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Habitat deterioration affects body condition of lizards: A behavioral approach with *Iberolacerta cyreni* lizards inhabiting ski resorts

Luisa Amo*, Pilar López, José Martín

Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain

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ABSTRACT

We analyzed whether habitat deterioration due to ski slopes affected lizards' behavior, and whether these changes in behavior had consequences for the body condition and health state of lizards. Results suggested that habitat deterioration in ski slopes not only implied a loss of optimal habitat for lizards, but also led to an increase in perceived risk of predation. Males seemed to adjust their movement patterns to differences in risk, increasing their movement speed during their displacements across risky areas within ski slopes, but as a consequence, they incurred loss of body condition. A laboratory experiment supported that fleeing at high speeds in areas without refuges can be a factor responsible for reduced body condition. However, changes in body condition did not affect sprint speed of lizards. Our study provides new evidence that behavioral strategies to cope with increased predation risk, due to human-induced habitat deterioration, may affect body condition of lizards. Our results have applications for the design of conservation plans for this endangered lizard species. Environmental impact studies should be performed before opening new ski slopes, but taking into account not only the presence of lizards but also their body condition. An effective way to decrease the effects of habitat loss may be the artificial restoration of some refuges to create safe corridors for movement.

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1. Introduction

One of the main strategies of prey to cope with predation risk is the selection of safe habitats where they can attend their requirements while minimizing predation risk (e.g., Lima, 1998; Amat and Masero, 2004). Habitat selection may decrease conspicuousness of prey, and provide refuges to hide from attacking predators (Arthur et al., 2004). However, natural vegetation appears nowadays deeply modified by human activities, and this change in habitat structure may increase perceived risk of predation (Whittingham and

Evans, 2004). For example, deterioration of vegetation may make animals more conspicuous and thus, more vulnerable to predators (Martín and López, 1998), which will require animals to increase the frequency of costly antipredatory behaviors.

One of these antipredatory behaviors is the modification of activity and locomotor patterns (Martín and Salvador, 1997a; McAdam and Kramer, 1998), such as a decrease in activity to avoid the attack of predators that localize their prey by their movement (Hecnar and M'Closkey, 1998; Downes, 2001; Weber and Van Noordwijk, 2002; Laurila et al., 2004), or, when

* Corresponding author. Tel.: +34 914111328; fax: +34 915645078.

E-mail address: luisa.amo@mncn.csic.es (L. Amo).

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movement is required, a modification of locomotor patterns (Martín and Salvador, 1997a; McAdam and Kramer, 1998) to decrease time exposed to potential predators (López and Martín, 2002; Miles, 2004). Antipredatory behaviors such as fleeing at high speed and refuge use are costly. For example, *Podarcis muralis* and *Psammotromus algirus* lizards submitted to a high predation pressure suffered a loss of body mass (Martín and López, 1999a; Pérez-Tris et al., 2004). Therefore, an excessive allocation of time and energy to antipredatory strategies can decrease body condition, with important consequences for short and long term fitness. Furthermore, the loss of body condition could also decrease the ability to invest in defense against parasites (Cooper et al., 1985; Smallridge and Bull, 2000). However, there are no studies about the costs, in terms of body condition and health state, of changes in movement patterns in response to increased predation risk.

The Iberian rock lizard, *Iberolacerta cyreni* (= *Lacerta monticola cyreni*), is an endemic endangered small diurnal lacertid found mainly in rocky habitats in some high mountains of the Iberian Peninsula (Martín, 2005). However, this lizard suffers a loss of optimal habitat due to the construction of ski infrastructures (Martín and Salvador, 1997b; Pérez-Mellado, 2003). The natural vegetation of the ski slopes is badly affected (Martín and Salvador, 1997b), causing a considerable impact on the whole ecosystem (Haslett, 1991; Illich and Haslett, 1994; Wipf et al., 2005). The lack of vegetation and rocks causes a loss of cover and potential refuges for lizards (Martín and Salvador, 1997b), and thus, it creates areas with higher level of predation risk.

Here we analyzed whether male lizards have different microhabitat use and locomotor patterns in areas with two levels of perceived predation risk, induced by anthropogenic changes in microhabitat structure (i.e., construction of ski slopes), and whether these differences had consequences on their body condition and health state. We choose males because they defend territories by performing continuous movements across their home range searching for females and expelling intruder males (Martín and López, 2000; Aragón et al., 2001). Therefore, males may be more susceptible than females to predation because they have higher movement rates and are more conspicuous (Martín and Salvador, 1997a; Martín and López, 1999b, 2000). We therefore examined the effects of habitat deterioration on: (a) microhabitat selection, (b) spontaneous movement patterns, and (c) body condition, immune response, and parasite load of male lizards. We predicted that males should not use microhabitat at random, and therefore, regardless of possible differences in cover of shrubs and rocks between areas, we expected that lizards selected similar and safe microhabitats in both areas (i.e., those close to refuges such as shrubs or rocks). However, because males need to patrol their entire home ranges, we also predicted that males would incur higher predation risk while moving in ski slopes. Thus, we expected that, in ski slopes, males would increase speed when crossing unsafe areas far from refuges to reduce time exposed to predators. However, since moving at high speed is more costly than moving slower (Kramer and McLaughlin, 2001; Gleeson and Hancock, 2002), we expected that these males would suffer a loss of body condition, which might also affect their health state.

Many factors other than speed during displacements may affect body condition of males. Therefore, we performed a laboratory study to analyze the effect of fleeing at high speed on body condition and health state of lizards. We expected that lizards that were forced to run by a simulated predator and did not have a close refuge for hiding might suffer a loss of body mass after several attacks, whereas lizards that did not need to run for longer, because they have a close refuge, would not decrease their body mass. Immediately after this experiment, we measured sprint speed of lizards when they were forced to flee to test whether differences in body condition affected escape speed. We did not expect differences in escape speed of lizards of similar body size regardless of their body condition.

2. Methods

2.1. Study area and species

We performed the study in the Guadarrama Mountains (Madrid Prov., Central Spain) at an elevation range of 1900–2200 m. Natural landscape at this altitudinal range is characterized by granite rock boulders and screes interspersed with shrubs (*Cytisus oromediterraneus* and *Juniperus communis*), meadows of *Festuca* and other grasses, and a few dispersed Scots pines (*Pinus sylvestris*), which form extensive forest at lower altitudes (Martín and Salvador, 1997b). This area is characterized by the presence of several ski resorts and associated infrastructures initially built in the second decade of 20th century but that are continuously maintained and enlarged. In anthropogenic-induced deteriorated areas, mostly in ski slopes, there is no cover of shrubs nor even grasses, and rocks boulders are scarce or have been eliminated. In this region, *I. cyreni* (snout-to-vent length, SVL, of adult lizards ranges between 65 and 90 mm) is active from May to September due to limiting environmental temperatures. Lizards mate in May–June and produce a single clutch in July (Elvira and Vigal, 1985; Pérez-Mellado, 1998). In natural areas and in ski slopes we have observed similar presence and numbers of several predators of this species (Martín, 2005), such as ravens, *Corvus corax*, booted eagles, *Hieraetus pennatus*, or smooth snakes, *Coronella austriaca*.

2.2. Microhabitat use by lizards

To evaluate habitat characteristics of natural areas and ski slopes, and microhabitat use by lizards in these areas, we walked haphazardly during May–June 2003 in days with favorable climate conditions (warm sunny days) and between 09:00 and 13:00 GMT, when lizards were active. When we detected an adult male lizard ($n = 103$), we marked the point where it was first observed. For each point we took four 1 m transects, one at each of the four cardinal orientations radiating from the point where each individual was sighted. We used a scored stick standing vertically at nine sample points (two points at 50 and 100 cm in each of the four transects, and the central point), and recorded the type of substrate found at each point (grass, leaf litter, bare soil, or rocks). We noted the presence of canopy tree cover (Scots pines) above each sample point, and the height from the ground to the first

contact with the stick of leaves of subarctic vegetation at each point. This later measure provided the shrub cover and an indication of the potential utility of vegetation as a refuge by lizards (Martín and López, 1998). Thus, a low vegetation height indicated that vegetation is close to the ground, providing a narrow refuge where to hide. Previous studies have shown the importance of plant cover at the ground level for lizards (Carrascal et al., 1989; Martín and López, 1998). We also noted the distance to the nearest available refuge, and to the nearest open sunny spot where lizards could bask. Although this lizard species prefers rock crevices as refuges (Martín and Salvador, 1997b) it also uses low bushes as refuges (Amo, López and Martín, personal observation). Therefore, we considered both rock crevices and bushes as available refuges.

We calculated percent cover values for each habitat variable in the area surrounding each lizard (i.e., % contacts with each substratum and vegetation type), average distances to refuges and to sunny spots, and average height of potential refuges (for a similar sampling methodology see Martín and López, 1998, 2002). Given the large size of the area surveyed and the high lizard density, and because we avoided sampling the same area twice, the probability of repeated sampling of the same individual was very low. We therefore treated all measurements as independent. To estimate the availability of microhabitats we recorded the same variables as described above at 128 points randomly chosen through all the sampled areas. We classified the sampled areas as 'natural' or 'ski slopes'.

We used principal component analysis (PCA) to reduce all the habitat variables to a smaller number of independent components. We performed one PCA on the points describing available microhabitats and the lizard-observed microhabitat points. Original data were normalized by means of square root transformation. The initial factorial solutions were rotated by the Varimax procedure (Nie et al., 1975). We used general linear models (GLM) to compare PC scores describing microhabitat characteristics in relation to the level of deterioration of the habitat (natural vs. ski slopes), and the type of point (available vs. used by lizards) to determine whether lizards used available microhabitats in a non-random fashion. We included the interaction between level of deterioration and type of point in the model to test for differences in microhabitat selection of lizards in areas with different level of deterioration (Martín and López, 1998, 2002).

2.3. Movement patterns

We performed this study in the same area described above during May–June to determine whether male lizards changed their spontaneous movement patterns in relation to the level of deterioration of the habitat. We haphazardly walked both natural areas and ski slopes, between 1000 and 1600 h GMT. When a lizard was sighted, we started focal observations using binoculars and at a distance of 7–10 m to avoid disturbing the lizard. We chose adult males ($n = 45$) of similar body size in both areas to avoid the potential effect of lizards' size on locomotor patterns. We recorded with a digital chronometer for approximately 10 min the time spent in movement, the

distance moved, and the duration of the observation. Since not all observations could have the same exact duration because some lizards were lost or unintentionally disturbed, we calculated the time in movement and the distance moved in relation to the total duration of the observation. We calculated average 'burst speed' by dividing the distance moved by the time spent in movement. Since temperature may affect movement patterns (e.g., Zhang and Ji, 2004), and because it was difficult to measure body temperature of lizards immediately after the trial, we measured air temperature with a digital thermometer to the nearest 0.1 °C which can give an indication of body temperature in this species (Martín and Salvador, 1993).

We used analyses of covariance (ANCOVA) to test for differences in time spent in movement, distance moved, or average burst speed (dependent variables) in relation to the level of deterioration of the area, with air temperature as a covariate.

2.4. Measurement of body condition and health state of lizards

We captured by noosing adult male lizards ($n = 86$) in natural areas and ski slopes, during the mating period (May–middle of June) and after the mating period has finished (middle of June–July) to examine their body condition and health state (parasite load and immune response). We took lizards to 'El Ventorrillo' Field Station, 5 km from the capture site, where lizards were individually housed in 60 × 40 cm PVC outdoor terraria. They were fed mealworm larvae (*Tenebrio molitor*) and water was provided *ad libitum*. All lizards were healthy and were returned to their exact capture sites 48 h after capturing. We weighed and measured (SVL) lizards. Parasites were quantified on blood smears taken from the postorbital sinus, as described in Amo et al. (2004, 2006). Number of intra-erythrocytic parasites (Haemogregarines, the only parasite found) was estimated at 1000× by counting the number of parasites per 2000 erythrocytes.

We measured cell-mediated immune (CMI) responsiveness of 32 male lizards in summer by using a delayed-type hypersensitivity test (Lochmiller et al., 1993; Merino et al., 1999; Svensson et al., 2001; Belliure et al., 2004; Amo et al., 2006). We injected the lizard's footpad of the right hind limb with 0.02 ml of phytohaemagglutinin solution (PHA-P, Sigma), and measured the swellings with a pressure sensitive spessimeter (to the nearest 0.01 mm) before and 24 h after the injection (Smits et al., 1999; Amo et al., 2006). Repeatability of this measure is high ($r > 0.95$, L. Amo, unpublished data).

We used ANCOVA to analyze differences in blood parasite load between seasons and levels of deterioration of the habitat, including the interaction between season and level of deterioration, and SVL as a covariate. We also used ANCOVA to analyze differences in body mass between seasons and levels of deterioration, including the interaction between season and level of deterioration, and SVL and blood parasite load as covariates. We corrected body mass by SVL of lizards, thus, we refer through the text indistinctly to body mass and body condition. Finally, we used ANCOVA to analyze the effect of level of deterioration on CMI of lizards, including SVL, body mass and blood parasite load as covariates.

2.5. Effects of fleeing at high speed on body condition

In July, we captured by noosing 29 adult male lizards in a nearby natural area to determine whether increasing the frequency of displacements at high speed to reach safe refuges influenced body condition, and health state (parasite load and immune response) of lizards. Lizards were taken to 'El Ventorrillo' Field Station and maintained in the same initial conditions than described above. All lizards were measured, and we extracted a drop of blood for parasite measurements (see above). These measures were taken again immediately after the experiment finished. At the end of the experiment we also performed the PHA test to assess CMI (see above). To avoid changes in body condition and parasite load of lizards due to captivity *per se*, they were held in captivity only one week before testing to allow acclimation to laboratory conditions. Lizards were healthy and were released at the end of the experiment at the exact place of capture. The experiments were performed under license from the Consejería del Medio Ambiente de la Comunidad de Madrid (Spain).

Terraria were placed in an open sunny location while shade was provided by one of the terrarium walls and the refuge (flat stones of similar size and shape). Thus, we allowed lizards to thermoregulate and attain their preferred body temperatures for at least 2 h before and during the trials (Martín and Salvador, 1993). Lizards were assigned to one of three treatments. In the 'control' treatment lizards were individually housed in outdoor terraria with a refuge, and they were not disturbed during the course of the experiment. In the two experimental treatments, lizards were submitted to simulated repeated persistent attacks of 15 s of duration. We performed an attack every 10 min each day from 1000 to 1400 h GMT, when lizards were fully active, across 8 days. The experimenter simulated a predatory attack by rapidly approaching the terraria and tapping lizards close to the tail with a brush to stimulate them to perform a fleeing response. With this procedure we simulated an attack from an avian predator coming from above the lizard. The same person performed all predatory attacks in a similar way. In the 'refuge' treatment lizards had a refuge in their terraria in which they could hide during the attacks. In the 'fleeing' treatment the experimenter removed the refuge just before the daily session of attacks. Thus, because lizards could not hide, they had to run all the time during the attacks. The refuge was replaced at 1600 h GMT, after the session of attacks finished. Terraria were placed separately from each other such that our approaches to a terrarium did not influence lizards in other terraria.

We used repeated-measures ANOVA to analyze changes in body mass or intensity of blood parasites between the beginning and the end of the experiment (within subject factor) and between treatments (between subject factor). We included the interaction to analyze whether changes in body mass or parasite load across time varied between treatments. We corrected body mass by SVL of lizards, thus, we refer through the text indistinctly to body mass and body condition. We used ANCOVA to analyze differences in CMI of lizards at the end of the experiment (dependent variable) between treatments, and taking into account final body mass, and final blood parasite load as covariates.

Immediately after the experiment finished we measured sprint speed of lizards to examine whether changes in body condition, resulting from the different experimental treatments, affected escape performance of lizards. Lizards were individually tested in a linear terrarium which length approximates to that of an escape attempt under natural conditions (80 × 30 cm) (Carrascal et al., 1992; López and Martín, 2002) with a carpeted floor, which provided excellent traction. Individuals were allowed to bask for at least 2 h before trials. Lizards were induced to flee at high speed by tapping them close to the tail with a brush (López and Martín, 2002). The escape sequences were performed during 1 min to avoid differences in speed if lizards became fatigued. Lizards passed all the trials without apparent signs of stress. Experiments were recorded on videotape using a video-camera (Hi-8 format, 25 frames/s) aligned perpendicularly over the centre of the arena. From each individual, we selected two escape sequences. We analyzed the sequences frame-by-frame to determine sprint speed of lizards. Measurements were based on calibrated distances measured (to the nearest 1 mm) from the video monitor using the tip of the snout as a position reference (Martín and Avery, 1998). For each sequence we measured the distance between the initial position (lizard paused) of the lizard's snout mark and the final position in the first pause after fleeing (escape distance), and the time interval between the initial and final position (escape duration). From these data, we calculated the average 'escape speed' (distance moved divided by time taken; Martín and Avery, 1998). We also recorded the 'maximal speed' within each sequence (the greatest speed recorded in a frame, 40 ms, during the escape response). For each individual, an average value was determined from the two sequences that were analyzed. We used ANCOVAs to analyze differences in escape or maximal speed (dependent variables) between treatments, with final body mass of lizards as a covariate.

Table 1 – Principal components analysis for available and lizard microhabitat data in areas with natural vegetation and areas with habitat deteriorated by ski infrastructures

| | PC-1 | PC-2 | PC-3 |
|----------------------------------|--------------|--------------|-------------|
| <i>Substrate</i> | | | |
| Rocks | 0.47 | 0.79 | -0.27 |
| Bare soil | 0.23 | -0.88 | -0.22 |
| Grass | 0.05 | -0.05 | 0.83 |
| Litter | -0.82 | 0.02 | 0.36 |
| <i>Vegetation</i> | | | |
| Shrub cover | -0.89 | 0.16 | -0.15 |
| Shrub minimal height | -0.54 | 0.20 | 0.11 |
| Tree cover | -0.06 | -0.05 | 0.79 |
| Distance to refuge | 0.37 | -0.77 | 0.17 |
| Distance to open and sunny spots | -0.76 | 0.003 | -0.11 |
| Eigenvalue | 2.94 | 2.10 | 1.41 |
| % Var. | 32.71 | 23.36 | 15.70 |

Emboldened values indicated correlations of variables with the principal components greater than 0.70.

3. Results

3.1. Microhabitat selection by lizards

The PCA for microhabitats available and those used by lizards produced three components that together accounted for the 72% of the variance (Table 1). The first PC (PC-1) was negatively correlated with substrates of leaf litter, with cover of shrubs, and with distance to a sunny open area. The second PC (PC-2) was positively correlated with cover of rocky outcrops, and negatively correlated with substrates of bare soil and distance to refuges. The third PC (PC-3) was positively correlated with substrates of grass and tree canopy.

There were significant differences in relation to all PCs between levels of deterioration (natural areas vs. ski slopes) (GLM, Wilks $\chi^2 = 0.87$, $F_{3,225} = 11.60$, $p < 0.001$) and between types of microhabitat points (available vs. used by lizards) (Wilks $\chi^2 = 0.54$, $F_{3,225} = 62.62$, $p < 0.001$). The interaction between level

of deterioration and type of point was significant (Wilks $\chi^2 = 0.86$, $F_{3,225} = 12.00$, $p < 0.001$; Fig. 1). The general model showed significant overall differences for all PCs (PC-1: $R^2 = 0.20$, $F_{3,227} = 18.44$, $p < 0.001$; PC-2: $R^2 = 0.37$, $F_{3,227} = 44.99$, $p < 0.001$; PC-3: $R^2 = 0.11$, $F_{3,227} = 10.48$, $p = 0.001$). There were significant differences between natural areas and ski slopes in PC-1 and PC-2 scores (Tukey's tests, $p < 0.02$ in both cases), but not in PC-3 ($p = 0.17$). Thus, in ski slopes, there was a lower cover of shrubs and of substrates with leaf litter or rocks, and higher cover of bare soil substrates. Also in ski slopes points were closer to open areas and farther from refuges than in natural areas. Regardless of these differences in availability, lizards selected similar microhabitats in both areas, i.e., there were not significant differences between areas in the PC scores of microhabitat used by lizards ($p > 0.87$ in all cases). Thus, in both areas lizards selected microhabitats with low cover of trees and shrubs, with substrates of rocks rather than bare soil, grass or leaf litter, and close to sunny areas and to refuges.

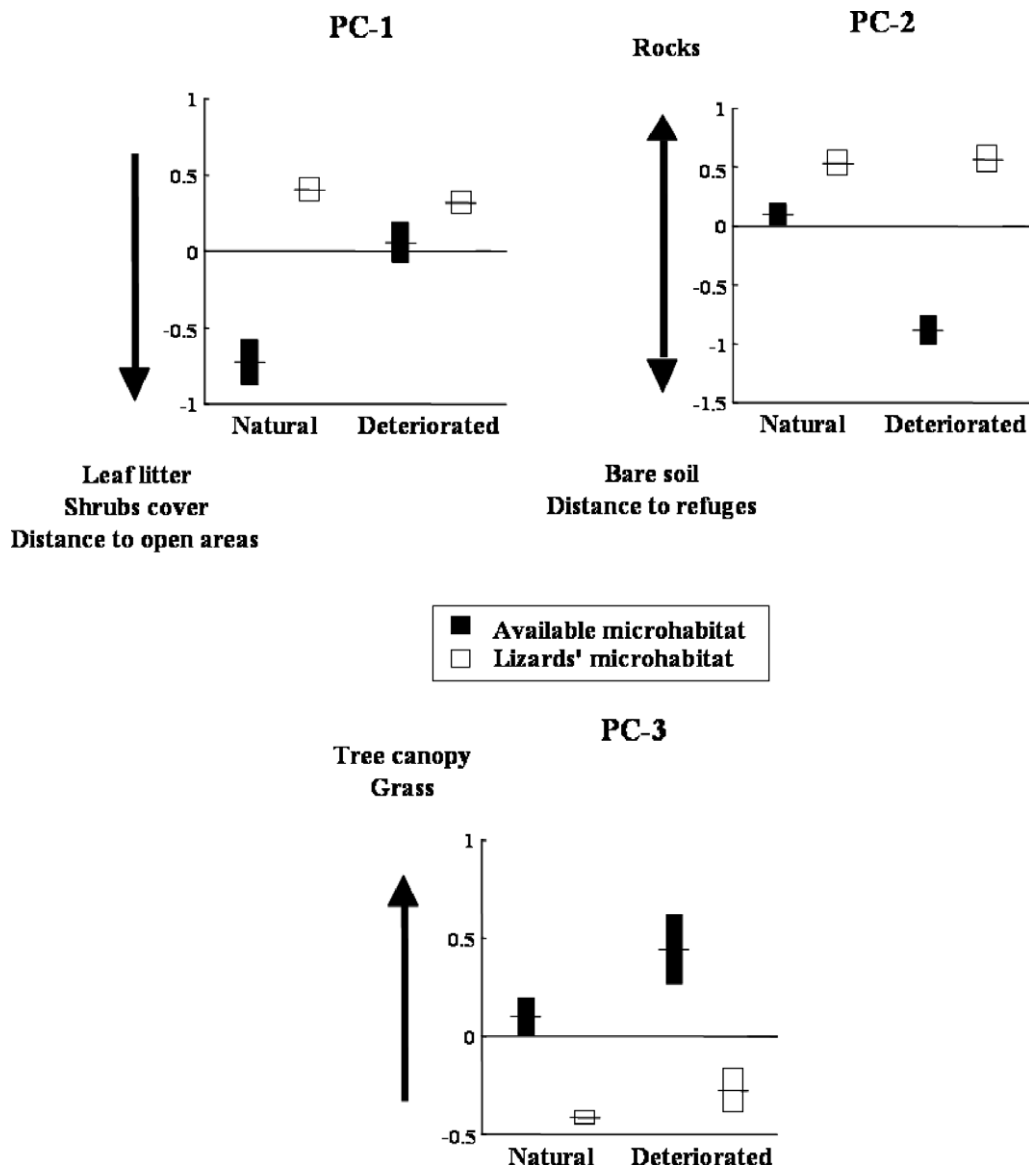


Fig. 1 – Means (\pm SE) PC scores for microhabitat available (black boxes) and microhabitat used by adult male *Iberolacerta cyreni* lizards (open boxes) in natural areas and areas deteriorated by ski infrastructures.

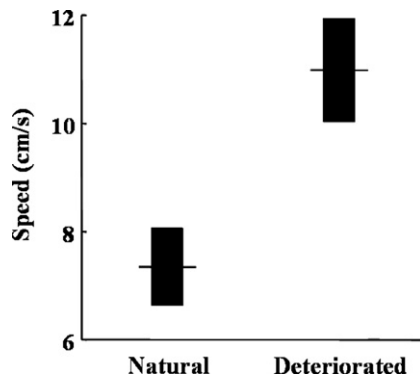


Fig. 2 – Mean (\pm SE) average burst speed (cm/s) of adult male *Iberolacerta cyreni* lizards while moving undisturbed in natural areas and in areas deteriorated by ski infrastructures.

3.2. Movement patterns

In relation to time spent in movement, the ANCOVA model was not significant ($R^2 = 0.11$, $F_{2,43} = 2.77$, $p = 0.07$). There were no significant differences between levels of deterioration (natural areas vs. ski slopes) (mean \pm SE, natural: $31 \pm 4\%$ time in movement, deteriorated: $30 \pm 3\%$; $F_{1,43} = 0.04$, $p = 0.85$), but lizards tended to decrease the time spent in movement when air temperature was higher ($F_{1,43} = 5.33$, $p = 0.03$). Lizards tended to move greater distances (27% more) in ski slopes than in natural areas (1.9 ± 0.2 m/min vs. 1.5 ± 0.2 m/min) but differences were not significant (ANCOVA, model: $R^2 = 0.10$, $F_{2,43} = 2.45$, $p = 0.10$; distance moved: $F_{1,43} = 3.16$, $p = 0.08$; air temperature effect: $F_{1,43} = 3.07$, $p = 0.09$). However, lizards moved at greater speeds (57% faster) in ski slopes than in natural areas (ANCOVA, model: $R^2 = 0.18$, $F_{2,43} = 4.79$, $p = 0.01$; level of deterioration effect: $F_{1,43} = 9.40$, $p = 0.004$; air temperature effect: $F_{1,43} = 0.18$, $p = 0.67$) (Fig. 2).

3.3. Parasite load and body mass of lizards

Larger lizards showed greater blood parasite loads (ANCOVA, model: $R^2 = 0.08$, $F_{4,81} = 1.77$, $p = 0.14$; body size effect: $F_{1,84} = 4.79$, $p = 0.03$), but there were no significant differences between natural areas and ski slopes (mean \pm SE, natural: 0.85 ± 0.13 parasites/2000 erythrocytes, deteriorated: 0.76 ± 0.25 ; $F_{1,81} = 1.16$, $p = 0.28$) nor between seasons (spring: 0.85 ± 0.19 , summer: 0.75 ± 0.14 ; $F_{1,81} = 0.05$, $p = 0.83$). The interaction between season and level of deterioration was not significant ($F_{1,81} = 0.80$, $p = 0.37$).

Body mass of lizards (ANCOVA, model: $R^2 = 0.78$, $F_{4,81} = 70.39$, $p < 0.0001$) was positively correlated to SVL ($F_{1,81} = 251.42$, $p < 0.001$). There were no significant overall differences between natural areas and ski slopes (mean \pm SE, natural: 7.9 ± 0.1 g, deteriorated: 7.9 ± 0.2 g; $F_{1,81} = 0.96$, $p = 0.33$) nor between seasons (spring: 7.2 ± 0.1 g, summer: 6.8 ± 0.2 g; $F_{1,81} = 0.45$, $p = 0.50$), but the interaction was significant ($F_{1,81} = 5.42$, $p = 0.02$; Fig. 3). Thus, in natural areas, there were no significant differences in relative body mass between seasons (Tukey's test, $p > 0.99$), but in ski slopes lizards showed lower relative body mass in summer than in spring

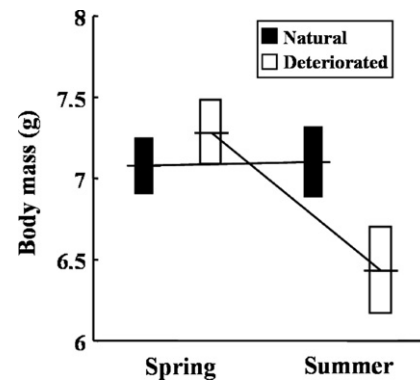


Fig. 3 – Mean (\pm SE) body mass (g) of adult male *Iberolacerta cyreni* lizards during the mating period (spring) and after the mating period had finished (summer) in natural areas (black bars) and areas deteriorated by ski infrastructures (open bars).

($p = 0.0002$). During spring, there were no significant differences in relative body mass between lizards of both areas ($p = 0.39$), whereas in summer, lizards inhabiting ski slopes had lower relative body mass than lizards in natural areas ($p < 0.001$). The effect of blood parasite load was not significant and it was removed from the final model.

There were no significant differences in the CMI of lizards during summer (ANCOVA, model: $R^2 = 0.24$, $F_{4,29} = 2.23$, $p = 0.09$) between natural areas and ski slopes (mean \pm SE, natural: 0.38 ± 0.05 mm, deteriorated: 0.60 ± 0.07 mm; $F_{1,29} = 3.48$, $p = 0.07$) nor in relation to the SVL ($F_{1,29} = 1.70$, $p = 0.20$), body mass ($F_{1,29} = 2.04$, $p = 0.16$) or blood parasite load ($F_{1,29} = 0.006$, $p = 0.94$).

3.4. Costs of fleeing to refuges on body condition

There were not overall significant differences between the initial and the final body mass of lizards (repeated-measures

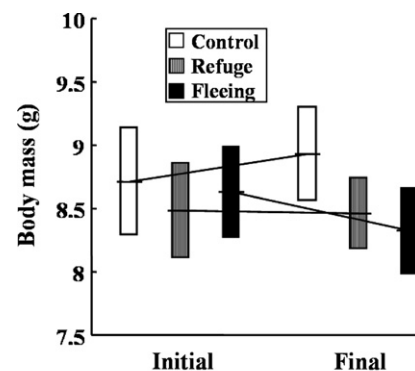


Fig. 4 – Changes in mean (\pm SE) body mass (g) of adult male *Iberolacerta cyreni* lizards after experiencing three treatments: (a) undisturbed lizards ('control', open bars); (b) lizards that could hide in refuges to avoid simulated attacks ('refuge', lined bars); (c) lizards that have to run continuously to avoid simulated attacks as there were not available refuges ('fleeing', black bars). Attacks were performed each 10 min during 4 h each day across 8 days.

ANOVA, $F_{1,27} = 0.22$, $p = 0.64$) nor between treatments ($F_{2,27} = 0.32$, $p = 0.73$). However, the interaction was significant ($F_{2,27} = 3.47$, $p = 0.046$; Fig. 4). Although post hoc comparisons did not show significant differences (Tukey's test, $p > 0.25$ in all cases), control lizards tended to increase their body mass, lizards that were attacked but could hide in a refuge tended to maintain their body mass, and lizards that were attacked but could not hide and, thus, were forced to flee, tended to decrease their body mass at the end of the experiment.

All lizards tended to decrease their blood parasite load in the course of experiment (mean \pm SE, 4.1 ± 0.9 vs. 3.3 ± 0.9 parasites/2000 erythrocytes; repeated-measures ANOVA, $F_{1,27} = 3.94$, $p = 0.06$), but there were no significant differences between treatments (control: 3.4 ± 1.6 , refuge: 6.0 ± 1.4 , fleeing: 1.8 ± 1.5 ; $F_{2,27} = 1.82$, $p = 0.18$), and the interaction was not significant ($F_{2,27} = 1.54$, $p = 0.23$).

The CMI of lizards (ANCOVA, $R^2 = 0.22$, $F_{4,25} = 1.81$, $p = 0.16$) did not differ between treatments (mean \pm SE, control: 0.66 ± 0.09 mm, refuge: 0.54 ± 0.06 , fleeing: 0.49 ± 0.05 ; $F_{2,25} = 1.18$, $p = 0.32$), and was not related to the final body mass ($F_{1,25} = 2.12$, $p = 0.16$) or the final blood parasite load ($F_{1,25} = 1.81$, $p = 0.19$).

Average escape speed of lizards was not affected by their body mass (ANCOVA, model: $R^2 = 0.12$, $F_{3,26} = 1.15$, $p = 0.35$; body mass effect: $F_{1,26} = 2.84$, $p = 0.10$), and there were not significant differences between treatments ($F_{2,26} = 0.42$, $p = 0.66$). Maximal speed was also not affected by body mass (ANCOVA, model: $R^2 = 0.02$, $F_{3,26} = 0.16$, $p = 0.92$; body mass effect: $F_{1,26} = 0.38$, $p = 0.54$), nor there were differences between treatments (mean \pm SE, control: 147 ± 11 cm/s, refuge: 145 ± 7 , fleeing: 149 ± 6 ; $F_{2,26} = 0.08$, $p = 0.92$). Thus, regardless of their body mass or treatment, lizards had similar escape and maximal speed when they were attacked and forced to run.

4. Discussion

To our knowledge, this is the first study showing a negative relationship between changes in movement patterns of male lizards, forced by the increased perceived predation risk in human-induced deteriorated habitats, and their body condition. Although there were differences in available microhabitats between natural areas and ski slopes, lizards selected similar microhabitats in both areas, such as rocky areas which offer basking sites (Hertz and Huey, 1981; Carrascal et al., 1992) as well as refuges (Martín and Salvador, 1997a,b). However, in ski slopes, the scarce cover of vegetation, and even of large rocks, implies a low availability of refuges. Animals often assess the level of predation risk accordingly to their distance to available refuges (Lima, 1993; Arenz and Leger, 2000). Thus, the greater distances to available refuges in ski slopes may increase the level of perceived predation risk for lizards. Lizards that moved through their territories may often need to move across risky areas far from refuges, where they would be more exposed to predators. Lizards seemed to perceive this increase in risk, and responded moving at faster average speed (i.e., 57% faster) in ski slopes, thus decreasing time exposed to potential predators.

In reptiles, the cost of locomotion is a significant component of the daily energy expenditure (Christian et al., 1997) and to perform frequently fleeing sequences at high speed is costly (Kramer and McLaughlin, 2001; Gleeson and Hancock, 2002). Our results showed that male lizards from ski slopes moved faster, suffered a loss of body mass in the course of season, probably due to energy expenditure associated with high speeds (Kramer and McLaughlin, 2001; Gleeson and Hancock, 2002). Differences in body mass between lizards inhabiting natural areas or ski slopes were significant in summer but not in spring because lizards have just emerged from refuges where they spent the winter period, and have similar body mass. However, in the course of season, lizards that inhabit ski slopes, and that have to move at higher speed suffer the accumulative physiological costs of this antipredatory behavior and suffer a progressive loss of mass. This result agrees with a previous study that showed that common wall lizards inhabiting tourist areas show lower body condition than lizards inhabiting areas without high frequency of visitants in summer but not in spring, due to physiological costs of frequent antipredatory behaviors (Amo et al., 2006).

Nevertheless, other factors rather, or in addition, than increasing speed may be also affecting body mass in the field. For example, the lower cover in ski slopes may make lizards more conspicuous and, thus, more frequently attacked than in natural areas. Therefore, in response to the direct attack of predators, lizards may also perform antipredatory behaviors (e.g., fleeing at high speed and increasing refuge use) that may also entail physiological costs (Martín and López, 1999a). Furthermore, habitat deterioration might also imply a decrease in food availability due to scarce vegetation and rocks of these areas. Another alternative explanation might be that lizards with a worse body condition per se were displaced from optimal habitats and were relegated to ski slopes areas across the season. However, our field observations suggest that lizards remained in the same area (natural area or ski slope) during all the annual activity period (Amo, López and Martín, personal observation).

In spite of all the potential causes affecting body condition, the results of the laboratory experiment seem to support that costs associated with continuous fleeing episodes alone can cause a decrease in body mass of lizards. Although differences did not reach significance level, lizards that were attacked and that could not hide and, thus, were forced to run, tended to decrease their body mass. Therefore, an increase in speed seems to be one of the causes of loss of body condition of lizards inhabiting in ski slopes, although other factors (as mentioned above) may also affect body condition of these lizards.

The loss of body mass of lizards inhabiting ski slopes during the breeding period may have important consequences because lizards in poor body condition may have a poorer immune response or be more susceptible to parasites (Cooper et al., 1985; Smallridge and Bull, 2000). However, our results did not show any effect of habitat deterioration on CMI response of lizards and haemogregarines' infection. However, our results should be interpreted with caution because CMI response, assessed by the PHA test is not well known in reptiles and our sample size was small.

Our results have applications for the design of conservation plans for this endangered lizard species. The deleterious effect of habitat deterioration in ski slopes on body condition of lizards might affect their fitness and affect populations. Therefore, environmental impact studies should be performed before opening new ski slopes (Stumpel et al., 1992; Martín and Salvador, 1997b), but taking into account not only the presence of lizards but also their body condition to ensure the correct management of this lizard species. Our results also highlight the importance of a high availability of refuges for the maintenance of lizards' populations, as has previously been found in other lizard species (Schlesinger and Shine, 1994; Hecnar and M'Closkey, 1998). Therefore, an effective way to decrease the deleterious effects of habitat loss, with the subsequent decrease in availability of refuges, may be the artificial restoration of some refuges to create safe corridors that connect good microhabitats for lizards. This strategy has previously proved to be successful in the restoration and maintenance of other endangered reptile species (Hecnar and M'Closkey, 1998; Webb and Shine, 2000; Souter et al., 2004).

In summary, habitat deterioration in ski slopes not only implied a loss of habitat for lizards, but led to a decrease in body condition, which could be a result of moving at faster speeds in ski slopes. However, more studies are needed to examine the effects of ski slopes on lizards' populations.

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