



## ARTICLES

# Sources of individual shy–bold variations in antipredator behaviour of male Iberian rock lizards

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Individual animals from the same population, sex, age and reproductive status often respond differently and consistently to predators. One important dimension of this behavioural variation is the shy–bold continuum. Innate differences in boldness might explain why individuals differ in their antipredator behaviour. In a laboratory experiment, we examined the sources of individual variation in antipredator behaviour of adult male lizards *Lacerta monticola*. We simulated in the laboratory repeated predatory attacks of low or high risk and analysed activity levels and refuge use in both situations. Multivariate analyses suggested the existence of two consistent and independent shy–bold continua. The first described a gradient from bold lizards that spent shorter times in the refuge after predatory approaches to shy lizards with longer emergence times, whereas the other described a gradient from bold lizards with a low propensity to hide when the predator was close but risk was low to shy lizards that hid more often. We analysed whether morphological characteristics, body condition and health (estimated from their T cell immunocompetence) of individuals might account for the differences observed. Bold individuals had smaller absolute body size, but relatively larger heads, better body condition and better health. Bold individuals with a low propensity to hide when risk was low had larger absolute body sizes, whereas relative head size, and body condition and health were not important. We suggest that the position of an individual in the shy–bold continua might reflect its optimal antipredator behaviour, which would be a function of its health, general quality and ability to evade predators.

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Predation is considered one of the most important selection pressures in shaping prey behaviour (Lima & Dill 1990; Lima 1998). Because natural selection favours individuals that avoid predators successfully, prey should have adjusted their antipredator behaviour over times. Thus, we might predict little variation between individuals in antipredator responses. Nevertheless, prey should optimize their antipredator responses by balancing antipredator demands with other requirements (Lima & Dill 1990; Sih 1992). Prey are known to adjust their escape response and refuge use to minimize costs such as the loss of opportunities, for example for mating or foraging, or physiological costs (Ydenberg & Dill 1986; Sih 1997). This flexibility may explain changes in the antipredator

response of the same individual depending on temporal changes in cost–benefit expectations (e.g. Martín & López 2000a, b; Martín et al. 2003a, b). In addition, because costs and benefits can vary between sexes or age classes, we predict differences in the responses of individuals of different classes (e.g. Martín & López 2003).

However, individual animals often behave in a way that distinguishes them from other members of their species of the same sex, state and age class. Antipredator behaviour may vary between individuals within populations, and understanding of the source of this variation is fundamental to evolutionary studies (Bennett 1987; Wilson 1998). For example, individual garter snakes, *Thamnophis ordinoides* (Brodie & Russell 1999) and salamanders, *Ambystoma jeffersonianum* (Brodie 1989) from the same population, sex and reproductive status respond differentially to predators. When these differences between individuals are consistent over time they have been considered 'behavioural styles', coping styles or personalities (Gosling & John 1999; Koolhaas et al. 1999; Réale

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et al. 2000; Gosling & Vazire 2002), which may have a genetic basis (Dingemanse et al. 2002, 2003; Drent et al. 2003; Van Oers et al. 2004). One important dimension of behavioural variation between individuals is the shy–bold continuum (Wilson et al. 1993, 1994; Coleman & Wilson 1998; Gosling 2001), boldness being defined as the willingness to take risks in novel or challenging situations (Wilson et al. 1994; Boissy 1995). The shy–bold continuum concept is relatively new, and, therefore, the taxonomic distribution and its evolutionary implications are little known (Wilson et al. 1994; Boissy 1995; Gosling & John 1999). Innate or heritable differences in boldness might explain why homogeneous individuals differ in their antipredator behaviour. If the degree of boldness when confronted with a predator was a relatively fixed characteristic of each individual, independently of environmental or variable intrinsic conditions, we would predict selection against nonoptimal responses. However, if this variability remains in the population, we should look for an evolutionary explanation.

Field studies have shown that lizards' escape decisions and patterns of refuge use are influenced by changes in the level of predation risk and the costs of refuge use (Cooper, 1997, 1998a, 1999, 2000; Martín & López 1999, 2000a, 2001). Studies of Iberian rock lizards, *Lacerta monticola*, have shown that they are able to modulate the risk of predation by modifying the distances to the nearest refuge and approach distances as a function of their ability to run (Carrascal et al. 1992; Martín & Salvador 1993) and of the thermal costs of refuge use (Martín & López 2000a, 2003). Their emergence times from a refuge may vary as a function of the level of the predation risk, the thermal conditions of the refuge, and foraging or mating expectations outside the refuge (Martín & López 1999, 2001; Martín et al. 2003a, b). In spite of these accurate behavioural modifications to balance costs and benefits of the antipredator response, anecdotal field observations suggest that there is an apparently clear and consistent variability in the responses of different individuals under similar conditions (J. Martín & P. López, personal observation). This variability does not seem to be caused by changes in environmental conditions, sex, state, or age classes, but we need more detailed studies to reveal the causes of variability in this lizard population.

We examined sources of variation in antipredator behaviour of a homogeneous group of adult male Iberian rock lizards. We limited the experiment to adult males (snout–vent length, SVL > 60 mm; Elvira & Vigal 1985) to separate the proportion of individual variation attributed to sex and age differences (e.g. Martín & López 2003; Martín et al. 2003b) from the resulting individual variation that could be due to different 'personalities'. We simulated in the laboratory repeated predatory attacks of high or low risk, and analysed (1) activity levels and refuge use in high- and low-risk situations, (2) the time spent in refuges after a high-risk predatory attack, and (3) the propensity to hide in refuges when the predator is close but not actually attacking (i.e. low risk). We analysed whether these responses are consistent within an individual, and whether small differences in morphological characteristics, which influence social dominance, and

in body condition and health might be related to the differences observed in antipredator behaviour.

## METHODS

During July 2002 we captured by noosing 34 adult males in 'Puerto de Navacerrada', Guadarrama Mountains, Central Spain. Lizards were individually housed at 'El Ventorrillo' Field Station (Navacerrada, Madrid Province) 5 km from the capture site in outdoor opaque plastic cages (80 × 50 cm and 60 cm high) containing rocks for cover. Food (mealworms and crickets) dusted with a multivitamin powder and water were provided ad libitum. Lizards were housed in these cages for at least a week to familiarize them with the novel environment prior to testing. All the animals were healthy during the trials, did not show any sign of stress, and at the end of the experiments were released at their initial sighting location before capture. All of them had maintained their original body mass through the experiment. The experiments were done under licence from the Madrid Environmental Agency (Consejería del Medio Ambiente de la Comunidad de Madrid).

### Morphology, Body Condition and Health

Bold individuals might simply be the winners in social competition, because more aggressive individuals in intraspecific contests would also be bold against predators (e.g. Tulley & Huntingford 1988; reviewed in Wilson et al. 1994). Thus, we tested whether morphological features, such as relative head size or colour badges, which reflect the potential social dominance of male lizards, are related to boldness. This and many other lizards are sexually dimorphic with respect to head size (Braña 1996), which affects the outcome of intrasexual agonistic contests of many lizards (Anderson & Vitt 1990) including this species: males with relatively larger heads are more dominant (López et al. 2002). Therefore, relative head size between males of similar age is an indicator of potential social dominance in this lizard (López et al. 2002). We measured lizard body size with a ruler (SVL,  $\bar{X} \pm \text{SE} = 73 \pm 1$  mm, range 60–80 mm) and their weight with a pesola spring scale ( $\bar{X} \pm \text{SE} = 7.7 \pm 0.2$  g, range 4.8–10.5 g). We used a digital calliper to measure ( $\pm 0.01$  mm) the head of males. Head height ( $\bar{X} \pm \text{SE} = 7.5 \pm 0.1$  mm, range 6.7–9.1 mm) was measured as the greatest vertical distance through the snout from the highest portion of the head to the bottom of the lower jaw. Head length ( $\bar{X} \pm \text{SE} = 16.2 \pm 0.2$  mm, range 13.8–18.0 mm) was the greatest horizontal distance between the tip of the snout and the posterior side of the parietal scales. Head width ( $\bar{X} \pm \text{SE} = 11.0 \pm 0.2$  mm, range 9.1–13.2 mm) was the greatest horizontal distance between the external sides of the parietal scales.

Many male lizards also have a conspicuous row of small but distinctive blue spots that runs along the side of the body on the outer margin of the belly. These spots also seem to have a role in intrasexual social relationships between males, as their number may function as a long-distance signal enhancing body size of dominant

larger/older males (P. López & J. Martín, unpublished data). We noted the number of blue spots on each side of the lizards and calculated an average number for both sides ( $\bar{X} \pm SE = 6.5 \pm 0.5$  spots/side, range 0–12.5 spots/side). We removed the influence of body size on head and spots measurements by regressing each against SVL (all variables log transformed) and used the residuals in further analyses.

We also hypothesized that boldness might be related to differences in the physical condition of otherwise similar individuals. Thus, we calculated body condition of each individual as the residuals from the regression equation of body mass (g) on SVL (mm), both variables log transformed, which may represent an index of the relative amount of fat stored, and, hence, of individual physical condition or nutritional status (Bonnet & Naulleau 1994; reviewed in Green 2000). To assess the health of lizards we used a delayed-type hypersensitivity test: the phytohaemagglutinin injection assay (PHA test). This test is a reliable measure of T-cell-dependent immunocompetence in vivo (McCorkle et al. 1980; Lochmiller et al. 1993), and has been used in many studies of many animals including lizards (Merino et al. 1999; Svensson et al. 2001). We marked a point with permanent ink on the foot pad of both hindlimbs. We then measured the thickness at this point with a pressure-sensitive spessimeter ( $\pm 0.01$  mm) to standardize pressure during measurements. Immediately after, we injected 0.02 mg of PHA dissolved in 0.01 ml of phosphate-buffered saline (PBS) water in the right foot pad, and the same volume of PBS in the left foot pad. Lizards were released in their terraria, and after 24 h we measured the foot pad thickness at the marked points. The cellular immune response index was calculated as the difference between pre- and postinjection measures on the right foot pad (PHA injected) minus the same difference on the left foot pad (control, PBS injected;  $\bar{X} \pm SE = 0.26 \pm 0.03$  mm, range 0.01–0.67 mm; Lochmiller et al. 1993). Because the thickness of the foot pad might be related to body size and, thus, affect the magnitude of the swelling response, we also calculated the residuals by regressing the immune response index against body mass (all variables log transformed). The only appreciable effect of the PHA injection was a slight swelling of the skin, caused by the immune response, which disappeared after 48 h. None of the lizards showed any sign of stress or pain for these tests, and all looked healthy after the trials.

Given the high correlation between all these measurements, we used principal components analysis (PCA) to reduce the 13 morphological and condition variables (Table 1) to a smaller number of independent components. The initial factorial solutions were rotated by the Varimax procedure (Sokal & Rohlf 1995). We then used factor scores of each principal component for further analyses.

### Antipredator Behaviour

We observed antipredator behaviour of lizards in outdoor conditions during July and August, from 1200 to 1600 hours GMT, when lizards were fully active. Terraria

**Table 1.** Principal components analysis (morphological principal components, MPC) for morphological measurements and body condition and health of lizards

	MPC1	MPC2	MPC3
Snout–vent length	<b>0.97</b>	–0.23	–0.02
Body mass	<b>0.92</b>	0.25	–0.06
Head height	<b>0.78</b>	0.23	–0.01
Head width	<b>0.82</b>	0.34	0.01
Head length	<b>0.91</b>	0.22	–0.13
Blue spots	0.30	0.34	–0.13
Immune response (PHA)	–0.15	0.01	<b>0.95</b>
Body mass residuals	0.16	<b>0.80</b>	–0.01
Head height residuals	0.14	<b>0.62</b>	0.02
Head width residuals	0.13	<b>0.75</b>	0.04
Head length residuals	0.16	<b>0.78</b>	–0.20
Blue spots residuals	–0.08	0.43	0.05
Immune response residuals	0.03	–0.10	<b>0.96</b>
Eigenvalue	4.90	2.37	1.83
% Variance	37.7	18.2	14.1

Bold type indicates correlations of variables with the principal components greater than 0.60.

were placed separately from each other, such that our approaches to a terrarium did not influence lizards in other terraria. We allowed lizards to thermoregulate and attain their preferred body temperatures for at least 2 h before the trials (Martín & Salvador 1993). Terraria were placed in an open sunny location while shade was provided by one of the terrarium walls and the refuge (flat stones of similar size and shape).

In each trial, we approached each terrarium several times to simulate predatory attacks, but previously noted whether the lizard was hiding inside the refuge, leaning out of the refuge (i.e. the lizard stayed inside the refuge but looked outside with the snout closer than 1 cm to the exit of the refuge), or outside the refuge. This was considered as a measure of the antipredator behaviour of lizards to the previous approaches of the experimenter. Lizards and other animals may react differentially to the approach of a predator as a function of the threat of the attack (Burger & Gochfeld 1990; Cooper 1997; Martín & López 1999). Thus, we approached terraria of lizards in one of two ways. In the ‘low-risk’ treatment, the experimenter walked slowly near (1 m) but tangentially to the terrarium, looking straight ahead and without paying attention to the lizard. Lizards could clearly see the experimenter from their terraria, as showed by alert behaviour and, eventually, escape responses of some lizards. In the ‘high-risk’ treatment, the experimenter simulated a predatory attack by rapidly approaching the terraria and tapping lizards close to the tail with a brush to stimulate them to run and hide in the refuge. With this procedure we simulated an attack from an avian predator coming from above the lizard. We are confident that with these procedures we simulated two risk levels of different intensity, because fleeing responses of lizards clearly differed between situations, and were similar to those observed in field experiments (Martín & López 1999). For each lizard, we simulated 24 attacks within a day (12 low-risk attacks every 10 min within 2 h, followed by 12 high-risk attacks every 10 min within 2 h) repeated over at least

48 h later. The same person performed all predatory attacks while another immobile and hidden person recorded the lizard's behaviour with binoculars from a vantage point. Lizards' behaviour was not affected by this hidden experimenter.

From the observations of the initial position of lizards taken every 10 min immediately before each of the 12 approaches, we calculated for the two trials the average number of times that a lizard was outside, inside or leaning out of the refuge during the high-risk and low-risk situations. Thus, we calculated an index of boldness for each individual under each risk level ranging, for example for the time spent outside, from 0 (if a lizard was hidden in the refuge in all observations; i.e. 'very shy') to 12 (if the lizard was always outside the refuge; i.e. 'very bold'). A similar index could be calculated for times when the lizard was seen inside the refuge (i.e. from 0 for 'bold' to 12 for 'shy').

In the high-risk treatment, after the lizard was forced to hide, we retreated and the hidden experimenter recorded from his vantage position the time that the lizard spent in the refuge until its head appeared from the refuge (appearance time), and the time until the lizard emerged entirely from the refuge (emergence time). If the lizard was inside the refuge when we simulated the attack, we touched the open end of the refuge with a paintbrush simulating another predatory attack, as if a predator were trying to flush the lizard from the refuge, and we assigned an emergence time of 10 min. We calculated for each lizard the average appearance and emergence times by considering all the attacks in the high-risk treatment in the two trials. We predicted that bold individuals would have shorter appearance and emergence times.

In the low-risk treatment, we noted the initial position of the lizard, and whether the lizard hid when the experimenter passed by close to the terrarium. We considered that if a lizard hid, it had overestimated the predation risk, given that the predator was passing by but not actually attacking the lizard. Although responding to all approaches by fleeing to the refuge would minimize potential predation risk, time and energy can be saved, and the costs of refuge use minimized, if lizards respond accurately only to actual predatory attacks (Ydenberg & Dill 1986; Martín & López 1999, 2000a). Then, we calculated the proportion of times that a lizard hid when it was outside the refuge, and when it was leaning out of the refuge. We predicted that bold individuals would have a lower proportion of these false-alarm superfluous flights.

Changes in refuge use between the high- and the low-risk treatments were evaluated with repeated measures one-way ANOVAs. Individual consistency in refuge use under the same risk level between the 2 days was calculated as the intraclass correlation coefficient based on variance components derived from a one-way ANOVA (Lessells & Boag 1987). Individual consistency in relative boldness with respect to refuge use across risk levels was tested with Spearman rank correlations (Sokal & Rohlf 1995).

Given the potential high correlation between all these measurements, we used principal components analysis (PCA) to reduce the eight antipredator behaviour variables

**Table 2.** Principal components analysis (antipredator principal components, APC) for the antipredator responses of lizards (see Methods)

	APC1	APC2
Inside refuge under high risk	<b>0.94</b>	0.07
Inside refuge under low risk	<b>0.77</b>	0.39
Outside refuge under high risk	<b>-0.93</b>	-0.11
Outside refuge under low risk	<b>-0.79</b>	-0.46
Appearance time after attack	<b>0.86</b>	-0.04
Emergence time after attack	<b>0.70</b>	0.31
False-alarm flights when leaning out	-0.03	<b>0.78</b>
False-alarm flights when outside	0.25	<b>0.76</b>
Eigenvalue	4.41	1.68
% Variance	55.1	21.1

Bold type indicates correlations of variables with the principal components greater than 0.60.

(Table 2) to a smaller number of independent components. The initial factorial solutions were rotated by the Varimax procedure. We then used factor scores of each principal component for further analyses. Thereafter, we used Pearson product-moment correlations to examine the possible relations between the average values of the PC scores reflecting antipredator behaviour and the average values of the PC scores reflecting morphology and condition of lizards (Sokal & Rohlf 1995).

## RESULTS

### Morphology, Body Condition and Health

The PCA for morphological measurements, body condition and health of lizards produced three components that together accounted for 70% of the variance (Table 1). The first morphology-PC (MPC1) was positively correlated with variables describing absolute body size. Thus, MPC1 described a gradient from smaller to larger lizards. The second PC (MPC2) was positively correlated with variables describing relative head size and body mass residuals, thus describing a gradient to lizards with relatively larger heads and with better body condition. The third PC (MPC3) was positively correlated with the immune response index and the residuals of this index, independently of body size, thus describing a gradient to lizards with better health, as indicated by their T-cell-dependent immunocompetence.

### Antipredator Behaviour

As predicted, lizards were more active (i.e. they were more often seen outside the refuge) in the low-risk than in the high-risk treatment ( $\bar{X} \pm \text{SE} = 4.9 \pm 0.3$  times versus  $3.4 \pm 0.4$  times; one-way repeated measures ANOVA:  $F_{1,33} = 48.25$ ,  $P < 0.0001$ ), and the responses of the same individuals were consistent between days (intraclass correlation coefficient, high risk:  $r = 0.68$ ,  $F_{33,67} = 5.33$ ,  $P < 0.0001$ ; low risk:  $r = 0.34$ ,  $F_{33,67} = 2.02$ ,  $P = 0.02$ ). In addition, individuals were consistent in refuge use across risk levels (Spearman rank correlation:  $r_s = 0.78$ ,  $N = 34$ ,  $P < 0.0001$ ). Thus, bold lizards in the high-risk

treatment (i.e. those that were seen outside the refuge more often than other individuals) were also bold in the low-risk treatment.

In contrast, leaning out of the refuge was not significantly different between treatments ( $\bar{X} \pm SE = 1.6 \pm 0.2$  times versus  $1.4 \pm 0.2$  times; one-way repeated measures ANOVA:  $F_{1,33} = 0.03$ ,  $P = 0.85$ ), but, nevertheless, individuals were consistent in their responses between days (intraclass correlation coefficient, high risk:  $r = 0.48$ ,  $F_{33,67} = 2.83$ ,  $P = 0.002$ ; low risk:  $r = 0.70$ ,  $F_{33,67} = 5.67$ ,  $P < 0.0001$ ) and across risk levels (Spearman rank correlation:  $r_s = 0.67$ ,  $N = 34$ ,  $P < 0.0001$ ).

Individuals varied in the time spent in the refuge after a simulated predatory attack of high risk. Average appearance times ranged between 184 and 533 s ( $\bar{X} \pm SE = 369 \pm 13$  s, coefficient of variation = 21.47), and average emergence times ranged between 258 and 586 s ( $\bar{X} \pm SE = 472 \pm 13$  s, coefficient of variation = 16.89). Individual consistency in time spent in refuges between days was high (intraclass correlation coefficient, appearance:  $r = 0.59$ ,  $F_{33,67} = 3.87$ ,  $P < 0.0001$ ; emergence:  $r = 0.88$ ,  $F_{33,67} = 15.36$ ,  $P < 0.0001$ ).

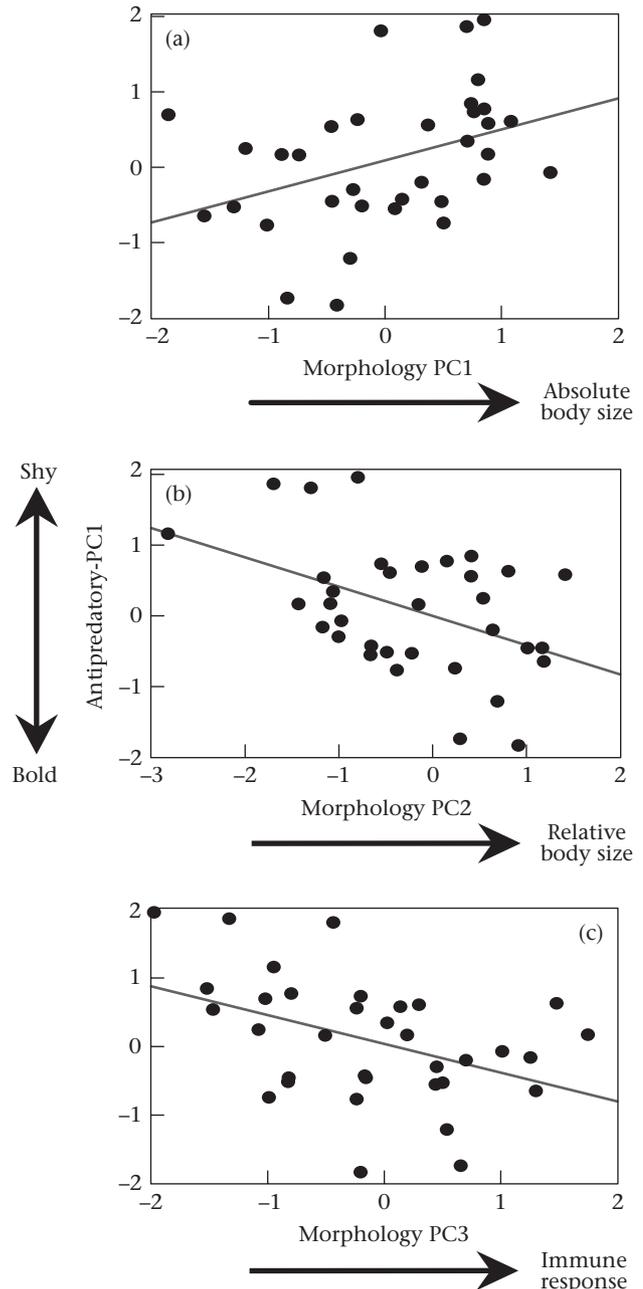
Individuals varied greatly in the proportion of false alarm flights to the refuge in the low-risk treatment. When lizards were leaning out of the refuge, some individuals always hid when the experimenter passed close by, whereas others never hid (proportion of false alarms:  $\bar{X} \pm SE = 0.41 \pm 0.06$ , range 0–1, coefficient of variation = 91.93). Similarly, when lizards were outside the refuge, some individuals hid frequently when the experimenter passed by, whereas others never hid (proportion of false alarms:  $\bar{X} \pm SE = 0.25 \pm 0.04$ , range 0–0.86, coefficient of variation = 90.91).

The PCA for antipredator measurements of lizards produced two components that together accounted for 76.2% of the variance (Table 2). The first antipredator-PC (APC1) was positively correlated with variables describing longer emergence times from the refuge after an actual predatory attack, and more times seen hidden inside the refuge (or fewer times seen outside refuges) in both the high- and the low-risk treatments. Thus, APC1 described a gradient from bold lizards that spent shorter times in the refuge after predatory approaches to shy lizards with longer emergence times. The second PC (APC2) was positively correlated with variables describing a high proportion of false-alarm flights to the refuge in the low-risk treatment. Thus, APC2 described a gradient from bold lizards with a low propensity to hide when the predator was close but risk was low to shy lizards that hid more often.

### Variation in Antipredator Behaviour

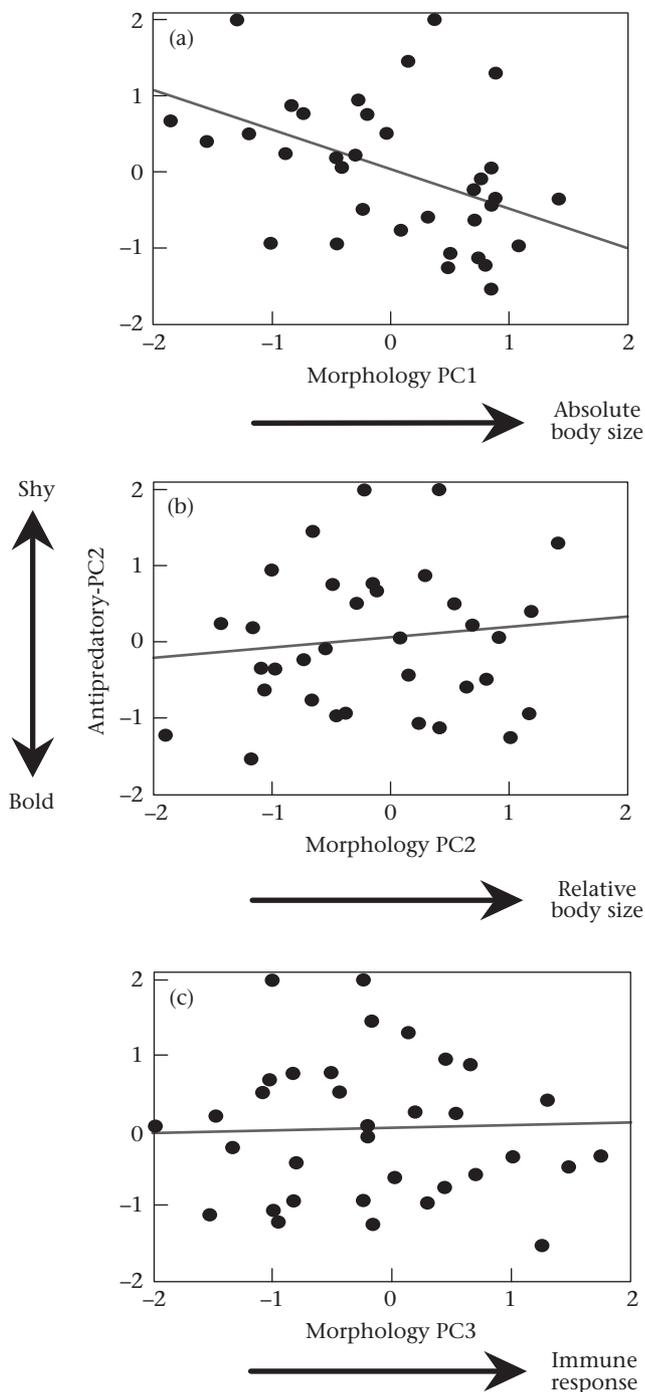
Correlations between MPC scores (i.e. those obtained from the morphology and condition PCA) and APC scores (i.e. those from the antipredator behaviour PCA) indicated that the shy–bold gradients in antipredator behaviour across individuals can be related to some of their morphology and condition characteristics. Thus, shy individuals that spent more time hidden in refuges (APC1) were

those with larger absolute body sizes (MPC1;  $r = 0.38$ ,  $F_{1,32} = 5.45$ ,  $P = 0.026$ ), but with relatively smaller head sizes and poorer body condition (MPC2;  $r = -0.44$ ,  $F_{1,32} = 7.85$ ,  $P = 0.008$ ), and with a worse immune system (MPC3;  $r = -0.43$ ,  $F_{1,32} = 7.26$ ,  $P = 0.01$ ; Fig. 1). However, shy individuals with a high propensity to hide when risk was low (APC2) were those with smaller absolute body sizes (MPC1;  $r = -0.43$ ,  $F_{1,32} = 7.49$ ,



**Figure 1.** Relation between morphology principal component (PC) scores (i.e. those obtained from the principal components analysis of morphology and condition variables) and the scores of the first antipredator-PC (i.e. APC1, which describes a gradient from bold lizards that spent shorter times in the refuge after predatory approaches to shy lizards with longer emergence times). (a) Absolute body size, (b) relative body size and (c) immune response.

$P = 0.01$ ), whereas relative body size (MPC2;  $r = 0.13$ ,  $F_{1,32} = 0.56$ ,  $P = 0.46$ ) and the immune system (MPC3;  $r = 0.03$ ,  $F_{1,32} = 0.03$ ,  $P = 0.86$ ) were not important (Fig. 2).



**Figure 2.** Relation between morphology principal component (PC) scores (i.e. those obtained from the principal components analysis of morphology and condition variables) and the scores of the second antipredator-PC (i.e. APC2, which describes a gradient from bold lizards with a low propensity to hide when the predator was close, but had not attacked, to shy lizards that hid more often). (a) Absolute body size, (b) relative body size and (c) immune response.

## DISCUSSION

Individual adult male *L. monticola* were consistently different in the magnitude of their antipredator responses under similar conditions of risk and costs. These differences in propensity to take risk could be caused by the existence of a shy–bold continuum within this lizard. Nevertheless, these differences might also be related to small subtle differences in morphology, body condition and health, which, however, can be considered as relatively fixed and phenotypically stable characteristics of an individual, at least within a season.

Our study further shows that there are at least two different, and not correlated, continua of antipredator behaviour in *L. monticola*. One gradient refers to time spent in refuges after predatory attacks or approaches of low risk, whereas the other refers to the propensity to hide when a predator is nearby but risk is low (i.e. preventive antipredator behaviour before an actual attack is launched). Thus, although individuals were consistent in their relative levels of refuge use under different levels of risk, individuals that were bold with respect to time spent in refuges after high-risk attacks were not necessarily bold with respect to the propensity to make false-alarm flights when the predator had not attacked. Similarly, sunfish *Lepomis gibbosus*, exposed first to threatening, novel but not dangerous, stimuli and later to a predator showed consistent individual differences in both situations, but these differences did not correlate across contexts (Coleman & Wilson 1998). These findings support the idea that boldness is context specific, and that there might be different behavioural gradients for each type of response.

The relations that we found between antipredator behaviour and morphology or condition might initially suggest that state-dependent factors may account for these shy–bold continua. Differences in absolute body size, although small in the lizards used here, might explain some differences. Patterns of refuge use may be influenced by the thermal conditions (Martín & López 1999, 2000a). Individuals with small body mass cool quickly, and can quickly reach an unfavourable body temperature (Carrascal et al. 1992), which might explain why smaller individuals have shorter emergence times from refuges (Martín & López 1999, 2003). Nevertheless, the differences observed in this experiment were much greater (the shyest individual had emergence times 2.3 times longer than the boldest one) than expected by a simple biophysical explanation (Martín & López 2003).

With respect to the propensity to hide even if an attack has not been launched, small lizards might flee early because they have lower absolute running escape performance (Martín & López 1995, 2003), and thus they might be under greater predation risk. Small, and thus more vulnerable, prey tend to show stronger antipredator behaviour than large prey (i.e. behavioural compensation for morphological vulnerability; Werner et al. 1983; Sih 1986; Dewitt et al. 1999). In addition, body size differences might be important because relative conspicuousness is one of the determinants of escape behaviour (Cooper 1998b; Martín & López 2000b). Larger individuals would be more conspicuous, and, thus, they might assess

that the probability of being detected by a predator passing by is higher, and flee to the refuge sooner (e.g. Martín & López 1995, 2003). In contrast, in this experiment we found the opposite trend, with smaller lizards having a high propensity to hide. Therefore, other explanations, such as the existence of behavioural differences between individuals, should be considered.

Relative head size, and its implications for social dominance, might also explain differences in antipredator behaviour. Male *L. monticola* with relatively larger heads were dominant in intrasexual encounters, and reached dominant status (López & Martín 2002; López et al. 2002). A high testosterone production increases the expression of these sexually dimorphic characters and also increases aggressiveness (Salvador et al. 1996). Bold individuals with respect to social interactions might also be bold under threatening situations because of high testosterone levels (Huntingford 1976; Kagan et al. 1988; Tulley & Huntingford 1988; Godin & Crossman 1994). However, differences that are adaptive in the context of predator avoidance are not necessarily adaptive in other contexts. Thus, the relation between relative head size, an index of social dominance, and boldness, may reflect a trade-off caused by the existence of behavioural correlations across situations (Sih et al. 2003). Nevertheless, it remains possible that bold individuals become dominant rather than dominant individuals becoming bold (Wilson et al. 1994). Another possibility is that dominant males are bold because they may face a conflict between hiding to avoid predators and defending a territory, which requires shorter emergence times from refuges (Cooper 1999; Díaz-Urriarte 1999).

Lizards in presumably worse health, as indicated by their worse T-cell immune response, were shyer. If health affected general performance, the ability of individuals in poor condition to evade predators may be lower, forcing them to adopt a shy strategy. In addition, shyness might be a consequence of having suffered some previous stress that had increased their levels of corticosteroids (Hanley & Stamps 2002), which have immunosuppressive effects (Lochmiller 1996; Cohn 1997; Svensson et al. 2001). For example, chronic stress predisposes hens, *Gallus gallus domesticus*, to react more fearfully to subsequent alarming events (Jones et al. 1988). Furthermore, fear in rats, *Rattus norvegicus* and hens increases with high levels of plasma corticosterone (Gamallo et al. 1986; Jones et al. 1988).

We suggest that the relative boldness of an individual might be a function of its health and associated ability to evade predators. There is a considerable amount of genetic variation for personality types in some mammals and birds, and this behavioural variation is heritable (Sluyter et al. 1995; Dingemans et al. 2002, 2003; Drent et al. 2003). Similarly, the consistency of the antipredator responses in this lizard might be explained because health may be a relatively long-term characteristic of an individual that may be heritable (Brinkhof et al. 1999; Svensson et al. 2001). Behavioural adjustments of the antipredator responses, according to individual characteristics, might allow different strategies to have similar fitness. This might explain the persistence of shy–bold continua in a population. Further studies are needed that

analyse in detail and manipulate the condition of individuals to reveal the sources of consistent behavioural differences between individuals.

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