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Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape?

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Predation risk may compromise the ability of animals to acquire and maintain body reserves by hindering foraging efficiency and increasing physiological stress. Locomotor performance may depend on body mass, so losing mass under predation risk could be an adaptive response of prey to improve escape ability. We studied individual variation in antipredatory behaviour, feeding rate, body mass and escape performance in the lacertid lizard *Psammodromus algirus*. Individuals were experimentally exposed to different levels of food availability (limited or abundant) and predation risk, represented by reduced refuge availability and simulated predator attacks. Predation risk induced lizards to reduce conspicuousness behaviourally and to avoid feeding in the presence of predators. If food was abundant, alarmed lizards reduced feeding rate, losing mass. Lizards supplied with limited food fed at near-maximum rates independently of predation risk but lost more mass when alarmed; thus, mass losses experienced under predation risk were higher than those expected from feeding interruption alone. Although body mass of lizards varied between treatments, no component of escape performance measured during predator attacks (endurance, speed, escape strategy) was affected by treatments or by variations in body mass. Thus, the body mass changes were consistent with a trade-off between gaining resources and avoiding predators, mediated by hampered foraging efficiency and physiological stress. However, improved escape efficiency is not required to explain mass reduction upon predator encounters beyond that expected from feeding interruption or predation-related stress. Therefore, the idea that animals may regulate body reserves in relation to performance demands should be reconsidered.

Predators may impair the ability of their prey to acquire and maintain energy resources (Lima & Dill 1990), and this has negative effects on life history traits such as growth (reviewed in Downes 2001) or adult body condition (Lilliendahl 1997; Carrascal & Polo 1999; Martín & López 1999; van der Veen 1999; Rands & Cuthill 2001). There is general agreement that predation risk may compromise energy management and increase starvation risk, and current research is devoted principally to unravelling the causes and consequences of losing mass under the risk of predation (reviewed in van der Veen & Sivars 2000; Rands & Cuthill 2001). The loss of body mass under the risk of predation may have three, not mutually exclusive, proximate causes (e.g. Rands & Cuthill 2001). First, individuals may lose mass from a decrease in foraging efficiency imposed by the presence of predators, because antipredatory behaviours take time that could otherwise be used to search for food (Lima 1986; McNamara & Houston 1990; Houston et al. 1993). Second, the presence of the predator itself may cause stress-induced hormonal responses in its prey, resulting in increased energy expenditure (Assenmacher 1973; Axelrod & Reisine 1984; Wingfield et al. 1998). Third, individuals may decide to eat less, not because of interruption or stress, but to keep body mass optimal for predator avoidance, because locomotor performance and hence escape efficiency may improve with a reduced body mass (Witter & Cuthill 1993). This hypothesis predicts that individuals should manage their body reserves in relation to feeding prospects and the probability of predation encounters, modulating their locomotor performance according to what is known as an adaptive fit-for-escape (Metcalfe & Ure 1995; Carrascal & Polo 1999; van der Veen 1999; van der Veen & Sivars 2000).

There is strong empirical support for the idea that predation risk compromises energy management. Both

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correlative studies on natural populations (Gosler et al. 1995; Tellería et al. 2001) and experimental studies (Lilliendahl 1997; Carrascal & Polo 1999; Martín & López 1999; van der Venn & Sivars 2000; Rands & Cuthill 2001) have shown that body mass of individuals decreased under increased predation risk. There is also evidence that being fat impairs the ability to escape during predator attacks (e.g. Lind et al. 1999). However, it remains unclear whether body mass is strategically regulated in relation to predation risk. Experiments have focused on separating feeding interruption and predation risk per se as causes of mass loss (Carrascal & Polo 1999; van der Veen & Sivars 2000; Rands & Cuthill 2001). However, it is unknown whether body mass lost from increased predation risk affects escape performance during predator attacks (Veasey et al. 1998; Olsson et al. 2000; van der Veen & Lindström 2000). Thus, whether animals adaptively reduce body mass to improve escape performance according to the fit-for-escape hypothesis remains to be shown (van der Veen & Sivars 2000).

The causes and consequences of body mass variation are particularly well studied in birds (see references above). However, energetic costs of antipredatory behaviours have also been found in lizards, which lose mass when forced to use refuges more often, probably as a consequence of impaired foraging and thermoregulation (Martín & López 1999; Downes 2001). Although body mass is likely to have a much lower impact on terrestrial locomotion than on flight, the loss of mass observed in reptiles might also be adaptive under the risk of predation, as assumed for birds (Martín & López 1999), as long as the locomotor performance of lizards improves with reduced body mass. For instance, sprint speed is impaired in gravid or pregnant female lizards (reviewed in Olsson et al. 2000), and individuals are less mobile when carrying large prey in the stomach (Martín 1996). However, whether predator-induced stress contributes to mass loss in reptiles independently of feeding interruption, and whether this mass loss favours escape performance, remain open questions. To our knowledge, the possibility that reptiles manage adult body reserves in relation to a trade-off between gaining resources and avoiding predators has not been studied.

We studied behavioural decisions and energy regulation by lacertid lizards *Psammodromus algirus* (L.) under different levels of predation risk and food abundance, and the effects of these changes on the vulnerability of lizards to predator attacks. A trade-off between predation avoidance and reserve maintenance predicts that the energetic cost of antipredatory behaviours should increase with decreasing feeding prospects. If the probability of obtaining food is high, individuals should be less penalized by predator-induced body mass losses than if food becomes limiting, when energy storage may be essential to maintain good physical condition (for territorial defence, mate acquisition or reproductive investment) and eventually to avoid starvation (Lima 1986). We studied whether lizards modify overall activity, antipredatory behaviour or feeding rate in response to experimentally manipulated levels of predation risk and food abundance, in an attempt to identify causes of potential variation in body mass. We also analysed whether behavioural responses under increased predation risk and the changes in body mass related to these behaviours resulted in improved escape efficiency of lizards when pursued by a (human) predator.

METHODS

Capture and Husbandry of Lizards

The study was authorized by the Agencia de Medio Ambiente (Junta de Castilla y León), and was conducted indoors at the Faculty of Biology, Universidad Complutense de Madrid, between 8 August and 8 September 2001. We captured adult lizards by hand or by noose at a mixed archipelago of evergreen, *Quercus rotundifolia*, and deciduous, *Q. pyrenaica*, oak forests in Lerma, northern Spain. Lizards were captured 2 months before the experiment, that is, in early June, to be used in a study of breeding performance (unpublished data). Individuals of both sexes were brought to the laboratory within 2 days of capture.

The laboratory had natural daylight and ventilation coming from opened full-wall windows. Lizards were caged in terraria (40×60 cm and 30 cm high) with white opaque walls, covered by a green net (0.5-cm mesh), which prevented escape, let daylight enter the cages and provided a shrublike shelter. Terraria were filled with a layer of moistened earth, averaging 10 cm deep and covered with leaf litter. Heat was supplied by an incandescent lamp, which created a photothermal gradient (circa 25–50°C), allowing thermoregulation within the preferred temperature range for this species (Díaz 1997). Lamps were on during four daily periods separated by dark intervals (0700–0900 hours, 0930–1130 hours, 1230–1430 hours and 1500–1600 hours GMT), for a total of 7 h of daily heat supply. An earthenware tile (circa 10×15 cm) and thin fallen wood provided lizards with additional shade and shelter. Lizards were fed crickets, *Acheta domesticus*, mealworms, *Tenebrio mollitor*, and waxworms, *Galleria mellonella*, ad libitum, dusted with a commercial diet supplement (Reptivite, ZooMed, Inc., San Luis Obispo, U.S.A.) that was delivered according to the manufacturer's recommendations. All individuals had access to water ad libitum.

During the 2 months before the experiment, disturbance was kept at the minimum necessary for routine inspections of individuals. All lizards became almost immediately acclimated to captivity, showing normal basking and feeding behaviours. After egg laying (early June to mid-July), we chose 10 males and 10 females of similar body size (mean ± SE snout–vent length: males: 75.60 ± 1.37 mm; females: 75.97 ± 1.56 mm; $F_{1,18} = 0.03$, $P = 0.86$; body mass: males: 12.09 ± 0.66 g; females: 10.55 ± 0.66 g; $F_{1,18} = 2.74$, $P = 0.15$) and an intact or completely regenerated tail. These lizards were placed in individual cages (alternating males and females), where they spent 1 week under the same housing conditions to allow further acclimation. Once the experiment had finished, lizards had 1 week under standard housing conditions before being released at their sites of capture.

Experimental Design

Each individual underwent four treatments, coded 1 (low risk and limited food), 2 (high risk and limited food), 3 (low risk and abundant food) and 4 (high risk and abundant food), and applied in the sequence 1–2–3–4–1, thus changing predation risk level with each treatment. To prevent order effects from confounding our treatments, each lizard was randomly assigned to one of four groups ($N = 5$ individuals each), and each group started with a different treatment according to a balanced design. Each treatment lasted 7 days, and an additional day was used to measure body mass and fleeing performance. Individuals were never handled during the treatments. All treatments were applied in each individual's cage, thereby reducing uncontrolled environmental variation.

We manipulated predation risk by changing shelter availability in the cages and simulating predator attacks. Different predators probably elicit different responses from lizards, but there is a general lack of knowledge on the relative importance of different predators in determining antipredatory behaviour in this species (Martín & López 2000). Nevertheless, these lizards prefer areas with abundant leaf litter, which they use as a refuge when attacked by humans and presumably also when attacked by other predators such as birds and mammals (Martín & López 2000). A low availability of leaf litter also increases conspicuousness in this species, and hence its exposure to many predators (Martín & López 2000). Because predation encounters were simulated by human attacks, we manipulated the amount of leaf litter in the cages to increase the perception of a high predation risk through decreasing shelter availability (Martín & López 2000). In treatments with high predation risk, leaf litter was removed, so that shelter was restricted to the earthenware tile and the burrows that lizards could dig. Simulated predator attacks were carried out every day during the treatment. If lizards were active when sighted, they were chased in the cage by hand tapping for 15 s or until they escaped into a sheltered site, usually under the tile. This simulated a realistic attack, which alarmed lizards without impairing their body condition from exhaustion (15 s is close to the maximum time required to catch a lizard in the cage for routine inspections). No lizard was captured during the chases to prevent confounding predation risk and capture as causes of stress. The human predator wore neutral clothes and started from the same edge of the cage to avoid varying the perception of predation risk (Cooper 1997). Four attacks per day were conducted at standard times (30 min after the start of each heating period), resulting in an average $\pm$ SE of 15.6 ± 0.9 attacks per treatment, depending on the activity of each lizard (to mimic a realistic predator–prey interaction, inactive lizards were not chased). Although variable numbers of predation attacks might have affected the response of lizards to our treatments, we checked that this was not the case for the behavioural or physiological variables studied (for all effects, $F_{1,16} < 1.85$, $P > 0.195$).

Cages simulating low predation risk had the ground completely covered with leaf litter and dispersed fallen wood, representing a sheltered environment in which conspicuousness of active lizards was low (Martín & López 2000). In these treatments, we recorded the behaviour of lizards without chasing them, thus mimicking the failure of an approaching predator to detect them. We disturbed individuals treated with low predation risk only when providing food, so that lizards were disturbed more often during treatments with abundant food than during treatments with limiting food.

We manipulated food abundance to supply either limited or nonlimited but controlled food resources. To keep diet quality as constant as possible, lizards were fed only crickets dusted with diet supplement during treatments. Crickets were weighed at the time of supply (± 0.01 g). Based on observation of the amount of food consumed by lizards when fed ad libitum before the experiment, treatments involving limited food received an average $\pm$ SE of 0.53 ± 0.02 g of crickets, with a supply of one small cricket every second day. Treatments involving abundant food received 2.80 ± 0.05 g of crickets, with a daily supply of one large cricket. Food was always delivered at 0830 hours, 1 h after the first chase in high-predation-risk cages, to minimize the variation in lizards' behaviour that could be caused by alertness induced by a recent pursuit.

Activity, Feeding Rate and Antipredatory Behaviour

We recorded the behaviour of all lizards immediately before chasing those undergoing predation treatments. Lizards were considered to be inactive when they were completely out of sight, usually buried or beneath the tile. Active individuals were sometimes hidden, for example, partially concealed under the tile, in a burrow or beneath leaf litter or fallen wood. These individuals were always alert, so we interpreted their behaviour as antipredatory responses aimed at decreasing exposure, in contrast to other forms of activity increasing conspicuousness, such as basking or walking (Martín & López 1999, 2000). Activity and behaviour (exposed or hidden) were thus recorded four times per day. We used the total numbers of occasions on which lizards were active or exposed during the treatment as measures of activity and exposure, but the first 2 days of each treatment were excluded from analyses because they were considered as a period of acclimation to the new conditions.

We also studied the willingness of lizards to feed under predation risk during each treatment. When we supplied food, we recorded the response time of active lizards. Individuals that did not attack the cricket within 30 s of receiving it were considered to be reluctant to feed in the presence of a potential predator, that is, the observer. These individuals displayed obvious antipredatory behaviours, remaining vigilant after having detected the cricket (detection of the prey was proved by head movements). A time limit of 30 s was adequate to decide whether lizards were reluctant to feed, because individuals that attacked the cricket did so in an average $\pm$ SE time of 5.9 ± 1.4 s. Because of the small number of trials (two to five food deliveries depending on treatment), a quantitative assessment of feeding incentive was impossible. Hence, we

considered that lizards were motivated to feed under predation risk if they attacked the cricket within 30 s at least once during the treatment. Based on this consideration, our tests for behavioural changes between treatments should be regarded as conservative. We tested for changes in feeding motivation by performing two complementary tests: first, we considered the null hypothesis that, if there is no effect of treatment, we should expect 25% of individuals changing behaviour in either direction (from feeding to not feeding and vice versa) and 50% of them maintaining behaviour between treatments. Second, we considered only individuals that changed behaviour between treatments, with a 50% probability of change in either direction as the null hypothesis. Because of the small sample sizes available for these chi-square tests, we report exact P values.

Two individuals lost their tails by autotomy, one on the first test day (when changing from treatment 3 to 4) and the other on the second test day (from treatment 2 to 3). Tail autotomy affects antipredatory behaviour of lizards in that tailless individuals reduce home range size by remaining in relatively sheltered sites and deserting the most exposed areas of their territory (Salvador et al. 1995). This behavioural response is probably mediated by a strong effect of tail loss on escape ability, which motivates individuals to remain close to refuges (Martín & Avery 1998; Downes & Shine 2001). However, this response does not involve variation in behavioural parameters such as foraging tactics or feeding rates (Martín & Salvador 1997 and references therein), and tailless individuals seem neither more easily detected nor preferred by predators (Downes & Shine 2001). Therefore, we assumed that tail loss did not affect the behaviour of the two tailless lizards, particularly given the small dimensions of the cage compared to natural home ranges.

Body Mass and Escape Ability of Lizards

Lizards were weighed ($\pm$0.1 g) on the test day following each treatment at 0800 hours using a digital balance. At the same time, we removed all crickets remaining in the terrarium and weighed them to determine the amount of food consumed by lizards during the treatment. Given that remaining crickets should have lost mass, this estimate was conservative with respect to feeding interruption under predation risk, because it assumes that lizards consumed more food than they actually did. For the two tailless individuals, we weighed the tail immediately after autotomy and added its mass to the body mass, assuming that tail regeneration did not affect energy consumption causing a detectable decrease in body mass (Fox & McCoy 2000).

Escape performance was measured on a runtrack (240$\times$30$\times$40 cm) with white opaque walls that resembled cage conditions. The floor was made of cork, providing excellent traction, and it was marked with perpendicular bands every 30 cm, dividing the runtrack into six stretches (the 30-cm ends of the runtrack were not considered in the analyses). Runs were recorded at 25 frames/s using a JVC GR-AX200 video recorder fixed on a tripod 75 cm above and 50 cm off the edge of the cage, so that the whole runtrack (except the 30-cm end closest to the camera, not used in the analysis) could be viewed on a single image.

Lizards ran twice every test day, at 1000 hours and at 1530 hours. Behavioural decisions made by lizards under different situations might affect body temperature, and this could influence sprint performance (Bauwens et al. 1995). To control for this possible effect, we measured body temperature immediately before placing lizards on the runtrack, using a Miller & Weber quick-reading cloacal thermometer (0.1°C precision). Average $\pm$ SE body temperature was 33.57 $\pm$ 0.24°C, well within the thermal range preferred by this species (Bauwens et al. 1995; Díaz 1997). In addition, *P. algirus* has an optimal temperature for sprint speed at 34.35 $\pm$ 0.56°C, and it performs at 80% of its maximum capacity or better in the 10.76 $\pm$ 1.07°C interval centred around that temperature (Bauwens et al. 1995). Therefore, we assumed that the temperatures at which lizards were tested did not impair performance. Lizards were placed on one edge of the runtrack and were forced to run by hand tapping close to the tail, simulating predator attacks like the ones applied during the treatments of high predation risk. Individuals were chased up and down along the runtrack until they refused to run despite insistent tapping, when we considered them to be 'exhausted'.

For each running session, we recorded fleeing distance (the distance covered by lizards in sprints performed from one baseline of the runtrack), which measures how far away from an attacking predator the lizard can move in a single run (Martín & López 2000). Fleeing distances thus measured a maximum of 180 cm, because of the dimensions of the runtrack, but this is a long distance for a medium-sized lacertid and fleeing further may not be necessary for increasing escape probability (Martín & López 2000). Given that lizards could decide not to perform at their maximum capacity on the runtrack (which would bias average values), we considered both the average and maximum fleeing distances in our analyses. We also recorded the total number of sprints until exhaustion, the distance covered in each sprint and the total distance covered, as different components of running endurance. The snout of lizards was used as a reference for measuring these distances on the screen ($\pm$1 cm), once we confirmed that variation in recording angle caused by position of the video recorder did not affect our measurements. Finally, we measured sprint speed as a major component of locomotor performance (Bauwens et al. 1995). We counted the number of video frames from the start to the end of each run and converted them into time ($\pm$0.02 s), to compute speed in cm/s. For each sprint, we recorded both average speed and top speed, with top speed measured in the fastest 30-cm stretch. For distances, we considered both the mean and the maximum values of average and top speed as variables in our study.

Statistical Analyses

Because all treatments were applied to all individuals, we analysed the response of lizards using repeated

measures analysis of variance (ANOVA; residuals were normally distributed; StatSoft, Inc. 1999). One male lizard (starting on treatment 2) died the week after the experiment, probably of disease, because it fed normally but still lost condition. One female (starting on treatment 1) was reluctant to escape when chased, both in the cage and on the runtrack. These two individuals were excluded from the analyses, leading to a final sample size of 18 lizards. Given that sprint speed and escape tactics are strongly influenced by tail possession in this species (Martín & Avery 1998), the analysis of escape performance excluded three lizards that suffered autotomy: the two individuals that lost the tail during the treatments and another one that became tailless during the last test day, at the end of treatment 2.

Ethical Note

Capture methods, housing conditions and release procedures were appropriate for this species. We were careful to provide lizards with adequate housing conditions (including cage dimensions, daylight supply and diet diversity and supplement) as determined by our experience with this species in the laboratory. Insects fed to lizards were in good condition, having access to water and fresh food according to supplier.

We observed no adverse effect of either the experiment or the housing methods on lizards' health. Variation in mass between the most extreme treatments in our design averaged 5.3% (range 0–10%) of total body mass (see Results), which we assumed to be within the range of natural variation, although there is little published information about this topic. For example, an increased use of refuges triggered by experimentally increased predation risk in free-ranging *Podarcis muralis* caused a loss of around 8% of total body mass (Martín & López 1999).

All individuals were in good condition, both during the experiment and when released at the site of capture, with the exception of the individual that died after the experiment apparently from disease. For ethical reasons, lizards were not treated with antibiotics or other medication; hence, we could not prevent this source of mortality. Mortality rate in the laboratory was lower than 5%, which is much lower than the natural mortality rate (average annual mortality estimated from recaptures in the field: 47–65%; Díaz 1993).

RESULTS

Activity and Antipredatory Behaviour

Overall, lizards did not change activity in response to food abundance or predation risk, although they delayed the start of activity when they were alarmed, leading to a significant interaction between time of day (the most important determinant of activity) and predation risk (Table 1). Thus, all lizards showed reduced activity at the end of the day but, in the first two heating periods, lizards were less active when subject to higher predation risk, reaching similar levels of activity afterwards independently of the risk of predation (Fig. 1). However, increased predation risk led to an overall lower frequency of exposure in alarmed lizards (which were found basking or walking less often; Table 1). Exposure matched the pattern of overall activity when the risk was low, but it decreased under increased predation risk (Fig. 1).

Feeding Rate and Antipredatory Behaviour

The amount of food delivered to lizards did not change between treatments involving variation in predation risk (food abundance: $F_{1,17} = 3675.8$, $P < 0.0001$; predation risk: $F_{1,17} = 0.52$, $P = 0.482$; food × risk: $F_{1,17} = 0.13$, $P = 0.725$). Lizards in the high-risk treatments fed at lower rates, and they eventually consumed less food than under low predation risk (risk: $F_{1,17} = 5.01$, $P = 0.039$; food abundance: $F_{1,17} = 270.54$, $P < 0.0001$). However, the effect of predation risk on the amount of food consumed varied in relation to food abundance, leading to an almost significant interaction ($F_{1,17} = 4.28$, $P = 0.054$). Lizards consumed virtually all crickets supplied when food was scarce, such that food intake did not vary in relation to predation ($F_{1,17} = 1.39$, $P = 0.254$). When food was abundant, lizards refused more crickets under high predation risk ($F_{1,17} = 4.85$, $P = 0.042$; Fig. 2).

Apart from reducing overall food intake if food was abundant, lizards tended to be reluctant to feed in the presence of a predator when they perceived a high risk of

Table 1. Three-way repeated measures ANOVA analysing variation in frequency of activity and exposure of lizards (behaviours increasing conspicuousness) in relation to time of day (four measuring times) and experimentally manipulated food abundance and predation risk

		Activity		Exposure	
	df	*F*	*P*	*F*	*P*
Food abundance	1,17	2.13	0.163	1.48	0.241
Predation risk	1,17	1.79	0.199	5.99	0.026
Food × risk	1,17	0.21	0.651	0.18	0.679
Time of day	3,51	16.93	<0.0001	16.05	<0.0001
Time × food	3,51	1.17	0.331	2.34	0.084
Time × risk	3,51	3.59	0.020	3.40	0.025
Time × food × risk	3,51	0.41	0.748	0.28	0.837

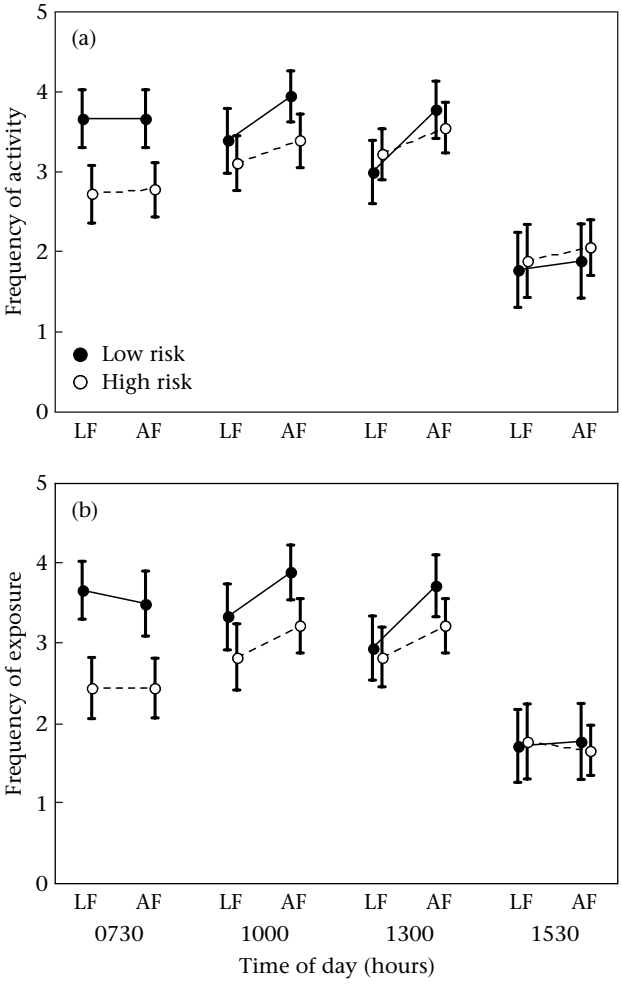

Figure 1. Daily pattern of (a) activity and (b) exposure (see Methods for definition) of lizards in relation to experimentally manipulated food abundance (LF: limited food; AF: abundant food) and predation risk. Means are shown ±SE.

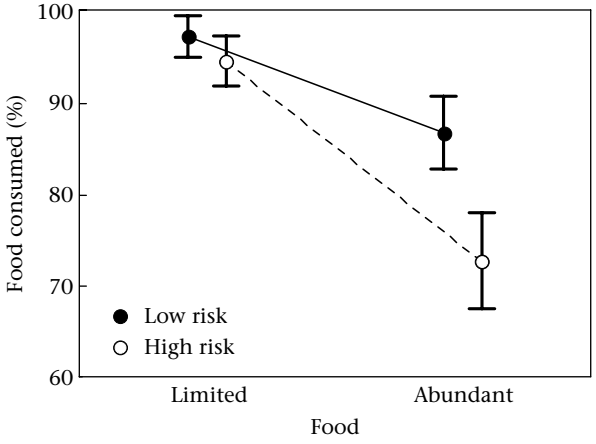

Figure 2. Mean percentage of food consumed ± SE in relation to variation in food abundance (limited versus abundant) and predation risk between experimental treatments.

being attacked, regardless of food abundance. However, because of the small sample size for this analysis, these trends were nonsignificant. Among seven lizards showing repeated activity during food supplying in treatments with limited food, two maintained the same response (both fed in the presence of the observer) when predation risk increased, five lost willingness to feed, and none adopted a higher propensity to feed ($\chi^2_2 = 8.42$, $P = 0.055$). The test of goodness-of-fit to homogeneity of behavioural changes with increasing risk (excluding individuals that did not vary in response) led to a similar conclusion ($\chi^2_1 = 5.0$, $P = 0.063$). In the same way, of 16 lizards showing repeated activity across treatments with abundant food, 10 maintained behaviour when predation risk increased (two of them kept feeding and eight never fed in the presence of the observer), six lost their willingness to feed, and none adopted a higher propensity to feed, but this heterogeneity of behavioural decisions did not reach statistical significance ($\chi^2_2 = 5.50$, $P = 0.068$). This result was caused by a high frequency of individuals that decided not to feed in the presence of predators when food was abundant, regardless of predation risk, as shown by a significant deviation from homogeneity of behavioural changes with increasing risk (excluding individuals that decided not to change behaviour: $\chi^2_1 = 6.0$, $P = 0.031$).

Variation in Body Mass

Lizards lost mass in response to both impaired feeding conditions ($F_{1,17} = 15.47$, $P = 0.001$) and increased predation risk ($F_{1,17} = 4.99$, $P = 0.039$; Fig. 3a). The interaction between these effects was nonsignificant ($F_{1,17} = 0.98$, $P = 0.337$). The difference in mass between the least stressful situation (abundant food and low predation risk) and the most stressful treatment (limited food and high risk) averaged 5.3% of total body mass. The effect of predation risk was small, averaging a loss of 2.9% of total body mass under limited food conditions and 1.1% when food was abundant.

We analysed the extent to which food interruption under the risk of predation may account for differences in body mass between predation treatments. To do so, we studied the association between changes in food intake and changes in body mass from low to high risk of predation in each treatment of food abundance, testing for the effect of intake as a changing covariate in a repeated measures analysis of covariance (ANCOVA) (StatSoft, Inc. 1999). Under limited food, variation in food intake did not significantly explain variation in body mass ($r^2 = 0.05$, $F_{1,16} = 0.81$, $P = 0.38$), consistent with the similar feeding rate of lizards during both treatments with limited food. When food was abundant, reduction in food intake under increased predation risk accounted for 34% of variation in mass loss ($F_{1,16} = 8.22$, $P = 0.011$): lizards lost about 0.5 g of body mass per g of crickets left (regression slope = −0.47), and they were not expected to decrease body mass without decreasing food intake (intercept = 0.08, which does not differ significantly from zero: t test: $t_{16} = 0.55$, $P = 0.58$; Fig. 3b). The two tailless individuals showed no anomalous pattern compared to other lizards, supporting the idea that autotomy did not affect reserve regulation (Fig. 3b).

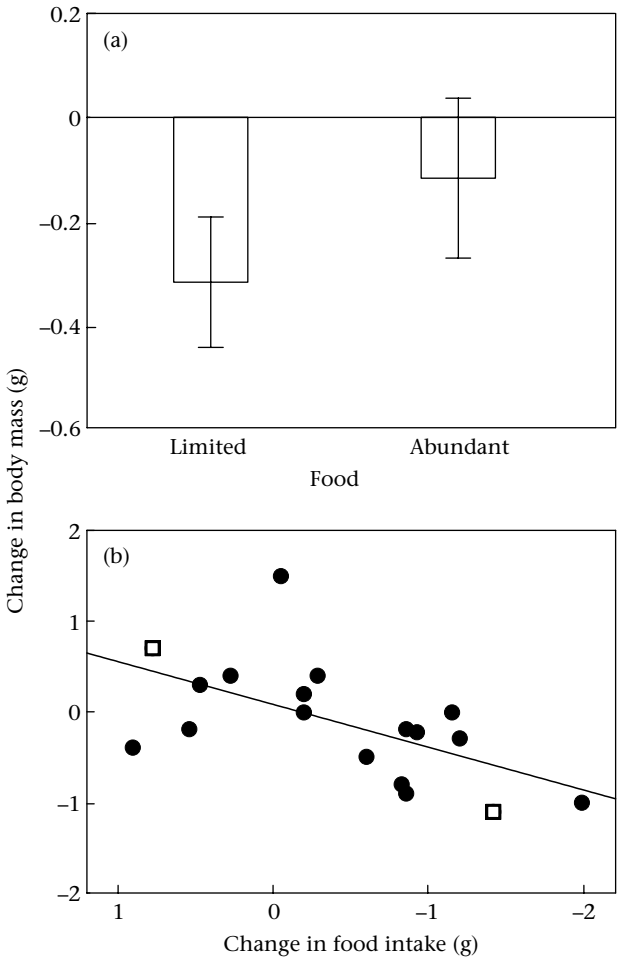

Figure 3. (a) Mean change in body mass ± SE from low predation risk to high predation risk, in each treatment of food abundance. (b) Correlation between the change in food intake from low predation risk to high predation risk and mass change of lizards, in treatments with abundant food. □: Individuals that lost tails during the experiment (see text for details).

Escape Performance of Lizards

Lizards showed a sprint performance similar to that reported in previous studies on the same species (Table 2; cf. Bauwens et al. 1995). A principal components analysis (PCA) with performance variables extracted two components that accounted for 75% of the variation in the correlation matrix (Table 2). The first (PC1) was a measure of escape capacity of lizards: the higher this score, the longer was the total distance covered and the faster the individual sprints. The second component was related to the organization of escape behaviour: high PC2 scores corresponded to few long flights, and low scores corresponded to many short runs, independently of the total distance covered or the speed in individual sprints (only top speed was correlated with PC2, and this effect was comparatively small). Therefore, these two components adequately described both the capacity of lizards to avoid predators at the critical moment of the attack (PC1) and the behavioural decisions made by individuals with respect to escape strategy (PC2).

Table 2. Average values for the different variables measuring escape performance of lizards ($N = 15$ individuals, distances in cm and speeds in cm/s) and results of PCA summarizing this variation ($N = 120$, eight trials per individual)

		Factor loading	
	Mean ± SE	PC1	PC2
Number of sprints	5.2 ± 0.2	0.240	−0.812
Total distance	526.3 ± 17.6	0.612	0.045
Mean fleeing distance	121.7 ± 3.9	0.315	0.877
Maximum fleeing distance	157.6 ± 2.8	0.346	0.674
Mean top speed	162.8 ± 3.2	0.847	0.411
Mean average speed	140.5 ± 2.7	0.891	0.166
Maximum top speed	202.4 ± 3.7	0.915	0.207
Maximum average speed	173.5 ± 3.2	0.929	−0.075
Eigenvalue		3.863	2.131
Variance explained (%)		48.29	26.63

Significance values for correlations between variables and components are not indicated because we used nonindependent measures in this analysis, which was aimed at summarizing variation in escape performance both within and between individuals.

A one-way ANCOVA with individual as a random effect and body temperature as the covariate showed substantial within-individual repeatability of both locomotor capacity and escape strategy (intraclass correlation: $r_i = 0.32$ for PC1 and 0.52 for PC2, $P < 0.0001$ in both cases). Given the behavioural nature of the variables and the temporal separation between measurements, these repeatabilities give reliability to our results. Sprint capacity depended more on body temperature than escape strategy (effect of temperature on PC1: $F_{1,14} = 5.13$, $P = 0.039$; effect on PC2: $F_{1,14} = 0.25$, $P = 0.622$).

None of the components of escape performance changed in relation to experimental treatments (Table 3), even though lizards lost mass in response to both food deprivation and increased predation risk. This lack of variation between treatments was not confounded by changes in temperature (effects of temperature as a changing covariate in an ANCOVA; PC1: $F_{1,13} = 0.06$, $P = 0.806$; PC2: $F_{1,13} = 0.05$, $P = 0.835$). We also checked the correlation between changes in body mass and performance by including body mass as a changing covariate in a repeated measures ANCOVA (using the averages for each test day, because lizards were weighed only in the morning). Variation in body mass did not affect variation in PC1 or PC2 (the largest possible effect is shown in Fig. 4), nor did it affect changes in any of the variables of performance originally measured (all 10 within-cell regressions were nonsignificant: $F_{1,13} < 1.25$, $P > 0.28$). The power of these analyses was small because of the small sample size ($N = 15$), and particularly because of the very small magnitude of the effects being tested. Thus, the largest possible within-subject effects of body mass on performance (differences in performance related to the greatest difference in body mass experienced by each lizard; Fig. 4) were very small (PC1: $r^2 = 0.017$, $F_{1,13} = 0.23$, $P = 0.63$; PC2: $r^2 = 0.022$, $F_{1,13} = 0.30$, $P = 0.59$); the sample size required to detect these effects with $\alpha = 0.05$

Table 3. Results of three-way repeated measures ANOVA analysing variation in body temperature measured before running, sprint capacity (PC1) and escape strategy (PC2) of lizards (for details of principal components of performance, see Table 2), in relation to time of measurement (morning or afternoon) and experimentally manipulated food abundance and predation risk

	Body temperature		Sprint capacity		Escape strategy	
	$F_{1,14}$	P	$F_{1,14}$	P	$F_{1,14}$	P
Food abundance	0.002	0.969	1.01	0.332	0.002	0.962
Predation risk	2.28	0.153	0.49	0.497	0.06	0.811
Food×risk	1.27	0.279	0.46	0.509	0.14	0.710
Time	1.29	0.276	0.02	0.886	2.20	0.160
Time×food	0.03	0.855	0.27	0.609	1.46	0.247
Time×risk	0.78	0.392	1.19	0.295	0.04	0.852
Time×food×risk	0.38	0.550	0.12	0.732	0.05	0.829

would be 324 and 243 lizards, respectively (assuming population correlations similar to the ones we found and having a conservatively low goal power of 0.65).

DISCUSSION

To our knowledge, this is the first experimental investigation of the trade-off between gaining energy and avoiding predation in adult lizards. It is also the first attempt to assess empirically to what extent mass losses caused by predation risk influence escape performance in any animal. Our results show that predation risk affected the behaviour of lizards, compromising the acquisition and maintenance of body reserves. Alarmed lizards lost mass not only because they interrupted feeding, but also because of stress in relation to predation risk per se (as it happened under limited feeding conditions). However, these predation-induced mass losses did not improve escape performance during predator attacks. We discuss below how the loss of body mass arises as a cost of antipredatory behaviours in lizards, which is apparently not counterbalanced by an improvement in escape efficiency.

Lizards responded behaviourally to predation risk. Alarmed lizards' behaviours reduced exposure, which probably impaired foraging and hence led to losing mass. During treatments involving high predation risk, lizards tried to decrease conspicuousness by using sheltered positions more often, showed increased reluctance to feed when a predator was present and decreased food intake if food was abundant. Increased use of refuges and feeding interruption are common behavioural responses to predation risk in vertebrates, which have been documented in reptiles (Carrascal et al. 1992; Martín & López 1999, 2001). These behaviours involve important costs; for example, they may reduce mating probability, impair territory defence and compromise thermoregulation (Salvador et al. 1995; Carrascal et al. 2001). Antipredatory behaviours are also performed at the expense of reduced energy acquisition and maintenance (McNamara & Houston 1990). This cost of antipredatory behaviour is probably lower for lizards than for endothermic animals, as long as reptiles can adjust metabolic rates by changing activity (e.g. Huey 1982; cf. Carrascal et al. 2001). Furthermore, lizards that reduce exposure bask less, probably have lower body temperatures and, consequently, lower metabolic costs (Huey 1982). However, interrupted activity is likely to have important costs in terms of territory defence or mating prospects (Salvador et al. 1995), which might outweigh starvation costs. In our study, lizards did not substantially reduce overall activity under increased predation risk, and they did not change

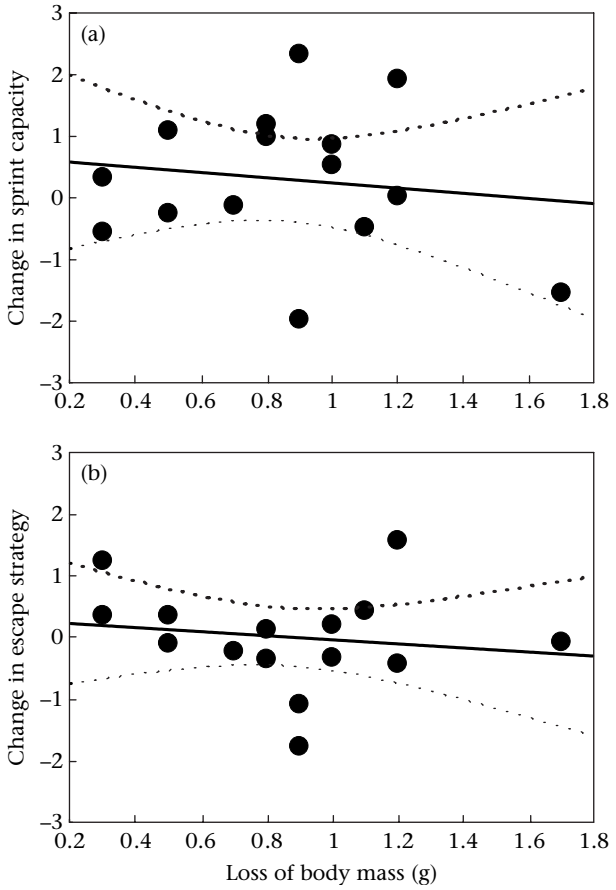

Figure 4. Changes in escape performance in relation to the largest difference in mass experienced by each lizard during the experiment. Performance was measured by (a) sprint capacity (high values indicate higher speed and endurance, PC1 in Table 2) and (b) escape strategy (high values indicate longer flees, PC2). The 95% confidence bands for the regression lines are shown.

activity at all when food was limited, eventually impairing their body condition in these circumstances. These results mean that, although the advantages of ectothermy could account for the lower decrease in body mass of alarmed lizards (1–3% of total body mass) compared to endotherms experiencing a similar predation risk (up to 8% of total body mass in birds; Carrascal & Polo 1999; van der Veen & Sivars 2000; Rands & Cuthill 2001), the need to remain active and to increase vigilance under predation risk eventually led to a loss of mass. Therefore, a reduction in adult body mass upon predator encounters can be expected also in ectotherms, as long as decreasing the probability of being predated compensates for the costs of impaired body condition (McNamara & Houston 1990; Martín & López 1999).

Because lizards do not respond to impaired feeding conditions by interrupting activity (which would save energy by reducing metabolic rate: Huey 1982), starvation costs should shape the trade-off between gaining energy and avoiding predators. If food becomes limited, behaviours aimed at reducing vulnerability should become more expensive in terms of energy maintenance, and being fat should become less costly or even beneficial. In turn, interrupted feeding caused by predator encounters should become more costly under impaired feeding conditions (Lima 1986; McNamara & Houston 1990). In our study, alarmed lizards reduced overall food intake if food was abundant, and this response accounted for a substantial amount of variance in mass loss under predation risk. However, when food became scarce, lizards maintained a similar, nearly maximum feeding rate independently of predation risk, supporting the idea that gaining energy was favoured under impaired feeding conditions. However, although this behavioural response was consistent with starvation costs shaping the trade-off between gaining reserves and avoiding predators (McNamara & Houston 1990), alarmed lizards lost as much mass as they did when interrupting feeding under nonlimited conditions. This result shows that factors other than impaired foraging induce alarmed lizards to lose mass.

The loss of body mass without decreasing food intake, and hence attributable to predation risk per se, could be caused by alarmed lizards entering a hormone-mediated 'emergency life history stage' (Wingfield et al. 1998). Threatening environmental events such as increased predation risk activate the hypothalamo-pituitary-adrenal axis, resulting in an elevation of glucocorticosteroid secretion. These hormones orchestrate physiological and behavioural changes including staying in refuges, escape from the high-risk area, increased vigilance and mobilization of stored fat reserves (Wingfield et al. 1998). The release of other hormones during stressful conditions may also increase energy expenditure (Assenmacher 1973; Axelrod & Reisine 1984). The combination of all these behavioural and physiological changes may explain not only the adoption of antipredatory behaviours, including feeding interruption, but also the loss of body mass beyond that expected from feeding interruption alone. In our study, this stress seemed more important under impaired feeding conditions. In fact, food shortages may be an additional stressing factor, causing an overresponse of lizards in terms of mass loss under predation risk (Wingfield et al. 1998). Further research is required to identify how starvation costs may shape the relative importance of impaired foraging and physiological stress as causes of mass loss in alarmed animals. However, our results suggest that stress related to impaired feeding conditions might mediate the physiological consequences of antipredatory behaviour in lizards.

Whether caused by feeding interruption or by physiological stress, mass losses might have fitness consequences for lizards. In many species, growth is indeterminate, and a larger body size at a given age favours mate acquisition (Díaz 1993; Martín & Forsman 1999) and increases breeding output (Downes 2001). Thus, an impaired body condition caused by exposure to predators may compromise future breeding success. Opposing these costs, it has been suggested that, for some prey, losing mass might be adaptive under predation risk, to the point that fit-for-escape strategies may have evolved to increase survival probability during predator attacks (e.g. van der Veen & Sivars 2000). In our study, however, predation risk did not affect either the physiological capacity or the behavioural strategy of lizards to escape from an attacking predator, despite predation-induced changes in body mass. The changes in escape performance of lizards were also not correlated with changes in body mass between running sessions. Losing mass from increased predation risk favoured none of a range of components of escape performance measured during simulated predator attacks, including endurance, sprint speed and fleeing strategy.

Alarmed lizards lost 1–3% of total body mass, which may be too little to improve escape performance. Much higher variations in the body mass of lizards have not affected their escape ability. Most studies on the relation between body mass and locomotor performance in lizards have pointed to a nonenergetic cost of reproduction, showing that gravid females have impaired performance (Bauwens & Thoen 1981; Cooper et al. 1990; Miles et al. 2000). However, this reproductive burden could be better related to physiological changes occurring during pregnancy than to the costs of carrying an extra load (as shown in the viviparous skink *Niveoscincus microlepidotus*; Olsson et al. 2000). The effects of reproduction on performance may also be offset behaviourally, for example by increasing crypsis (Bauwens & Thoen 1981; Cooper et al. 1990). Reduced locomotor activity after eating large prey (reviewed in Martín 1996) might be more directly related to variation in performance in relation to energy storage in lizards. In juvenile *Psammodromus algirus*, individuals fed to satiation decreased routine mobility, probably as a consequence of being less compelled to search for food (movement was substituted by basking in fat individuals; Martín 1996). However, fat lizards did not show an impaired performance when escaping from simulated predator attacks, despite being 8% heavier than lean individuals, thus failing to support an effect of body mass on vulnerability (Martín 1996).

The fit-for-escape hypothesis stems from the abundant literature on the trade-off between starvation and predation in birds, including both a loss of body mass in the presence of predators and a negative effect of body mass on flight performance (reviews in, respectively, Rands &

Cuthill 2001; Lind et al. 1999). However, whether mass reduction from predation encounters improves escape ability is not as clear as it is usually assumed. Birds exposed to manipulations of predation risk similar to those in our study lost 4–8% of their total body mass (Carrascal & Polo 1999; van der Veen & Sivars 2000; Rands & Cuthill 2001). However, impaired locomotor performance of fat individuals, a necessary condition for the fit-for-escape hypothesis, has been revealed only in (1) extremely heavy birds putting on fat during migration (Kullberg et al. 1996; Lind et al. 1999), (2) females in the laying period for which a physiological burden could outweigh the cost of increased mass (Lee et al. 1996; Kullberg et al. 2002 and references therein) and (3) birds flying with an artificially increased mass load (Witter et al. 1994). Daily fattening, which is closer in magnitude to variation in body mass upon predator encounters, affected climbing ability in nonalarmed birds (Metcalfe & Ure 1995), but not in birds exposed to simulated predator attacks (Kullberg 1998; Veasey et al. 1998, who repeated Metcalfe & Ure's 1995 experiment on alarmed birds). These studies indicate that the negative impact of carrying a high fat load during a predator attack has probably been overestimated in birds (Veasey et al. 1998; van der Veen & Lindström 2000).

In summary, predation risk may compromise both the acquisition and the maintenance of energy reserves, which are likely to have fitness consequences for animals. The costs of losing mass may be compensated by improved predator avoidance from increased alertness and reduced exposure. However, the frequently advocated strategic loss of body mass under predation risk remains to be documented, showing that individuals experimentally induced to lose mass under predation risk escape better during predator attacks. According to the current study and others cited here, being fat under predation risk may be costly, because devoting time to acquire and maintain energy reserves compromises antipredatory behaviours (Lima 1986), but fit-for-escape is not required to explain the loss of mass. Therefore, it would be more parsimonious to consider the loss of mass not as a part, but as just a cost of antipredatory defence.

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