ORIGINAL PAPER

Habituation to low-risk predators improves body condition in lizards

Iñaki Rodríguez-Prieto · José Martín ·
Esteban Fernández-Juricic

Abstract Habituation to nonlethal predation stimuli may provide benefits for animals living in areas with frequent encounters with low-risk predators. On the other hand, individuals can be very consistent in their antipredator responses, with shy individuals showing greater degree of responsiveness than bold individuals. However, the link between habituation or boldness and individual benefits has not been thoroughly investigated. We established whether and how two behavioral components associated with antipredator responses (habituation and boldness, and their interaction) would influence body condition, which is a parameter related to fitness. We conducted an outdoor semi-natural experiment with Iberian wall lizards (*Podarcis hispanica*). Individual boldness was consistent across contexts, but we did not find any effect of boldness or the interaction between boldness and habituation on body condition. However, those individuals that habituated more readily to a frequent predatory stimulus were able to increase their body condition more relative to lizards that habituated less. This finding highlights the importance of individual differences in behavioral plasticity, which could influence traits related to fitness. Habituation can provide benefits for individuals exposed to low-risk predators;
however, individuals more prone to habituation could also experience mortality costs by wrongly habituating to a dangerous predator.

Keywords Behavioral plasticity · Behavioral syndrome · Body condition · Boldness · Fitness · Habituation · Personality

Introduction

Animals are subject to two main costs as a result of predation: direct mortality and nonlethal costs arising from behavioral changes while trying to reduce predation risk (Fraser and Gilliam 1992; Creel and Christianson 2008). To maximize fitness, animals should adjust their antipredator behavior to match the actual level of predation risk, balancing the risk of being captured with the costs incurred in predator avoidance (Cooper and Frederick 2007; Lima and Dill 1990; Ydenberg and Dill 1986). If an individual experiences a history of frequent nonthreatening encounters with a particular predator, it can learn that the predator exerts low levels of predation risk. Consequently, it can reduce the antipredator responses toward that predator via habituation (Domjan 2003; Ellenberg et al. 2009; Rodriguez-Prieto et al. 2009). Habituation is a special case of behavioral plasticity (Hemmi and Merkle 2009) and is defined as a behavioral response decrement that results from repeated stimulation and that does not involve sensory or motor fatigue (Rankin et al. 2009). Individuals may also vary consistently in several personality traits (Réale et al. 2007), including boldness, which can be defined as the reaction of an individual to risky situations such as those elicited by predators or humans. Generally, shyer individuals show stronger responses than bolder individuals (Réale

I. Rodríguez-Prieto · J. Martín
Departamento de Ecología Evolutiva,
Museo Nacional de Ciencias Naturales, CSIC,
José Gutiérrez Abascal 2,
28006 Madrid, Spain

E. Fernández-Juricic (✉)
Department of Biological Sciences, Purdue University,
915 W. State Street,
West Lafayette, IN 47907, USA
e-mail: efernan@purdue.edu

et al. 2007). Habituation and boldness are not mutually exclusive; an individual can be bold or shy, but at the same time it can show habituation to a specific predator.

It is usually assumed that habituation, through reduction of unnecessary antipredator responses, is beneficial for individuals in areas with a high frequency of encounters with low-risk predators (e.g., humans; Fox and Madsen 1997; Sutherlan 2007). Furthermore, some authors have suggested that antipredator boldness could be advantageous for increased growth and mass gain (Brown et al. 2007; Ward et al. 2004). However, despite the growing number of studies on habituation and boldness, the assumption that they provide specific benefits for individuals has not received enough empirical support. A simple reduction in antipredator responses could be a weak predictor of the consequences of predation risk if not accompanied by other measures more directly related to the costs and benefits of antipredator behavior or even fitness (Gill et al. 2001; Tarlow and Blumstein 2007).

Previous studies have found that body condition is negatively affected by predation risk in many taxa, including reptiles (e.g., Amo et al. 2006; Martín and López 1999), birds (e.g., Féret et al. 2003; Müllner et al. 2004), and mammals (e.g., Hjeljord and Histøl 1999; Pauli and Buskirk 2007). This suggests that body condition is affected by the nonlethal costs associated with the time, energy, and resources lost when fleeing or hiding from predators (Amo et al. 2007; Brown and Kotler 2004), when avoiding risky habitats (Béchet et al. 2004; Peluc et al. 2008), and when predator presence is accompanied by stress responses (e.g., increase in glucocorticoid levels, Sapolsky 1992; Sheriff et al. 2009). A reduction in body condition may imply less body reserves available for traits related to fitness, such as survival and reproductive success (Schulte-Hostedde et al. 2005).

We established whether and how body condition changes could be associated with habituation and boldness. We developed a semi-natural experimental scenario to expose Iberian wall lizards (*Podarcis hispanica*) to controlled levels of low predation risk (human intrusions) and measured changes in behavior and body condition over a short period of time.

The ability of individuals to habituate has been shown to vary within a population (Ellenberg et al. 2009; Olson et al. 1997; Runyan and Blumstein 2004; Stolen 2003). We predicted that individuals that habituate more readily would increase their body condition relative to those individuals that habituate less readily due to their reduction of unnecessary responses to the risk stimuli. We also predicted that bold individuals would increase their body condition relative to shy individuals because the costs of non-lethal predation risk could be higher for shy individuals given their relatively greater degree of responsiveness to a predator (Carrete and Tella 2010). We also explored whether habituation and boldness would interact. We expected the effect of habituation on body condition to be more detrimental to shy than to bold individuals. The effects of non-lethal predation risk on bold individuals could be so low that an additional habituation-driven decrease in responsiveness to the predation stimuli may not have a significant effect on body condition. Shy individuals, on the contrary, could benefit more from a decrease in their high-antipredator responses.

A measurable effect of habituation is the progressive reduction in magnitude of a behavioral response to the repeated application of a stimulus over time (Rankin et al. 2009). Therefore, we used the progressive reduction of flight initiation distance (FID) as our proxy for habituation to repeated human intrusions. Reduction in FID has been commonly used as a proxy for habituation in both vertebrate and invertebrate systems (e.g., Hemmi 2005; Hemmi and Merkle 2009; Ikuta and Blumstein 2003; Lord et al. 2001; Magle et al. 2005; Martínez-Abraín et al. 2008; Mccleery 2009; Rodriguez-Prieto et al. 2009; Runyan and Blumstein 2004).

Materials and methods

Thirty-two adult Iberian wall lizards were captured by noosing from a population in the Guadarrama Mountains (Central Spain) and were transported to El Ventorrillo field station, 3 km from the capture site. We only used lizards with intact tails since lizards with autotomized tails may show altered antipredator behavior (e.g., Cooper 2003; Cooper and Wilson 2008; Salvador et al. 1995) Lizards were individually housed outdoors in plastic cages (48× 29×24 cm) for 2 weeks. We added a ceramic refuge to each cage and provided water ad libitum and mealworms and crickets as daily food. While in these cages, lizards were behaviorally tested for boldness (see below). After the boldness tests were completed, lizards were transferred to large outdoor enclosures to study habituation and change in body condition.

Boldness

To position each individual lizard in the shy–bold gradient, we followed the methodology of López et al. (2005). We tested the lizards between 1615 and 1815 hours, when all individuals were active. We placed the individual cages separately from each other in an open and sunny location, but the cage walls and the ceramic refuge provided partial shade. We simulated several consecutive attacks to each lizard, recording at the start of each attack whether the lizard was hiding inside the refuge (body and head inside

the refuge), leaning out of the refuge (i.e., individual's body was inside the refuge, but its head was sticking out), or outside of the refuge (body and head outside of the refuge) (López et al. 2005). One observer (IRP) performed the attacks by first crawling slowly on the ground to avoid being seen by the lizards in the contiguous cages. The observer then suddenly appeared over the cage walls simulating a predator attack by tapping the lizard close to its tail with a little stick, which made the animal run and hide in the refuge. For each lizard, we simulated one attack every 10 min in a 2-h window (12 attacks per day). We repeated the same procedure the next day, with another 12 attacks. If the lizard was still hiding in the refuge from the previous attack, the observer tapped the refuge entrance with the stick. The purpose of all these "attacks" was to create a context of constant high risk and to record the lizards' responses (i.e., the number of times they were outside versus the number of times they were inside the refuge out of 12 attacks during the 2-h period).

We counted the number of times that each individual was outside, inside, or leaning out of the refuge in each of the 2 days of the experiment. We included six variables (number of times inside the refuge on day 1, number of times leaning out on day 1, number of times outside the refuge on day 1, and the same variables on day 2) in a principal component analysis (PCA) to obtain a composite variable indicative of boldness following López et al. (2005). Instead of directly summing up the values of each response for the 2 days (e.g., number of times inside the refuge on day 1+number of times inside the refuge on day 2), we maintained them as separate variables while entering them in the PCA because the lizards could have been affected by different confounding factors (e.g., slight weather differences) during each testing day.

We obtained two factors with eigenvalues >1 (percentage of total variance explained: PC1, 55.6%; PC2, 23.0%). PC1 (hereafter 'boldness index') correlated positively with the number of times outside the refuge on day 1 (factor loading= 0.88) and on day 2 (factor loading=0.92), and negatively with the number of times inside the refuge on day 1 (factor loading= −0.90) and on day 2 (factor loading=−0.93). PC1 represented a gradient from shy to bold individuals. Shy individuals responded to the simulated predator attacks with stronger antipredator behavior than bold individuals, reducing their predation risk by staying under the refuge longer. PC2 correlated with the number of times the lizards leaned out of the refuge on day 1 (factor loading=−0.83) and on day 2 (factor loading=−0.75). PC2 represented a gradient of the frequency of leaning out of the refuge. A leaning lizard could be trying to ascertain whether the predator that attacked it was still in the vicinity of the refuge or not (Polo et al. in press). PC2 was not associated with body condition change (r=0.12, $F_{1,29}$=0.44, P=0.514), so we excluded it from the main analysis.

We believe that it would be unlikely that our boldness index was influenced by habituation to humans developed through the boldness tests. An attacked lizard could only see a hand, a stick, and part of a face appearing suddenly and briefly over the rim of their cage, which simulated a dangerous attack that actually ended in a physical interaction with the lizard or the refuge entrance.

Enclosures

After finishing the boldness tests, lizards were transferred to four 6×4-m outdoor enclosures placed in an open area surrounded by woodland (Fig. 1), where the habituation and body condition experiment was performed. Enclosures had a natural herbaceous substrate. We supplied water to the lizards by refilling at night four semi-buried water cups per enclosure, but we did not supply any food, so that the lizards were forced to search and capture naturally occurring invertebrates within the enclosures. Lizards were not able to climb the walls, which were made of polyethylene sheets partially buried in the substrate. However, there was a constant flux of arthropods, resulting in diverse and abundant prey availability in the enclosures. We completed each enclosure with a standardized array of rocks, tiles, and bricks for refuge and thermoregulation (Fig. 1).

Individual lizards were assorted by size (four categories) and sex, and eight lizards were allocated at random into each of the four enclosures (n=32 individuals). The proportions of body size and age classes were the same in each enclosure. Lizard snout to vent length (SVL) ranged from 53 to 64 mm in males, and from 53 to 60 mm in females. Body mass ranged from 3.94 to 6.62 g in males and from 2.68 to 5.49 g in females. Lizards went through an acclimation phase in the enclosures from mid-June to mid-August (post-reproductive period). Three days prior to
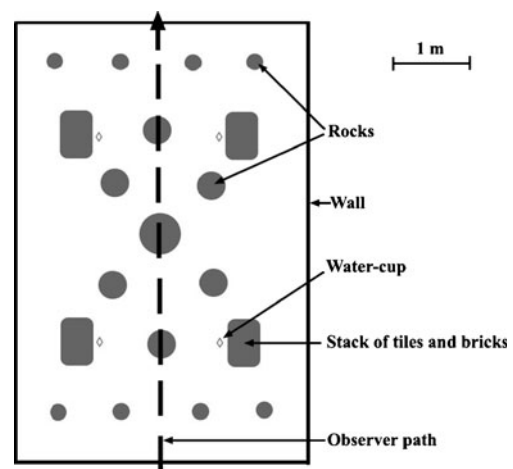

Fig. 1 Enclosure layout showing the different elements used to create refuge for Iberian lizards

the experiments, each individual was dorsally marked with three painted dorsal color circles to allow visual identification.

Habituation protocol

Lizards were subjected to a 6-day habituation protocol. Previous studies found that even less than 6 days of treatment were enough to observe habituation effects (Ellenberg et al. 2009; Walker et al. 2006). One observer (IRP), wearing dull-colored clothes entered and longitudinally crossed each enclosure (Fig. 1) every 20 min during the peak activity period (1200 to 1400 hours and 1645 to 1845 hours; 12 intrusions per enclosure per day). Lizard activity was very low outside these peak activity periods due to the shadows projected by surrounding trees before 1200 hours and after 1900 hours, and to high temperatures between 1400 and 1630 hours. Flight initiation distance (FID) was defined as the distance between the observer and the lizard when the latter moved away in response to the approaching threat. As the observer crossed the enclosure, he was able to mark his own position and the positions of the lizards as they individually flushed on a detailed scaled map of the enclosure. When the observer reached the end of the enclosure, he went back to the marked points of the crossing path and measured FID with a measuring tape without stepping out of the crossing path. We did not sample individuals located at less than 40 cm from the enclosure walls. When the lizards were in these locations, they had to choose between fleeing towards our crossing path in order to reach a refuge and hiding under the shadow cast by the walls. Thus, they had different fleeing costs and benefits than when they were in the main area of the enclosure, which could have added uncontrolled noise to our analysis. We also measured the distance to the nearest refuge, but it did not affect the FID significantly ($r=0.04$, $P=0.524$). We obtained 12.90 ± 0.74 (mean±SE) FID measurements per individual during the habituation protocol (range, four to 20 measurements).

We estimated the reduction of the FID over the course of the 6-day experimental phase by regressing the FID over time for each individual. We were not interested in whether the changes in FID were significant or not over the duration of the experiment, but on the relative magnitude of the gradual change, so we used the slope of the regression to measure the rate of reduction. Some individuals maintained their FID almost unaltered over the course of the experiment (slope of the FID/time regression close to zero), but other individuals experienced a strong decrease in FID over time (high negative slopes), with a gradient of FID reduction between these extremes. Some individuals even showed a tendency to slightly increase their FID, (low positive slopes). Thus, we used the slope of individual FID/time regressions to characterize each individual's response to the habituation protocol. For clarity, we multiplied the slopes by negative

one in order to obtain a "habituation index" with higher scores indicating rapid habituation.

Exposure index

When performing the habituation treatment and just before entering each enclosure, the observer also recorded the identity of all the lizards that were out of the refuges. Since the enclosures were relatively small and lacked tall vegetation, we are confident that we detected all the lizards that were not in the refuges. Summing all observations over the course of the habituation treatment, we obtained an exposure index that represented the number of times each individual was exposed to low-risk stimuli. Lizards were exposed 23.55 ± 0.86 times (range, 13 to 36 times). We included this variable in the present analysis to control for its potential effect on body condition change.

Body condition

We measured lizard mass with a digital balance ($\pm$ 0.01 g) and SVL with a steel ruler (±1 mm) (1) at the start of the acclimation phase (first measurement), (2) 3 days prior to the habituation experiment (second measurement), and (3) at the end of the habituation experiment (third measurement). All measurements were performed at night when lizards were lethargic to minimize potential handling effects. The body condition index was calculated for each of the 31 lizards at each of the measurement periods as the residuals from the regression equation of body mass on SVL; both of these variables were log-transformed (Jakob et al. 1996; Schulte-Hostedde et al. 2005). We calculated body condition change through the habituation period as the difference in body condition between the third and second measurements. Body condition change under no-habituation conditions (acclimation phase) was the difference between the second and the first measurements.

The captures and experiments were done under license (Ref. 10/054082.5/05, resolución 6516/05) from the Madrid Environmental Agency (Consejería de Medio Ambiente de la Comunidad de Madrid). The experimental protocol and procedures were in compliance with the European Communities Council Directive of 24 November 1986 (86/609/ EEC). At the end of the experiment the lizards were released at their exact capture points after ensuring that they were healthy and in good condition.

Statistical analyses

We removed an individual that lost its tail during the acclimation phase from the dataset. All variables were checked for normality and the SVL was log-transformed. We used Statistica 6.0 (Statsoft Inc.) for all statistical analyses.

Boldness was not affected significantly by sex ($F_{1,27}=$ 0.79, $P=0.380$), absolute body size ($F_{1,27}=0.30$, $P=$ 0.586), or relative body size ($F_{1,27}=0.31$, $P=0.582$). We tested whether the individual lizard's shy–bold response was consistent across situations: for each lizard, we calculated the mean FID during the first day of the habituation protocol and we used Spearman's rank correlation analysis to compare it with the boldness index obtained in the cage tests. Because we considered these two measures to be different aspects of the same trait (i.e., boldness), we expected the lizards ranked as bold in the cage tests to show short FID at the start of the habituation treatment.

We used a general linear model to assess the effects of habituation and boldness (boldness index from the cage tests) on body condition change. All enclosures were similar in design and composition. However, their specific positions relative to the surrounding trees led to slight differences in the total time of direct sunlight received by each enclosure. Consequently, we included an enclosure identity factor in the model and the interaction between the enclosure effect and habituation. Additionally, we included in the model sex, exposure index, SVL, and the body condition of the lizards at the second measurement period because the body condition change could be influenced by whether individuals started the experimental phase with low-body condition. We also included the interaction between the effects of the habituation ability and boldness on body condition change. Following Whittingham et al. (2006), we included all the variables in the same model instead of using stepwise procedures.

Given the duration of the habituation treatment, most body condition change resulted from absolute mass change, with very low SVL growth detected over the course of the experiment. We preferred the use of body condition change as our dependent variable instead of absolute mass change, since the proportional nature of body condition can control for any allometric relationship between mass change and body length; for instance, a 0.1-g change in body mass may not represent the same benefit for a big lizard as for a small one. Nevertheless, we repeated the same analysis using body mass change as the dependent variable in order to provide a more complete picture of the effects of habituation.

Finally, we used Spearman's rank correlation to assess whether the lizards that were better at improving their body condition during the experimental phase were also those better at improving body condition during the acclimation phase. An association between these two variables might indicate that consistent individual differences in the ability to capture or process food could account for individual differences in body condition change during the experiment.

Results

Habituation responses differed among lizards; some individuals reduced their FID over the course of the experimental phase and others maintained or slightly increased their FID. The change in the FID slope ranged from –14.1 (suggesting strong habituation) to +4.7 (suggesting slight sensitization). These slopes, multiplied by negative one, were used as the habituation index for each individual as explained above.

The position of each individual in the shy–bold gradient was consistent across contexts, with the individual boldness index obtained in the cage tests being negatively correlated with the individual mean FID obtained during the first day of the habituation protocol (Spearman's rank correlation, $r_s=-0.47$, $N=31$, $P=0.008$).

Mass change during the experimental period varied among individual lizards from –0.12 to 0.58 g ($0.25\pm$ 0.03 g). With sex, body condition at the start of the experiment, and enclosure statistically controlled, body condition change during the experimental period was significantly related to the habituation index (Table 1). This means that greater ability of individuals to habituate was associated with improved body condition (Fig. 2). There was a significant enclosure effect, with body condition change varying among enclosures (Table 1). Boldness did not affect body condition change ($P>0.95$, Table 1), nor did the interaction between habituation ability and boldness ($P>$ 0.95, Table 1) or the interaction between habituation ability and enclosure ($P>0.80$, Table 1).

We repeated the analysis using the body mass change as dependent variable instead of the body condition change and

Table 1 Effects of habituation, boldness, initial body condition, snout to vent length, times exposed to the habituation stimuli, sex, enclosure, the interaction between habituation and boldness, and the interaction between habituation and enclosure on the body condition change of Iberian lizards

	F	D.F.	P
Intercept	2.96	1, 17	0.103
Habituation index	6.13	1, 17	**0.024**
Boldness index	0.01	1, 17	0.974
Initial body condition	0.12	1, 17	0.736
SVL (log)	2.72	1, 17	0.118
Exposure index	0.27	1, 17	0.608
Sex	0.01	1, 17	0.902
Enclosure	3.40	3, 17	**0.025**
Habituation × enclosure	0.33	3, 17	0.802
Habituation × boldness	0.01	1, 17	0.957

Significant results are in bold
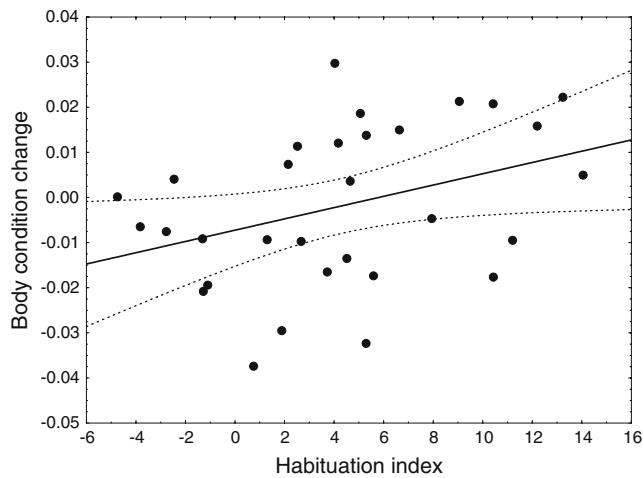
D.F. Degress of Freedom

Fig. 2 Relationship between habituation index and body condition change (r^2=0.13) in Iberian wall lizards with 95% confidence intervals

obtained the same main result; greater ability to habituate was associated with greater body mass gain ($F_{1,20}$=12.12, P= 0.002). We also found a significant effect of enclosure ($F_{3,20}$=10.61, $P<0.001$), but no other variables affected body mass change significantly ($F_{1,20}$ ranged from 0.01 to 1.38, $P>0.05$).

Finally, body condition change during the experimental phase was not significantly associated with body condition change during the acclimation phase (Spearman's rank correlation, r_s=0.07, P=0.698).

Discussion

This is the first study that shows that ability to habituate to a low-risk predator is positively associated with body condition gain. Those individual lizards that quickly decreased their antipredator responses over the course of the experiment were able to increase their body reserves more than those lizards that showed a lesser degree of habituation to the non-lethal predator stimuli. Contrary to our expectations, boldness did not influence changes in lizard body condition. Individual boldness did not affect the habituation ability of lizards either (Rodríguez-Prieto et al., in review).

We did not find an association between body condition gained during the acclimation phase and the subsequent gains during the habituation experiment. Thus, we believe our results are not directly influenced by a differential ability to capture or process food. The enclosure where lizards were housed influenced body condition, probably reflecting differences in food abundance and thermoregulatory opportunities due to the varying cover of surrounding trees. Nonetheless, we controlled for this enclosure effect statistically. Sex did not influence change in body condition, which could be explained by the experiments being carried at least 2 months after the

period of oviposition. At the end of August, both males and females must gain energetic reserves before winter.

Our results support the idea that boldness is consistent across contexts (Ward et al. 2004; Wilson and Godin 2009). Those lizards that were more prone to leave a refuge under simulated attacks in the plastic cage were also found to initiate flight at closer distances in the semi-natural enclosure more than 2 months later. However, our results suggest that boldness had no effect on the ability of lizards to maintain or increase their body condition. The effect of habituation in our particular scenario may have overridden any other behavioral effect on body condition. Alternatively, the lack of an effect may be related to our experimental scenario, because the effects of boldness in traits related to fitness can vary between contexts (Smith and Blumstein 2008). Further research is needed to ascertain the causes of this lack of association between boldness and body condition change.

Those individuals that habituated more readily to a frequently encountered low-risk predator (as shown by their faster decrease in FID) would have a relative advantage over those individuals unable to adjust that rapidly. This resulted in greater body condition improvement for lizards with higher habituation ability. This could arise from a reduction in the energetic, foraging, and thermoregulatory costs associated with fleeing to a refuge (Amo et al. 2006; Martín and López 1999). The mechanism implicated merits more research particularly in light of recent findings. For instance, more habituated individuals might also reduce their physiological stress responses to the predation stimuli (Ellenberg et al. 2009) parallel to the measured reduction in FID. Heart rate increase (Ellenberg et al. 2009) and glucocorticoid secretion (Sapolsky 1992; Sheriff et al. 2009; Walker et al. 2006) are common stress responses to predation risk that can affect body condition; high levels of glucocorticoids reduce body condition if maintained for several days (Sapolsky 1992). The lack of association between the exposure index or boldness and body condition change (Table 1) further supports the idea that some non-behavioral process associated with habituation (e.g., reduction in physiological stress responses) may play a role in the variation in body condition.

Under the risk allocation hypothesis (Lima and Bednekoff 1999), antipredator behavior at any given time is influenced not only by the present predation risk, but also by the history of temporal variation in risk. Risk allocation may produce a reduction in antipredator responses in frequently disturbed areas, similar to that produced by habituation (Rodriguez-Prieto et al. 2009). Risk allocation and habituation are not mutually exclusive, and both processes can act simultaneously (Rodriguez-Prieto et al. 2009). However, while risk allocation predicts reduced antipredator responses as the frequency of predator encounters increases, we measured

habituation as the progressive reduction in antipredator responses over the course of several days under a constant frequency of predator encounters, which could not be produced by risk allocation.

One could argue that the association between the decrease in FID over time (i.e., habituation) and the increase in body condition actually may work the other way round: some lizards may decrease their FID because they have attained a greater body condition, since antipredator responses may be condition-dependent in animals (Beale and Monaghan 2004). However, (1) we controlled for initial body condition in the analysis, (2) antipredator responses do not appear to be condition-dependent in lizards (Pérez-Tris et al. 2004), and (3) even if condition dependence is prevalent in our system we would actually expect it to produce the opposite pattern; individuals gaining body condition would increase their FID because higher energy reserves would allow them to allocate higher effort into antipredator behavior (Beale and Monaghan 2004). Similarly, we would expect individuals with high-body condition to increase their FID in order to protect their higher future expected fitness (Clark 1994; Cooper and Frederick 2007).

Body condition is used in ecology as an estimate of nutritional state and is a good predictor of survival and/or reproductive success (Jakob et al. 1996; Schulte-Hostedde et al. 2005). This positive association between body condition and fitness, while not universal (see Dibattista et al. 2007), is widespread in many taxa, such as amphibians (e.g., Garner et al. 2009; Reading 2007), reptiles (e.g., Salvador et al. 2008; Shine et al. 2001), birds (e.g., Buenestado et al. 2009; Taylor and Jamieson 2007), and mammals (e.g., Dobson and Michener 1995; Wauters and Dhondt 1995). Animals with better body condition have higher energy reserves and may allocate more resources to reproduction and maintenance (Van Noordwijk and de Jong 1986), being better prepared to initiate the breeding season (e.g., Naulleau and Bonnet 1996), to fight off parasites and diseases (e.g., Amo et al. 2006; Garner et al. 2009), and to gain greater access to receptive females (e.g., Hofman and Henle 2006; Salvador et al. 2008). Moreover, better body condition usually allows the production of larger clutches (e.g., Radder and Shanbhag 2004) or offspring of larger size (e.g., Hofman and Henle 2006), which in turn may lead to higher offspring survivorship (e.g., Díaz et al. 2005; Sinervo et al. 1992).

Our findings suggest that habituation ability may be adaptive for individuals living in areas with a high frequency of human disturbance. This supports the potential use of habituation as a management tool for some wild animal populations endangered by an excess of outdoor recreation, as suggested by others (Davies et al. 2007; Fox and Madsen 1997; Geist 1975, 1978; Martínez-Abraín et al. 2008; Nisbet 2000; Sutherlan 2007; Taylor and Knight

2003). Recent studies on the specificity of antipredator habituation in wild animals have found no transfer of habituation from target predator stimuli (i.e., a low-risk predator) to other predator stimuli (i.e., a high-risk predator) (Coleman et al. 2008; Deecke et al. 2002; Hemmi and Merkle 2009; Martínez-Abraín et al. 2008; but see Mccleery 2009). Moreover, Labra and Leonard's (1999) results, while not focused on habituation transfer, imply that lizards from human-habituated populations retained, or even increased, their responsiveness to raptor predators. However, not all species may be suitable for habituation (e.g., Humboldt versus yellow-eyed penguins; Ellenberg et al. 2006, 2009), while some species may actually exacerbate human-wildlife conflicts if habituated (e.g., *Cervus elaphus*, Kloppers et al. 2005; Thompson and Henderson 1998). Overall, we caution that habituation of wild populations could have unintended consequences, and a better understanding of the mechanisms of habituation is needed before implementing it as a management tool.

The ability to habituate can provide benefits for individuals exposed to low-risk predators, which may be favored by natural selection. However, those individuals more prone to habituation could also be more exposed to the costs of habituation to the wrong predators (Frid and Dill 2002). For instance, if a dangerous predator does not show predatory behavior for several consecutive encounters with a prey individual, this individual could become incorrectly habituated to the predator provided it has a high propensity for habituation. This could have lethal consequences in future encounters. Depending on the context (e.g., prevalence of low-risk predators in the area), the cost of habituation to the wrong predator could counteract the benefits of rapid habituation ability, thus creating a trade-off contributing to the maintenance of widespread individual variation in habituation potential (Olson et al. 1997; Stolen 2003; Runyan and Blumstein 2004; Ellenberg et al. 2009, this study).

References

Amo L, López P, Martín J (2006) Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizards. Biol Conserv 131:402–409

Amo L, López P, Martín J (2007) Refuge use: a conflict between avoiding predation and losing mass in lizards. Physiol Behav 90:334–343

Beale C, Monaghan P (2004) Behavioural responses to human disturbance: a matter of choice? Anim Behav 68:1065–1069

Béchet A, Giroux J-F, Gauthier G (2004) The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. J Appl Ecol 41:689–700

Brown C, Jones F, Braithwaite VA (2007) Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcope*. J Fish Biol 71:1590–1601

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Lett 7:999–1014

Buenestado FJ, Ferreras P, Blanco-Aguiar JA, Tortosa FS, Villafuerte R (2009) Survival and causes of mortality among wild Red-legged Partridges *Alectoris rufa* in southern Spain: implications for conservation. Ibis 151:720–730

Carrete M, Tella JL (2010) Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. Biol Lett. doi:10.1098/rsbl.2009.0739

Clark CW (1994) Antipredator behavior and the asset-protection principle. Behav Ecol 5:159–170

Coleman A, Richardson D, Schechter R, Blumstein DT (2008) Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)? Biol Lett 4:250–252

Cooper WE Jr (2003) Shifted balance of risk and cost after autotomy affects use of cover, escape, activity and foraging in the keeled earless lizard (*Holbrookia propinqua*). Behav Ecol Sociobiol 54:179–187

Cooper WE Jr, Frederick WG (2007) Optimal flight initiation distance. J Theor Biol 244:59–67

Cooper WE Jr, Wilson DS (2008) How to stay alive after losing your tail. Behaviour 145:1085–1099

Creel S, Christianson D (2008) Relationships between direct predation and risk effects. Trends Ecol Evol 23:194–201

Davies M, Newsome D, Moncrieff D, Smith A (2007) Conserving the Black-flanked Rock-wallaby (*Petrogale lateralis lateralis*) through tourism: development of a habitat ranking system for translocated animals and the need for on-going management. Conserv Sci W Aust 6:1–12

Deecke VB, Slater PJB, Ford JKB (2002) Selective habituation shapes acoustic predator recognition in harbour seals. Nature 420:171–173

Díaz JA, Pérez-Tris J, Tellería JL, Carbonell R, Santos T (2005) Reproductive investment of a lacertid lizard in fragmented habitat. Conserv Biol 19:1578–1585

Dibattista JD, Feldheim KA, Gruber SH, Hendry AP (2007) When bigger is not better: selection against large size, high condition and fast growth in juvenile lemon sharks. J Evol Biol 20:201–212

Dobson FS, Michener GR (1995) Maternal traits and reproduction in Richardson's ground squirrels. Ecology 76:851–862

Domjan M (2003) The principles of learning and behavior. Belmont, California

Ellenberg U, Mattern T, Seddon PJ, Luna-Jorquera G (2006) Physiological and reproductive consequences of human disturbance in Humboldt penguins: the need for species specific visitor management. Biol Conserv 133:95–106

Ellenberg U, Mattern T, Seddon PJ (2009) Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. Anim Behav 77:289–296

Féret M, Gauthier G, Béchet A, Giroux J-F, Hobson KA (2003) Effect of a spring hunt on nutrient storage by greater snow geese in southern Quebec. J Wildl Manage 67:796–807

Fox AD, Madsen J (1997) Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. J Appl Ecol 34:1–13

Fraser DF, Gilliam JF (1992) Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. Ecology 73:959–970

Frid A, Dill LM (2002) Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol 6:11

Garner TWJ, Walker S, Bosch J, Leech S, Rowcliffe JM, Cunningham AA, Fisher MC (2009) Life history tradeoffs influence mortality associated with the amphibian pathogen *Batrachochytrium dendrobatidis*. Oikos 118:783–791

Geist V (1975) On the management of mountain sheep: theoretical considerations (and discussion). In: Trefethen JB (ed) The wild sheep in modern North America. Boone & Crockett Club, Alexandrai, pp 77–105

Geist V (1978) Behavior. In: Schmidt JL, Gilbert DL (eds) Big game of North America: ecology and management. Stackpole Books, Harrisburg, pp 283–296

Gill JA, Norris K, Sutherland WJ (2001) Why behavioural responses may not reflect the population consequences of human disturbance. Biol Conserv 97:265–268

Hemmi JM (2005) Predator avoidance in fiddler crabs: 1. Escape decisions in relation to the risk of predation. Anim Behav 69:603–614

Hemmi JM, Merkle T (2009) High stimulus specificity characterizes anti-predator habituation under natural conditions. Proc R Soc B 276:4381–4388

Hjeljord O, Histøl T (1999) Range–body mass interactions of a northern ungulate—a test of a hypothesis. Oecologia 119:326–339

Hofman S, Henle K (2006) Male reproductive success and intrasexual selection in the common lizard determined by DNA-microsatellites. J Herpetol 40:1–6

Ikuta LA, Blumstein DT (2003) Do fences protect birds from human disturbance? Biol Conserv 112:447–452

Jakob EM, Marshall SD, Uetz GW (1996) Estimating fitness: a comparison of body condition indices. Oikos 77:61–67

Kloppers EL, St Claire CC, Hurd TE (2005) Predator-resembling aversive conditioning for managing habituated wildlife. Ecol Soc 10:31

Labra A, Leonard R (1999) Intraspecific variation in antipredator responses of three species of lizards (*Liolaemus*): possible effects of human presence. J Herpetol 33:441–448

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lima SL, Bednekoff PE (1999) Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat 153:649–659

López P, Hawlena D, Polo V, Amo L, Martín J (2005) Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards. Anim Behav 69:1–9

Lord A, Waas JR, Innes J, Whittingham MJ (2001) Effects of human approaches to nests of northern New Zealand dotterels. Biol Conserv 98:233–240

Magle S, Zhu J, Crooks KR (2005) Behavioral responses to repeated human intrusion by black-tailed prairie dogs (*Cynomis ludovicianus*). J Mammal 86:524–530

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

Martínez-Abraín A, Oró D, Conesa D, Jiménez J (2008) Compromise between seabird enjoyment and disturbance: the role of observed and observers. Environ Conserv 35:104–108

Mccleery RA (2009) Changes in fox-squirrel anti-predators behaviors across the urban-rural gradient. Landscape Ecol 24:483–493

Müllner A, Linsenmair KE, Wikelski M (2004) Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). Biol Conserv 118:549–558

Naulleau G, Bonnet X (1996) Body condition threshold for breeding in a viviparous snake. Oecologia 107:1432–1939

Nisbet ICT (2000) Disturbance, habituation, and management of waterbirds colonies. Waterbirds 23:312–332

Olson TL, Gilbert BK, Squibb RC (1997) The effects of increasing human activity on brown bear use of an Alaskan river. Biol Conserv 82:95–99

Pauli JN, Buskirk SW (2007) Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog Cynomys ludovicianus. J Appl Ecol 44:1219–1230

Peluc SI, Sillett TS, Rotenberry JT, Ghalambor CK (2008) Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behav Ecol 19:830–835

Pérez-Tris J, Díaz JA, Tellería JL (2004) Loss of body mass under predation risk: cost of antipredatory behaviour or adaptive fit-for-escape. Anim Behav 67:511–521

Polo V, López P, Martín J (2010) Uncertainty about future predation risk modulates monitoring behaviour from refuges in lizards. Behav Ecol (in press)

Radder RS, Shanbhag BA (2004) Factors influencing offspring traits in the oviparous multi-clutched lizard, Calotes versicolor (Agamidae). J Biosci 29:105–110

Rankin CH et al (2009) Habituation revisited: an updated and revised description of the behavioral characteristics of habituation. Neurobiol Learn Mem 92:135–138

Reading CJ (2007) Linking global warming to amphibian declines through its effects on female body condition and survivorship. Oecologia 151:125–131

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse N (2007) Integrating animal temperament within ecology and evolution. Biol Rev 82:291–318

Rodriguez-Prieto I, Fernández-Juricic E, Martín J, Regis Y (2009) Antipredator behavior in blackbirds: habituation complements risk allocation. Behav Ecol 20:371–377

Runyan AM, Blumstein DT (2004) Do individual differences influence flight initiation distance? J Wildl Manage 68:1124–1129

Salvador A, Martín J, López P (1995) Tail loss reduces home range size and access to females in male lizards, Psammodromus algirus. Behav Ecol 6:382–387

Salvador A, Díaz JA, Veiga JP, BloorP BRP (2008) Correlates of reproductive success in male lizards of the alpine species Iberolacerta cyreni. Behav Ecol 19:169–176

Sapolsky RM (1992) Neuroendocrinology of the stress response. In: Becker JB, Breedlove SM, Crews D (eds) Behavioral Endocrinology. Massachusetts Institute of Technnology Press, Cambridge, pp 287–324

Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ (2005) Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163

Sheriff MJ, Krebs CJ, Boonstra R (2009) The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. J Anim Ecol 78:1249–1258

Shine R, LeMaster LP, Moore IT, Olsson MM, Mason RT (2001) Bumpus in the snake den: effects of sex, size, and body condition on mortality of red-sided garter snakes. Evolution 55:598–604

Sinervo B, Doughty P, Huey RB, Zamudio K (1992) Allometric engineering: a causal analysis of natural selection on offspring size. Science 258:1927–1930

Smith BR, Blumstein DT (2008) Fitness consequences of personality: a meta-analysis. Behav Ecol 19:448–455

Stolen ED (2003) The effects of vehicle passage on foraging behavior of wading birds. Waterbirds 26:429–436

Sutherlan WJ (2007) Future directions in disturbance reearch. Ibis 149:120–124

Tarlow E, Blumstein DT (2007) Evaluating methods to quantify anthropogenic stressors on wild animals. Appl Anim Behav Sci 102:429–451

Taylor AR, Knight RL (2003) Wildlife responses to recreation and associated visitor perceptions. Ecol Appl 13:951–963

Taylor SS, Jamieson IG (2007) Factors affecting the survival of founding individuals in translocated New Zealand Saddlebacks Philesturnus carunculatus. Ibis 149:783–791

Thompson MJ, Henderson RE (1998) Elk habituation as a credibility challenge for wildlife professionals. Wildl Soc Bull 26:477–483

Van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Walker BG, Boersma PD, Wingfield JC (2006) Habituation of adult magellanic penguins to human visitation as expressed trough behavior and corticosterone secretion. Conserv Biol 20:146–154

Ward AJW, Thomas P, Hart PJB, Krause J (2004) Correlates of boldness in three-spined sticklebacks (Gasterosteus aculeatus). Behav Ecol Sociobiol 55:561–568

Wauters LA, Dhondt AA (1995) Lifetime reproductive success and its correlates in female Eurasian red squirrels. Oikos 72:402–410

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol 75:1182–1189

Wilson ADM, Godin JGJ (2009) Boldness and behavioral syndromes in the bluegill sunfish, Lepomis macrochirus. Behav Ecol 20:231–237

Ydenberg RC, Dill LM (1986) The economics of fleeing from predators. Adv Study Behav 16:229–249