsalis*. – J. Comp. Physiol. 11: 1–6.

Harwood, R. H. 1979. The effect of temperature on the digestive efficiency of three species of lizards, *Cnemidophorus tigris*, *Gerrhonotus multicarinatus* and *Sceloporus occidentalis*. – Comp. Biochem. Physiol. A 63: 417–433.

Huey, R. B. 1982. Temperature, physiology and the ecology of reptiles. – In: Gans, C. and Pough, F. H. (eds), Biology of the Reptilia. Vol. 12. Academic Press, New York, pp. 25–91.

Koivula, K., Rytkönen, S. and Orell, M. 1995. Hunger-dependency of hiding behaviour after a predator attack in dominant and subordinate willow tits. – Ardea 83: 397–404.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. – Ecology 65: 689–701.

Licht, P. 1974. Response of *Anolis* lizards to food suplementation in nature. – Copeia 1974: 215–221.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

Martín, J. 1996. Effects of recent feeding on locomotor performance of juvenile *Psammodromus algirus* lizards. – Funct. Ecol. 10: 390–395.

Martín, J. and Salvador, A. 1992. Tail loss consequences on habitat use by the Iberian Rock lizard *Lacerta monticola*. – Oikos 65: 328–333.

Martín, J. and Salvador, A. 1993a. Thermoregulatory behaviour of rock-lizards in response to tail loss. – Behaviour 124: 123–136.

Martín, J. and Salvador, A. 1993b. Tail loss and foraging tactics of iberian rock-lizards, *Lacerta monticola*. – Oikos 66: 318–324.

Martín-Vallejo, J., García-Fernández, J., Pérez-Mellado, V. and Vicente-Villardon, J. L. 1995. Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of central Spain. – Herpetol. J. 5: 181–188.

Pond, C. M. 1981. Storage. – In: Townsend, C. R. and Calow, P. (eds), Physiological ecology. Blackwell Scientific, Oxford, pp. 190–219.

Rice, W. R. 1989. Analyzing tables of statistical tests. – Evolution 43: 223–225.

Ruxton, G. D. 1995. Short term refuge use and stability of predator-prey models. – Theor. Popul. Biol. 47: 1–17.

Schwarzkopf, L. and Shine, R. 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. – Behav. Ecol. Sociobiol. 31: 17–25.

Sih, A. 1986. Antipredator responses and the perception of danger by mosquito larvae. – Ecology 67: 434–441.

Sih, A. 1987. Prey refuges and predator-prey stability. – Theor. Popul. Biol. 31: 434–441.

Sih, A., Krupa, J. and Travers, S. 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider, *Gerris remigis*. – Am. Nat. 135: 84–290.

Sih, A., Kats, L. B. and Moore, R. D. 1992. Effects of predatory sunfish on the density, drift and refuge use of stream salamander larvae. – Ecology 73: 1418–1430.

Sinervo, B. 1990. Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). – Oecologia 83: 228–237.

Sinervo, B. and Adolph, S. C. 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. – Ecology 75: 776–790.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry 3rd ed. – Freeman, New York.

Stevenson, R. D., Peterson, C. R. and Tsuji, J. S. 1985. The thermal dependence of locomotion, tongue flicking, digestion and oxygen consumption in the wandering warter snake. – Physiol. Zool. 58: 46–57.

Tossini, G., Jones, S. and Avery, R. A. 1994. Effects of feeding on set point temperatures and thermoregulatory behaviour in the lizards *Podarcis muralis* and *Lacerta vivipara*. – Amphibia-Reptilia 15: 257–265.

Weatherhead, P. J. and Robertson, I. C. 1992. Thermal constraints on swimming performance and escape response of northern water snakes (*Nerodia sipedon*). – Can. J. Zool. 70: 94–98.

Werner, E. E., Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. 1983. An experimental test of the effects of predation risk on habitat use. – Ecology 64: 1540–1548.

Witter, M. S., Cuthill, I. C. and Bonser, R. H. C. 1994. Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. – Anim. Behav. 48: 201–222.

Wolf, N. G. and Kramer, D. L. 1987. Use of cover and the need to breathe: the effects of hypoxia on vulnerability of dwarf gouramis to predatory snakeheads. – Oecologia 73: 127–132.

Ydenberg, R. C. and Dill, L. M. 1986. The economics of fleeing from predators. – Adv. Stud. Behav. 16: 229–249.