Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards

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Abstract: Deforestation may increase predation risk for prey because it may make prey more conspicuous and limit the number of refuges suitable to avoid predators. Therefore, prey may need to increase the magnitude of escape responses. However, excessive antipredatory effort might lead to a loss of body mass and a decrease in defense against parasites, with important consequences for short- and long-term fitness. We analyzed whether *Psammodromus algirus* (L., 1758) lizards that inhabit patches with different levels of deterioration of the vegetation within the same oak forest differed in relative abundance numbers, microhabitat use, antipredatory strategies, and health state. Results showed lizards selected similar microhabitats regardless of the level of deterioration of the vegetation and relative abundance of lizards was similar in both areas. However, habitat deterioration seemed to increase predation risk, at least for females, because they were detected at longer distances in deteriorated areas. Females seemed to adjust their antipredatory behavior accordingly to high risk of predation by increasing approach distances allowed to predators. The costs associated with frequent antipredatory displays might explain why females in deteriorated habitats had lower body condition and greater blood parasite loads than females in natural areas. This loss of body condition and increased parasitemia might have deleterious consequences for female fitness and therefore affect the maintenance of lizard populations in the long-term.

Résumé : La déforestation peut accroître le risque de prédation chez les proies parce qu'elle peut mettre les proies plus en évidence et réduire le nombre de refuges adéquats pour éviter les prédateurs. En conséquence, les proies peuvent devoir augmenter l'importance de leurs réactions de fuite. Cependant, un effort démesuré pour éviter la prédation pourrait entraîner une perte de masse corporelle et une réduction de la défense antiparasitaire, avec des conséquences importantes sur la fitness à court et à long termes. Nous avons examiné si des lézards *Psammodromus algirus* (L., 1758) qui vivent dans un même habitat de chênaie, mais dans des taches avec différents degrés de détérioration de la végétation, se distinguent par leur densité relative, leur utilisation des microhabitats, leurs stratégies antiprédatrices et leur état de santé. Les résultats montrent que les lézards choisissent des microhabitats semblables indépendamment du degré de dégradation de la végétation et que l'abondance relative des lézards est la même dans les deux régions. Cependant, la détérioration de l'habitat semble augmenter le risque de prédation, au moins chez les femelles, parce qu'elles peuvent être repérées à de plus grandes distances dans les zones dégradées. Les femelles semblent ajuster leur comportement antiprédateur en conséquence de ce risque élevé de prédation en augmentant les distances d'approche qu'elles tolèrent chez les prédateurs. Les coûts associés à ces manifestations antiprédatrices fréquentes peut peut-être expliquer pourquoi les femelles dans les habitats dégradés ont une condition corporelle inférieure et des charges parasitaires sanguines plus importantes que les femelles vivant dans les zones naturelles. Cette perte de condition corporelle et cette parasitémie accrue peuvent avoir des conséquences négatives sur la fitness des femelles et ainsi affecter le maintien à long terme des populations de lézards.

[Traduit par la Rédaction]

Introduction

Predation risk is a major force in the evolution of several morphological and behavioral characteristics of animals (Lima and Dill 1990; Lima 1998). One of the first antipredatory strategies of animals is the selection of safe habitats where they can attend their requirements such as thermoregulation (Martín and López 2002; Scheers and Van Damme 2002; Sabo 2003) or foraging (Díaz and Carrascal 1991; Yasué et al. 2003) while minimizing predation risk (Pitt 1999). Prey should select microhabitats where they can reduce their conspicuousness (Merilaita and Tullberg 2005) and find refuge in case of attack (Milne and Bull 2000; Webb and Shine 2000; Souter et al. 2003; Arthur et al. 2004). Thus, microhabitat characteristics may influence risk perceived by prey, as well as their antipredatory behavior, once a predator has launched an attack.

Theoretical models and empirical evidence suggest prey should wait to perform an escape response until costs of not responding are higher than costs of such a response (Ydenberg and Dill 1986; Dill and Houtman 1989; Bonenfant and Kramer 1996). Therefore, when prey perceive an increase in

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predation risk that is mediated by habitat characteristics (e.g., low availability of refuges), they may begin their escape earlier than if they perceive a lower risk of capture. Factors such as the extent of reliance on refuges to avoid predators and other components of risk such as the probability of detection by predators may strongly affect escape decisions (Lima and Dill 1990). Previous studies have shown that escape responses vary in relation to habitat characteristics (Bulova 1994; Martín and López 1995). Therefore, as microhabitat characteristics can affect predation risk and in turn influence the type of escape strategy, human-induced changes in habitat characteristics may affect predation risk and force changes in escape behavior of prey. For example, deterioration of natural vegetation could decrease the availability of cover that prey use as refuges. This would increase risk and could change prey behavior by increasing the magnitude of their escape response (e.g., greater approach distances) in deteriorated areas.

Antipredatory behaviors such as escape sequences or refuge use are costly, not only in terms of losing time to perform other activities such as foraging (Koivula et al. 1995; Dill and Fraser 1997; Martín et al. 2003*a*; Cooper and Pérez-Mellado 2004) or reproduction (Sih et al. 1990; Crowley et al. 1991; Martín et al. 2003*b*), but also in terms of body condition (Martín and López 1999*a*; Pérez-Tris et al. 2004; Amo et al. 2006). For example, lizards experimentally submitted to a high predation pressure have been shown to suffer a loss of body mass (Martín and López 1999*a*; Pérez-Tris et al. 2004; Amo et al. 2006, 2007*a*). Moreover, the loss of body condition could decrease the ability to invest in defense against parasites because nutritional status can influence the capacity for an immune response to infection (Cooper et al. 1985; Smallridge and Bull 2000; Amo et al. 2006). This may increase the negative effects of parasites on their host, with important negative consequences for short- and long-term fitness of individuals, and probably for maintenance of lizard populations. However, the effect of habitat deterioration on predation risk, escape behavior, body condition, and parasite load of lizards has scarcely been analyzed in natural conditions (but for experiments in seminatural enclosures see Oppliger et al. 1998).

The lizard *Psammodromus algirus* (L., 1758), a medium-sized lacertid lizard inhabiting Mediterranean forests of the Iberian Peninsula, usually escapes by fleeing into patches of tree leaf litter under cover of shrubs (Martín and López 1995, 2000). Today, this species is suffering a loss of habitat owing to human activities (Carretero et al. 2002). Montane forests of deciduous Pyrenean oaks (*Quercus pyrenaica* Willd.) of the Iberian Peninsula have been traditionally used for timber production and for extensive livestock grazing, and are being progressively deforested in some areas. Deforestation of oak forests not only occurs at the tree level but also at the shrub level, as shrubs are often eliminated to increase open areas for grazing. The loss of trees also entails a loss of oak-leaf litter on the ground that offers refuge to lizards. Therefore, deforestation may increase predation risk because it may make lizards more conspicuous and may also limit the number of refuges suitable to avoid predators (Martín and López 1998), thereby forcing lizards to increase the frequency of their escape responses. Thus, this species offers a good model to analyze how habitat deterioration and associated changes in vegetation structure affect antipredatory behavior, body condition, and health state of lizards.

In areas with different levels of vegetation deterioration (natural vs. deteriorated), we first examined (*i*) the relative abundances of lizards, (*ii*) the characteristics of microhabitats available and selected by lizards, and (*iii*) the conspicuousness of lizards in the microhabitats where they were initially located, which may reflect the probability of being detected by predators. Then we simulated predator attacks and analyzed (*iv*) the escape strategies and approach and flight distances of lizards. Finally, we captured lizards in different areas to measure their (*v*) body condition and (*vi*) parasite load (ectoparasites and blood parasites). Because microhabitats and refuges optimal for lizards may be limited and fragmented in deteriorated areas, we hypothesize lizards may be more conspicuous and vulnerable to predators and would need to run earlier, farther, and more frequently to avoid predators. Because of the energetic costs of antipredatory behaviors (Amo et al. 2007*a*), we hypothesize lizards inhabiting deteriorated areas will show worse body condition than lizards inhabiting natural areas. Furthermore, lizards with decreased body condition might not be able to allocate enough resources to parasite defense. Therefore, the deleterious effects of parasitemia should be more evident in deteriorated areas. We also expected to find differences in relative abundance of lizards between both areas, lizards being more abundant in natural areas than in deteriorated areas. Alternatively, lizards might adjust their antipredatory behavior according to local microhabitat characteristics. In that way, they could minimize the negative effects of antipredatory behavior but still maintain good body condition and low parasite load regardless of levels of habitat deterioration.

Material and methods

Study area and species

The study was performed during 3 consecutive years (2002–2004) in the Guadarrama Mountains (Madrid Province, central Spain) within two large oak forests that included several areas ($n = 8$) with two levels of deterioration of the vegetation (natural vs. deteriorated). Minimum size of areas was 10 ha. One of the forest areas was located near the village of Miraflores de la Sierra (hereinafter Miraflores) and the other one was near the village of Cercedilla (hereinafter Golondrina). In both forests, vegetation in natural areas consisted primarily of trees and small saplings of *Q. pyrenaica*, with scattered dispersed subarboreal perennial shrubs. Of these, *Cistus laurifolius* L. was dominant, whereas *Rosa pouzini* Tratt., *Rubus ulmifolius* Schott, *Genista florida* L., *Crataegus monogyna* von Jacquin, and *Cytisus scoparius* (L.) were less frequent. Oak-leaf litter is abundant on the ground year-round. In deforested areas, the absence of oak trees was the most obvious characteristic; the remaining vegetation consisted of patches of *C. laurifolius* shrubs interspersed with open grassy areas. Thus, we easily classified areas as natural or deteriorated according to this criterion. In both forest areas, we observed similar numbers and types of lizard predators such as feral cats, corvids (*Pica pica* (L., 1758), *Corvus corone* L., 1758, *Garrulus glandarius* (L., 1758)), shrikes

(*Lanius excubitor* L., 1758), raptors (*Buteo buteo* (L., 1758), *Milvus milvus* (L., 1758), *Circaetus gallicus* (J.F. Gmelin, 1788)), and owls (*Athene noctua* (Scopoli, 1769), *Otus scops* (L., 1758)).

Relative lizard abundance and microhabitat use by lizards

To evaluate relative lizard abundance and microhabitat characteristics of areas with different levels of deterioration, as well as microhabitat use by lizards in these areas, we marked 52 line transects that were each 200 m long. Transects were performed in natural and deteriorated areas. All transects were located at least 1–2 km from each other. During April and May 2002, coinciding with the mating season in this species, we walked each transect once in days with favorable climate conditions (warm sunny days) and between 0900 and 1300 GMT (when lizards are most active). We noted the number of lizards observed in each transect and in a 10 m wide belt, 5 m on each side of the survey line. When we detected an adult lizard, we marked the point where the lizard was first sighted to later record microhabitat characteristics. After finishing the transect, we returned to the marked points where we detected a lizard. For each one of these points, we used 10 cm graduated staffs to mark four 1 m lines, radiating towards the four cardinal directions. At 50 cm intervals, we recorded the type of substrate (grass, leaf litter, bare soil, or rocks) at a total of nine points, two in each direction and including the point of detection. We noted the presence of canopy tree cover above each sample point, as well as the cover and the height from the ground to the first contact between the staff and the leaves of subarboreal vegetation at each point. This latter variable provided an indication of the suitability of vegetation as a refuge for these lizards (Martín and López 1998). A low vegetation height provided a narrow refuge in which to hide. The total height of subarboreal vegetation was not considered significant because lizards move on the ground, below the vegetation. We also noted the distance to the nearest available refuge and to the nearest sunny spot where lizards could bask.

We calculated percent cover values for each habitat variable in the area surrounding each lizard (i.e., percent contacts with each substratum and vegetation type), mean distances to refuges and sunny spots, and mean height of potential refuges (for a similar sampling methodology see Martín and López 1998, 2002). 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 along each transect, we also recorded the same measures as above at three points per transect (at 70, 140, and 200 m along the progression line).

We used general linear models (GLM) to analyze differences in relative abundances of lizards to the level of habitat deterioration (natural vs. deteriorated). 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 (number of contacts) were normalized by means of a square-root transformation. The initial factorial solutions were rotated by the varimax procedure (Nie et al. 1975). We used GLM to analyze differences in the PC scores that reflect characteristics of microhabitat selected in relation to the level of deterioration of the vegetation (natural vs. deteriorated) and to determine whether male and female lizards used available microhabitats in a nonrandom fashion (available vs. males vs. females). We included in the model the interaction between level of deterioration and type of microhabitat to examine whether microhabitat use by lizards changed with deterioration.

Escape behavior

During April 2003 and 2004, we simulated predatory attacks to adult lizards in areas with different levels of deforestation within the Golondrina forest area. We recorded lizards' escape behavior and the microhabitat used before the attack. We walked randomly in days with favorable climate conditions and between 0900 and 1300 GTM until a lizard was detected. We noted the distance at which the lizard was detected by the observer (detection distance) and how the lizard was first detected (i.e., whether we saw it or we heard it). Noisy escape responses are especially notorious in this lizard species (Martín and López 2001). We then attempted to approach the lizard directly. The same person performed all approaches, walking at the same moderate speed (about 0.67 m/s) and wearing the same clothing to minimize effects on the lizards' risk perception (see Burger and Gochfeld 1993; Cooper 1997). We only performed one approach to the lizard. When the lizard began to escape we stopped. We noted the approach distance as the distance between the lizard and the observer when the lizard started its escape (a straight line measured to the nearest 0.1 m) and the flight distance as the distance the lizard ran during an episode of escape. We noted the escape strategy used, distinguishing between (*i*) lizards that fled to hide in the nearest available refuge, (*ii*) lizards that fled to hide in another refuge, and (*iii*) lizards that fled but stopped outside of refuges. We noted the distance from the initial location of the lizard to the nearest available refuge that to us was apparently suitable, as well as the distance to the refuge that was actually used. Once the escape episode had finished (when the lizard stopped), we used the same methodology as before to record the microhabitat characteristics at the point where the lizard was first sighted.

We used backward stepwise general regression models (GRM) to analyze the differences in detection, approach, or flight distances (dependent variables) in relation to the level of deterioration of the vegetation (explanatory variables), the PC scores describing microhabitat characteristics at the initial location of lizards, the distance to the nearest refuge, and the sex of lizards. We included in the initial model the interaction between level of deterioration and sex.

We used generalized nonlinear models (GLZ) to examine the effects of the level of deterioration, the PC scores defining microhabitat characteristics, and sex on the type of detection (dependent variable), with this latter variable following a binomial distribution (lizards seen or heard). We included the interaction between sex and level of deterioration in the model. We also used GLZ to assess the effect of deterioration level, microhabitat characteristics, distance to the nearest refuge, and sex on the type of escape strategy used by lizards (dependent variable). This variable was considered a multinomial ordinal variable (classifying lizards that hid in the nearest refuge, lizards that fled to another refuge, and lizards that fled but did not hide).

Measurement of body condition and parasite load of lizards

During April 2003 and 2004, we captured 48 adult lizards by noosing in areas with different levels of deterioration of the vegetation within the Golondrina forest. Immediately after capture, we weighed lizards, measured snout–vent lengths (SVL), and noted the number of ticks observed that were fixed on their body, usually in skin pockets (Salvador et al. 1996, 1999).

To assess blood parasite load, we made a smear on a microscope slide of blood taken from the postorbital sinus by using one 9 μL heparinized hematocrit tube. Blood smears were air-dried, fixed in absolute methanol for 10 min, and then stained in Giemsa diluted 1:9 with phosphate buffer (pH 7.2) for 40 min before the smears were examined for parasites. We scanned entirely at 200× magnification one longitudinal half of the smear, randomly chosen, to look for extra-erythrocytic protozoa (Merino and Potti 1995; Amo et al. 2004). The number of intra-erythrocytic parasites (i.e., haemogregarines, the only parasite found) was estimated, at 400× magnification, by counting the number of parasites per 2000 erythrocytes. Lizards were released at the exact location of capture. The experiments were performed under license from the Consejería del Medio Ambiente de la Comunidad de Madrid (Spain).

We used backward stepwise GLM to analyze differences in the intensity of tick infection in relation to sex and body size (SVL) of lizards and to the level of deterioration of the vegetation. The interactions between sex and level of deterioration, and between these two variables and SVL, were included in the initial model. We also used backward stepwise GLM to analyze differences in the intensity of haemogregarine infection in relation to the sex, SVL, tick load, and level of deterioration. We included in the initial model the interactions between sex and level of deterioration, as well as between each of these variables with SVL and tick load. Backward stepwise GLM were also used to analyze the effect of sex, size, intensity of infection by ticks and haemogregarines, and level of deterioration on body mass, including in the initial model the interactions between the categorical and the continuous variables.

Results

Relative lizard abundance and microhabitat use by lizards

There were no significant differences in relative lizard abundance between natural and deteriorated areas (number of lizards per transect — natural: 0.7 ± 0.3 (mean ± SE); deteriorated: 1.4 ± 0.3; GLM: R^2 = 0.04, $F_{[1,51]}$ = 2.22, p = 0.14). The PCA for microhabitats available and those used by lizards produced three components that together accounted for 59.9% of the variance (Table 1). The first PC (PC-1) was negatively correlated with the cover of shrubs and with the distance to a sunny area where lizards could bask, and it was positively correlated with distance to the nearest refuge and with the cover of grass substrates. The second PC (PC-2) was positively correlated with substrates of leaf litter and with the cover of trees. The third PC (PC-3) was positively correlated with the cover of rocky outcrops.

Table 1. Principal component (PC) analysis of data pertaining to available and used microhabitats by *Psammodromus algirus* in 52 transects made in natural and deteriorated areas within oak forests.

	PC-1	PC-2	PC-3
Substrate			
Rocks	0.01	–0.05	**0.95**
Bare soil	0.02	–0.45	0.07
Grass	**0.71**	–0.05	–0.37
Litter	–0.26	**0.73**	–0.28
Vegetation			
Shrub cover	**–0.90**	0.03	–0.13
Shrub minimal height	0.34	0.44	0.04
Tree cover	0.32	**0.75**	0.11
Distance to refuge	**0.75**	0.20	–0.09
Distance to sunny areas	**–0.67**	0.19	–0.17
Eigenvalue	2.62	1.58	1.19
Percent variance	29.10	17.54	13.26

Note: Values in boldface type indicated correlations of variables with principal components >0.60.

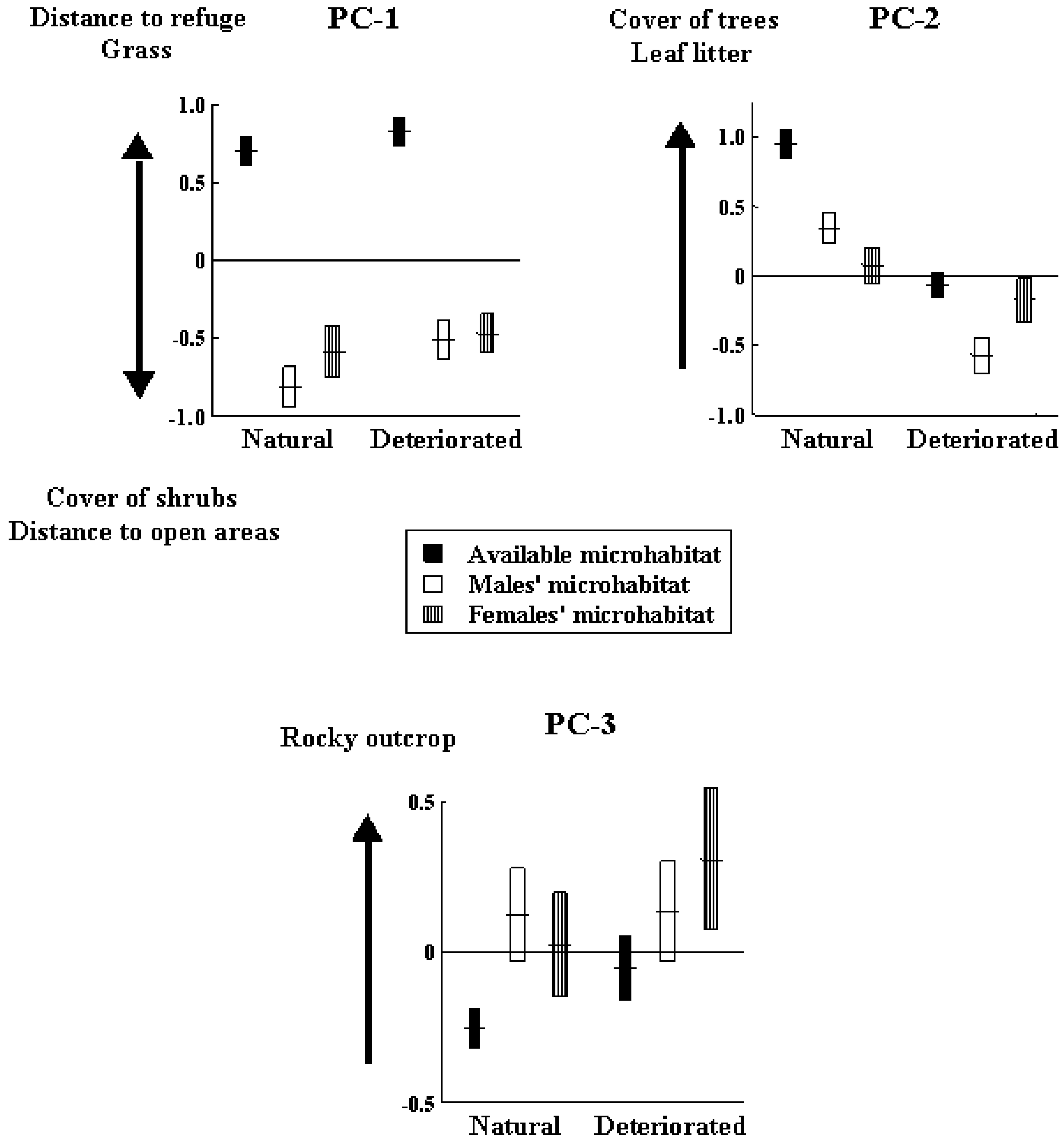
The model obtained by GLM analysis when analyzing PC scores in relation to type of point (available vs. selected by lizards) and level of deterioration (natural vs. deteriorated) showed significant differences with respect to PC-1 (R^2 = 0.43, $F_{[5,285]}$ = 42.46, p < 0.0001) and PC-2 (R^2 = 0.28, $F_{[5,285]}$ = 21.96, p < 0.0001), but not in relation to PC-3 (R^2 = 0.04, $F_{[5,285]}$ = 2.09, p = 0.07). Vegetation characteristics defined by the PC scores differed significantly between levels of deterioration of the vegetation (GLM: Wilks' χ^2 = 0.86, $F_{[3,283]}$ = 15.31, p < 0.0001; Fig. 1) and between available microhabitats and those selected by lizards (Wilks' χ^2 = 0.50, $F_{[6,566]}$ = 38.91, p < 0.0001). The interaction between these factors was not significant (Wilks' χ^2 = 0.97, $F_{[6,566]}$ = 1.68, p = 0.12); thus, lizards always selected similar microhabitats regardless of the level of deterioration of an area.

Microhabitats available in deteriorated areas had less tree cover and leaf litter than those available in natural areas (PC-2: Tukey's test, p < 0.0001) but did not differ with respect to other characteristics (p > 0.09 in all cases). There were no significant differences in the microhabitats selected by males and females (Tukey's test, p > 0.59 in all cases). There were significant differences in PC-1 and PC-2 between available microhabitats and those selected by male and female lizards (p < 0.001 in all cases). However, differences in PC-3 between available microhabitats and those selected by lizards were significant in females (p = 0.04) but not in males (p = 0.11). Thus, male and female lizards preferred substrates with low grass cover and leaf litter and tree canopy, high cover of shrubs, far from open areas, and close to refuges (PC-1 and PC-2); females also preferred rock substrates (PC-3).

Escape behavior

There were significant overall differences (GRM: R^2 = 0.15, $F_{[1,81]}$ = 7.27, p = 0.001) in the distance at which lizards

Fig. 1. PC scores (mean ± 1 SE) of microhabitats available (solid boxes) and used by male (open boxes) and female (hatched boxes) adult *Psammodromus algirus* in natural and deteriorated areas within oak forests.



were detected by the observer between levels of deterioration of the vegetation ($F_{[1,81]} = 8.93$, $p = 0.004$), but the interaction between level of deterioration and sex was also significant ($F_{[1,81]} = 4.26$, $p = 0.04$; Fig. 2). Thus, females were detected at longer distances in deteriorated areas than in natural areas (Tukey's test, $p = 0.005$), but males were detected at similar distances in both areas ($p = 0.74$). Microhabitat characteristics at the initial location did not significantly influence detection distances and were removed from the final model.

The type of detection differed in relation to microhabitat characteristics. Thus, when the percentage of rocky outcrop increased, lizards were more often detected by sight than sound (PC-3 — GLZ: Wald's $\chi^2_{[1]} = 9.14$, $p = 0.002$), whereas there were no significant differences when other microhabitats changed (PC-1 and PC-2: $p > 0.23$ in both cases). There were no significant differences in these observations between levels of deterioration ($p > 0.23$) or between sexes ($p > 0.99$); the interaction between sex and level of deterioration was not significant ($p > 0.99$).

Approach distances (i.e., the distance between the lizard and the observer when the lizard began to escape) (GRM: $R^2 = 0.29$, $F_{[4,78]} = 7.89$, $p < 0.0001$) differed between levels of deterioration ($F_{[1,78]} = 12.47$, $p = 0.0007$), showing differ-

Fig. 2. (*a*) Detection and (*b*) approach distances (cm; mean ± 1 SE) of male (black boxes) and female (open boxes) adult *P. algirus* in natural and deteriorated areas within oak forests.

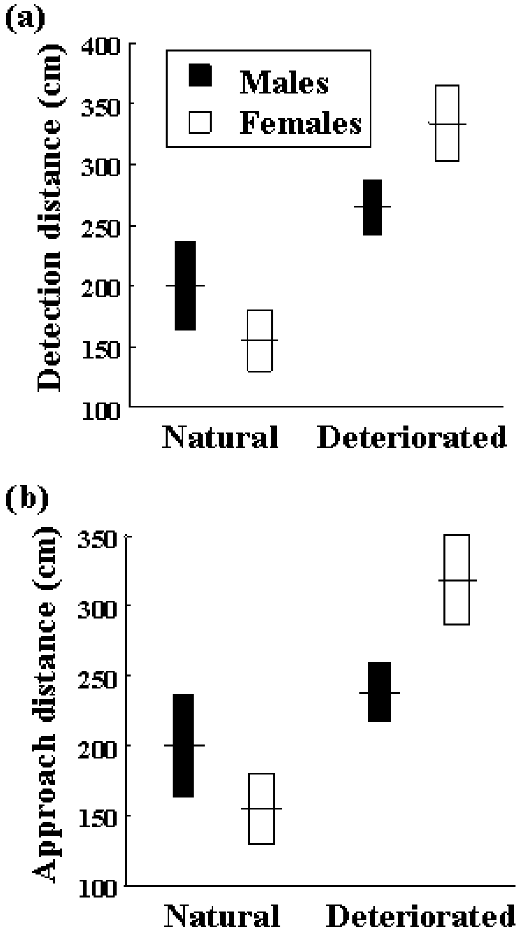
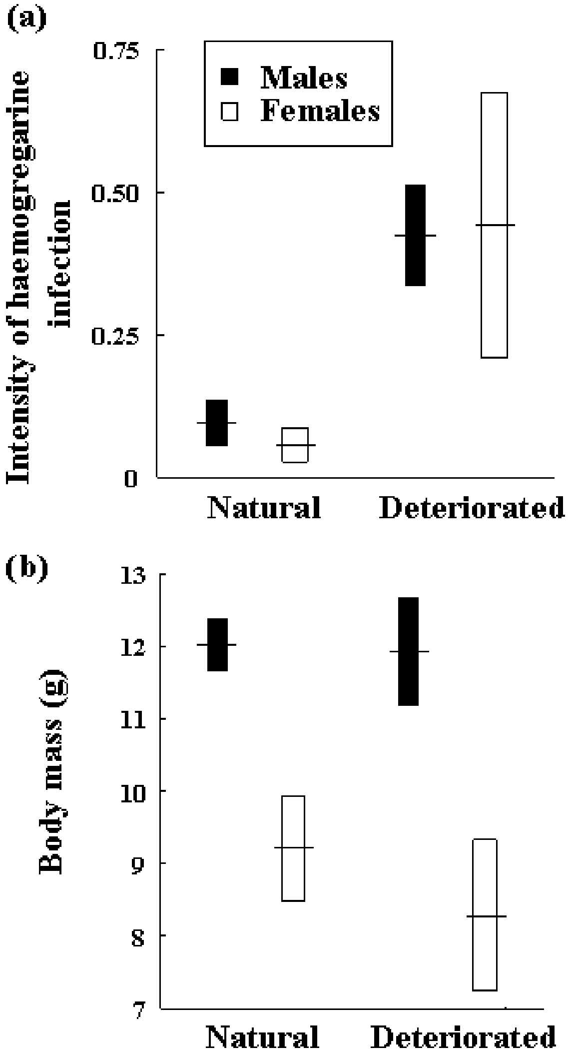


Fig. 3. (*a*) Infection intensity (mean ± 1 SE) of haemogregarines and (*b*) body mass (mean ± 1 SE) of male (black boxes) and female (open boxes) adult *P. algirus* in natural and deteriorated areas within oak forests.



ent antipredatory responses. The interaction between sex and level of deterioration was also significant ($F_{[1,78]} = 4.64$, $p = 0.03$; Fig. 2). Thus, approach distances of females were longer in deteriorated areas (Tukey's test, $p = 0.005$), whereas there were no significant differences in males ($p = 0.91$). Microhabitat characteristics also affected approach distances of lizards, which were longer when the cover of trees was greater and when substrates had more leaf litter (PC-2: $F_{[1,78]} = 9.35$, $p = 0.003$), and when there was a low cover of rocky outcrops (PC-3: $F_{[1,78]} = 7.95$, $p = 0.006$). Other variables did not significantly affect approach distances and were removed from the final model.

The escape strategy of lizards was related to the distance to the nearest refuge (Wald's $\chi^2_{[1]} = 5.60$, $p = 0.02$). When lizards were far from refuges they escaped by fleeing without using refuges, whereas when the nearest refuge was closer lizards escaped by hiding in this or another refuge. There were no significant differences in relation to the level of deterioration, sex, or microhabitat characteristics defined by the PC scores ($p > 0.11$ in all cases), and the interaction between sex and level of deterioration was not significant ($p = 0.29$). Flight distances (i.e., distance that a lizard moved during an escape episode) were positively correlated to the distance to the nearest refuge (GRM: $R^2 = 0.30$, $F_{[1,82]} = 35.15$, $p < 0.0001$), but they were not dependent on microhabitat characteristics, level of deterioration, or sex.

Parasite load and body condition of lizards

Males showed significantly higher intensities of infection by ticks than did females (GLM: $R^2 = 0.46$; model: $F_{[2,44]} = 19.05$, $p < 0.0001$; sex: $F_{[1,44]} = 19.30$, $p < 0.0001$), and lizards of similar body size showed significantly higher tick loads in natural than in deteriorated habitats (size × deterioration: $F_{[1,44]} = 10.55$, $p = 0.002$). Other variables and interactions were not significant and were removed from the final model. In contrast, the intensity of infection by haemogregarines in blood was significantly higher in deteriorated areas (GLM: $R^2 = 0.27$, $F_{[1,45]} = 16.28$, $p = 0.0002$; Fig. 3*a*). Other variables and interactions were not significant and were removed from the final model.

Body mass of lizards (GLM: $R^2 = 0.93$; model: $F_{[8,38]} = 61.11$, $p < 0.0001$) covaried with SVL ($F_{[1,38]} = 287.53$, $p < 0.0001$). Males were heavier than females ($F_{[1,38]} = 4.66$, $p = 0.04$), and males were heavier than females of equivalent

SVL (sex × SVL: $F_{[1,38]} = 7.60$, $p = 0.009$). Females were heavier in relation to SVL in natural habitats, whereas males were not significantly different in natural and deteriorated areas (sex × deterioration: $F_{[1,38]} = 6.32$, $p = 0.02$; Fig. 3*b*). Also, in deteriorated areas, there was a negative relationship between body mass and infection intensity of haemogregarines, whereas in natural areas there was no such relationship (blood parasites × deterioration: $F_{[1,38]} = 8.27$, $p = 0.007$). However, this effect of blood parasites on body mass was noted only in females (sex × blood parasites: $F_{[1,38]} = 8.91$, $p = 0.005$). The other variables and interactions were not significant and were removed from the final model.

Discussion

This study shows a relationship between levels of human-induced habitat deterioration and antipredatory behavior, parasite load, and body condition of lizards under natural conditions. In relation to habitat selection, our results show that lizards do not use habitat at random, as has previously been shown in this and other lacertid species (e.g., Castilla and Bauwens 1992; Martín and López 2002; Díaz et al. 2005). Although there were differences in microhabitat characteristics between natural and deteriorated areas, lizards selected similar places in both types of areas. Microhabitats preferred by lizards were present in both areas, which may explain why we did not find differences in relative lizard abundance between natural and deteriorated areas.

Males and females selected similar microhabitats, but there were sexual differences in exposure of lizards to predation between natural and deteriorated areas. The distance at which females were detected was higher in deteriorated areas, as has been previously observed in the common chameleon (Cuadrado et al. 2001). This may increase predation risk for females. However, females in deteriorated habitats seemed to compensate for the higher detectability by showing greater approach distances when attacked. Thus, females seemed able to assess their higher conspicuousness in deteriorated areas and fled earlier, in accordance with theoretical models of escape behavior (Ydenberg and Dill 1986) and previous results with this (Martín and López 1995, 1999*b*, 2000) and other lizard species (Cooper 1998, 2003). Furthermore, males with similar conspicuousness in natural and deteriorated areas exhibited similar approach distances in both areas. The similar detection distances of males between natural and deteriorated habitats might be explained because males have higher movement rates during the mating period, searching for females or patrolling their territory to defend them from rival males (Salvador et al. 1995, 1996), which makes them conspicuous. Furthermore, the bright nuptial coloration of males (see Díaz 1993; Salvador et al. 1995; Martín and López 1999*b*) could make them equally conspicuous in both areas.

Distance to available refuges might be expected to influence approach distances (Dill 1990; Bonenfant and Kramer 1996), because prey that are farther from a refuge may perceive a higher risk. However, our results did not show any relationship between approach distance and distance to the nearest refuge in contrast to previous results with this species in natural areas (Martín and López 2000). Thus, it seems that increased probability of detection by predators owing to the deterioration of the vegetation affected escape decisions more strongly than distances to refuges. Distance to the nearest refuge still affected the type of escape strategy and flight distances. When lizards were far from refuges, they escaped by fleeing without using refuges and had longer flight distances; however, when refuges were closer, lizards escaped by hiding in refuges.

The energetic costs of antipredatory behaviors may explain why females inhabiting deteriorated areas, where they exhibited greater antipredatory behaviors (i.e., greater approach distances), had lower body mass than females inhabiting natural areas. Loss of body condition under high risk of predation has been observed previously in this species under laboratory conditions (Pérez-Tris et al. 2004). Furthermore, in other lizard species, antipredatory behavior has been shown to entail a loss of body condition (Martín and López 1999*a*; Amo et al. 2006, 2007*a*, 2007*b*). Previous evidence also showed that habitat deterioration influences lizard antipredatory behavior and this change in antipredatory behavior influences body condition (Amo et al. 2007*a*).

The loss of body condition may cause a decrease in the allocation of resources to the immune function, and therefore a decrease in parasite defense (Cooper et al. 1985; Smallridge and Bull 2000). Our results show that intensity of infection by blood parasites (i.e., haemogregarines) was higher in deteriorated than in natural areas, despite lizards inhabiting natural areas supporting higher levels of ticks, the haemogregarine vector. Our results also show a negative relationship between the intensity of haemogregarine infection and the body condition in females in deteriorated habitats. This pattern supports previous results from seminatural experimental enclosures where common lizards (*Lacerta vivipara* Jacquin, 1787) showed higher levels of parasitemia in poor-quality habitats (Oppliger et al. 1998). Our results also show tick load was higher in natural than in deteriorated areas. Low availability of litter substrates in deteriorated areas may explain the lower tick infection levels (Chilton and Bull 1993). Hence, habitat degradation may influence the prevalence and intensity of parasitic arthropods through changes in microhabitat and microclimatic conditions, as has been previously observed in birds (Merino and Potti 1996). However, despite this high intensity of ectoparasite infection, we did not find a negative effect of tick load on body condition of lizards as previously found in other lizard species (Olsson et al. 2000). Our results showed males supported a higher intensity of tick infection than females, possibly because their higher movement rate makes them more susceptible to encounter ticks and (or) because of the immunosuppresor effects of testosterone (Salvador et al. 1996; Olsson et al. 2000; Klukowski and Nelson 2001).

In summary, this study shows an effect of habitat deterioration on antipredatory behavior, body condition, and parasite load of lizards. Oak forest deterioration leads to an increase in risk of predation, at least for females. Females seemed to adjust their antipredatory behavior according to increased predation risk in areas with deteriorated vegetation. Females inhabiting deteriorated areas also exhibit a lower body condition and greater blood parasite load. Costs of antipredatory behavior may explain this loss of body condition and health state. The poor body condition of female lizards in deteriorated habitats may have effects on their fitness, which in the long term may endanger *P. algirus* populations inhabiting these areas. Therefore, although there were no differences in relative lizard abundance, variables other than abundance should be considered when analyzing the effects of habitat modification on lizard populations. Therefore, much more research effort is needed to examine the effects of habitat deterioration on behavior, body condition, and survival of lizards.

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