

Conspicuousness-dependent antipredatory behavior may counteract coloration differences in Iberian rock lizards

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Sexual selection favors more conspicuous male displays, whereas natural selection (via predator pressure) favors less conspicuous displays. However, this trade-off might be altered if males with more conspicuous displays could compensate behaviorally for their increased conspicuousness by acting more cautiously toward predators. The aim of this study was to explore in 2 species of Iberian rock lizards whether or not conspicuous coloration was associated with antipredatory behavior and whether conspicuousness-dependent regulation of antipredatory behavior existed. Our results suggested that male lizards may compensate for the negative effects of conspicuous sexual coloration on predation risk by modulating their antipredatory behavior (time inside refuges, false alarms, etc). We found that male *Iberolacerta monticola*, but not male *Iberolacerta cyreni*, compensated for the negative effects of blue lateral ocelli, which increased visual conspicuousness. However, male lizards did not compensate for relatively unexposed ventral spots. We also found that male *I. monticola* in better condition and with more blue lateral ocelli were shier, whereas male *I. cyreni* in better condition and with more ventral spots were bolder. These 2 lizard species live in habitats that differ in refuge availability and in the number of potential predators, which may promote differences in the trade-off between predation risk and social behavior and may explain the observed interspecific differences in antipredatory behavior. This suggests that regulation of antipredatory behavior may also function as a condition-dependent cost promoting costly (honest) sexual signaling in some species. *Key words:* antipredatory behavior, conspicuous coloration, lizards sexual signals, predation costs, predation risk. [*Behav Ecol* 20:362–370 (2009)]

Sexual selection arises from competition among individuals of one sex for access to mates, giving rise to the evolution of extravagant secondary sexual characters or signals that are used in attraction of mates or in fights for access to mates (Andersson 1994). This raises the question of why males of some species have evolved bright colors, whereas others, even in the same genus, are dull colored. The function and evolution of such variation is usually explained by a balance between sexual selection and species recognition (via female choice), which usually favor conspicuous signals, and natural selection (via predator pressure), which favors cryptic individuals (Endler 1978, 1980; Andersson 1994; Møller and Nielsen 1996; Deutch 1997; Zuk and Kolloru 1998). However, high predation exposure may be compensated for by antipredator behavior (Forsman and Appelqvist 1998; Martín and López 1999b; Losos et al. 2004). Flexible antipredator behaviors are very common across taxa (Lima and Dill 1990). Animals are able to assess predation risk and modify their antipredator behavior depending, for example, on microhabitat characteristics (e.g., Martín and López 1995; Losos and Irshick 1996) or locomotory abilities (Braña 1993; Martín 1996). If males with more conspicuous displays could compensate behaviorally for their increased conspicuousness by acting more cautiously toward predators, the trade-off between sexual and natural selection might be altered. However, the influence of conspicuousness on antipredator behavior remains little

explored (but see Eterovick et al. 1997; Forsman and Appelqvist 1998; Hedrick 2000; Cuadrado et al. 2001; Lewkiewicz and Zuk 2004; Lindström et al. 2007).

Iberian rock lizards (*Iberolacerta* spp.) comprise a group of closely related species of medium sized lizards found mainly in rocky habitats in the Iberian Peninsula (Mayer and Arribas 2003; Carranza et al. 2004). The Carpetane rock lizard, *Iberolacerta cyreni* (formerly *Lacerta monticola cyreni*) is found at high altitude mountains in Central Spain (above 1800 m asl and until 2400 m asl) where it reaches higher population densities than the closely related Iberian rock lizard, *Iberolacerta monticola* (formerly *L. monticola cantabrica*), which is found in lower mountains (below 1500 m asl) and lowland valleys, even at the sea level, in North-western Spain (Galán and Fernández-Arias 1993; Martín 2005a,b). Both species of Iberian rock lizards select microhabitats with high cover of large rocks with crevices that provide refuges (Martín and Salvador 1997; see results) and are typical prey for snakes and mammals and also for many avian predators such as raptors or shrikes (see results; Martín 2005a,b). The lowland lizard species (*I. monticola*) develops more extensive and colorful breeding coloration (i.e., dorsal and ventral bright green coloration, blue spots on lateral ventral scales and blue ocelli over shoulders) than *I. cyreni* (i.e., dull blue-green coloration and a high number of blue spots on lateral ventral scales but none or rarely just one blue ocellum over shoulders) (Arribas 2001, Galán 2008). Blue spots and ocelli of lacertid lizards reflect ultraviolet (UV) light (Arribas 2001; Thorpe and Richard 2001), and both lizards and avian predators can perceive the reflectance of UV light (Fleishman et al. 1993; Cuthill et al. 2000). Bright colors render male lizards more conspicuous, possibly resulting in a greater susceptibility to

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predators (e.g., Martín and López 2001; Stuart-Fox et al. 2003; but see Olsson 1993); thus, we expected that a higher number of UV blue spots increased conspicuousness of Iberian rock lizards, at least, to avian predators. Then, the first goal of this study was to explore whether conspicuousness-dependent regulation of antipredatory behavior in Iberian rock lizards exists and whether it might explain interspecific differences in coloration/conspicuousness. Between-species differences in conspicuousness of signals or predation risk level may affect cost of signaling, which may also affect the adaptive value of conspicuousness-dependent regulation of antipredatory behavior. Lizard populations at high elevations enjoy high survivorship and reach higher densities than those at lower elevations (Bashey and Dunham 1997), likely because of reduced predation (Van Damme et al. 1989; Fox et al. 1994), abundant food, and the uniform distribution and abundance of appropriate thermal microhabitats. We hypothesized that if predation cost of signaling (i.e., high predation risk level) was high, the strength of conspicuousness-dependent regulation of antipredatory behavior may be higher. Typically, it is assumed that 2 localities differ in predation risk when they differ in predator density or community (McLaughlin and Roughgarden 1989, Van Damme and Castilla 1996) or in the availability of protective cover (Snell et al. 1988). Avian predators rely on visual active searching, whereas snakes and mammals rely mainly on chemical cues to locate prey. Thus, to estimate relative predation risk to visual predators on both species of Iberian rock lizards, we surveyed published studies to know the number of potential avian predator species at each population. We also measured microhabitats available and used by lizards to estimate availability of refuges and examined whether potential differences in visual backgrounds (vegetation and substrate cover in the microhabitats selected by lizards) may render one species to be more conspicuous than the other against their respective visual backgrounds.

Finally, behavioral compensation of conspicuousness may be costly (condition dependent) and, therefore, may affect by itself costs of signaling. One prominent model of sexual selection, the handicap model, assume that the marginal costs of signaling must be lower for males in good condition than for males in poor condition (Grafen 1990; Rowe and Houle 1996; Tomkins et al. 2004). Because the empirical evidence for direct fitness costs created by predators on sexual signals is scarce (Kotiaho 2001; but see Zuk and Kolluru 1998), it is not well understood whether predation costs increase in proportion to the expression of the signal or whether they are related to the condition of the males (see Candolin 1997, 1998; Kotiaho et al. 1998; Hedrick 2000; Lewkiewicz and Zuk 2004). Therefore, regulation of antipredatory behavior may compensate for the predation costs of increased sexual signaling. If individuals in better condition are better at escaping predation, and if signaling rate is positively dependent on condition, then the condition-dependent escape rate would reduce the cost of signaling in males that are signaling the most, thus fulfilling the assumptions of good genes sexual selection theory (Kotiaho 2001).

To examine whether antipredator behavior varied between individuals, within each species, in relation to individual conspicuousness, we simulated predatory attacks to lizards in the laboratory. We predicted that only visual signals that increased conspicuousness to visual predators may promote antipredatory behavior compensation. We used the number of UV-blue shoulder ocelli as a measure of visual conspicuousness because, in these ground dwelling lizards, these ocelli are clearly visible from above by predators. In contrast, UV-blue ventral spots are less visible from above, and we considered them as signals relatively less visible to predators. We hypothesized that if predation cost of signaling (i.e., high predation risk level) was high

(due to higher number of predator species or lower number of refuges), the strength of conspicuousness-dependent regulation of antipredatory behavior may be higher. Thus, we explored whether there were between-species differences in the strength of the relationships between conspicuousness and antipredatory behavior. Finally, we also included body condition in our within-species comparisons to test whether interspecific differences may promote differences in condition dependence of conspicuousness-dependent antipredatory behavior.

METHODS

Study animals

Between February and April 2005, we captured by harmless noosing 15 recently posthibernation emerging adult male lizards *I. cyreni* (snout-to-vent length, SVL, mean \pm SD = 77 \pm 3 mm) in alpine habitat at the Guadarrama Mountains in Madrid (40°77'N, 4°1'W; 1950 m asl), and 16 adult male lizards *I. monticola* (SVL = 77 \pm 2 mm) in moist and vegetated lowland habitat at coastal valleys in Galicia (43°70'N, 7°98'W; 100 m asl). At least 2 months before testing, to allow acclimation to laboratory conditions and to homogenize previous recent predation risk experience, lizards were individually housed at "El Ventorrillo" Field Station (Navacerrada, Madrid province), in outdoor 60 \times 40 cm PVC terraria containing rocks for cover. The photoperiod and ambient temperature were those of the surrounding region, and water and mealworm larvae dusted with multivitamin powder were provided ad libitum. Experimental lizards were fed ad libitum to ensure top foraging condition and to avoid individual differences in foraging abilities that might distort antipredatory behavior. However, we did not find differences in male body condition between time of capture and time of experiments (repeated-measures analyses of variance [ANOVAs], *I. monticola*: $F_{1,11} = 0.0047$, $P = 0.94$; *I. cyreni*: $F_{1,9} = 0.40$, $P = 0.54$), which suggests a lack of food limitation in natural conditions. Thus, although individual differences in body condition could depend on food intake, differences among our experimental individuals seem rather due to physiological requirements mediated by the health-dependent "individual quality", which may influence antipredatory behavior (see López et al. 2005). All lizards were healthy during the trials and were returned to their exact capture sites at the end of experiments.

We measured SVL and tail length to the nearest 1 mm with a ruler and counted the number of shoulder ocelli and ventral spots on the right and left side (2–4 counts per animal). Ocelli or spots with bright blue color reflect UV light (Arribas 2001; Thorpe and Richard 2001; unpublished data) were classified as "blue shoulder ocelli" or "blue ventral spots," and small ones or those with dull blue or white coloration (which do not reflect UV; Cabido C et al., unpublished data) were classified as "dull shoulder ocelli" or "dull ventral spots."

Antipredator behavior

We studied antipredator behavior of male lizards (*I. cyreni*: $n = 15$; *I. monticola*: $n = 16$) in outdoor conditions during July and August, from 1100 to 1400 h GMT, when lizards were fully active. We allowed lizards to thermoregulate and attain their preferred body temperatures for at least 1 h before the trials (Martín and Salvador 1993). Terraria were placed separately from each other, such that our approaches to a terrarium did not influence lizards in other terraria.

To examine antipredator responses, we 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, and then walked slowly, stopped close (50 cm) to each terrarium, and looked directly to the lizard during 10 s, verifying that lizards could clearly see the experimenter from their terraria. The same person performed all predatory threats. We simulated 1618 predatory attacks to each lizard within a day (one every 10 min within 3 h), which we repeated over 24 h later. From the observations of the initial position of lizards taken every 10 min immediately before each approach, we calculated the average number of times that a lizard was outside, inside, or leaning out of the refuge, which were considered as a measure of the antipredator behavior of lizards to the previous approaches of the experimenter. We also noted whether the lizard hid in the refuge when the experimenter stopped close to the terrarium and looked directly inside it. We considered that if a lizard hid, it perceived a high predation risk, given that the predator was looking to but not actually attacking the lizard. Although responding to all approaches by fleeing to the refuge would minimize predation risk, time and energy can be saved, and costs of refuge use minimized, if lizards responded accurately only to actual predatory attacks (Ydenberg and Dill 1986; Martín and López 1999a). Thus, we calculated the proportion of times that a lizard that was initially outside or leaning out of the refuge hid ("false alarms"), and the proportion of times that was initially outside the refuge and remained outside ("undisturbed") after the experimenter approached. We considered that a high number of "false alarms" indicated shyness, whereas a low number indicated boldness (López et al. 2005). With this procedure, we simulated a threat of a predator coming from above the lizard because it is likely that lizards respond to human beings as if they were visual predators (Cooper 2003). We predicted that more conspicuous individuals should respond to simulated predatory attacks with shyer antipredatory behavior (higher proportion of time inside the refuge and higher number of "false alarms") whereas less conspicuous individuals should respond with bolder antipredatory behavior (more time outside the refuge and lower number of "false alarms") (López et al. 2005). To test for possible effects of habituation to simulated predator attacks, we tested for individual consistency in antipredator behavior between both days. Repeatability was calculated as the intraclass correlation coefficient based on variance components derived from a 1-way ANOVA (Lessells and Boag 1987). All antipredator behavioral variables were significantly repeatable in both days ($0.43 < r < 0.82$, $0.04 > P > 0.0001$ in all cases) except "time leaning out the refuge" ($P > 0.08$). Thus, for the subsequent analyses, we discarded this variable and used the average values of the 2 days for all the other variables.

To examine the possible relations between the average values of the antipredator behavior variables (time inside refuge, false alarms, undisturbed) and number of shoulder ocelli and ventral spots reflecting conspicuousness of lizards (all variables log transformed), we developed general linear models (GLMs) (using Statistica 6.0 software) within each species separately. Data normality was verified by Shapiro-Wilk's tests, and tests of homogeneity of variances (Levene's test) showed that variances were not significantly heterogeneous after transformation. However, lateral ocelli in *I. cyreni* did not fit the assumptions of normality and were analyzed with Spearman's rank order correlations. We did not compare the 2 species in a single analysis because interspecific differences in ocelli and spots numbers did not comply with the assumption of homogeneous slopes between groups (Engqvist 2005). We also included body condition (calculated as the residuals from the regression equation of body mass (g) on SVL (mm), both variables log transformed) in the models because behavioral responses might be related to differences in the physical

condition of otherwise similar individuals. Body condition of each individual may represent an index of the relative amount of fat stored and, hence, of individual physical condition or nutritional status (reviewed in Green 2000). To decide what variables best predicted antipredator behavior of males, we used a "best-subsets" approach in conjunction with stepwise methods (Neter et al. 1985). We chose the most parsimonious model as having the lowest Akaike information criterion (AIC), and we checked its coincidence with the equivalent stepwise solution. Residuals from the final models were normally distributed (Grafen and Hails 2002).

Sympatric avian predator species

To obtain a rough between-species comparison of numbers of bird species that are known to prey on Iberian rock lizards, we compiled a list of potential predator species based on published studies, most of them made in the same area or very close geographical area (Martín and López 1990; Salvador and Veiga 2003; Martín 2005a,b; Martí and del Moral 2003). We also obtained from published sources (Martí and del Moral 2003) data on the presence and densities of these predators in both study sites.

Microhabitat selection

We measured microhabitat use by lizards to obtain a between-species comparison of refuge and visual background (vegetation and substrate cover) selection and availability. Visual background was examined because although both species differ in the number of blue shoulder ocelli and ventral spots, this might result in equal conspicuousness if visual background were different.

We searched for lizards by walking during April between 07:00 and 14:00 h (GMT) with consistent sampling effort in the 2 study sites. We recorded microhabitat data at the point where each individual was first sighted (*I. cyreni*: $n = 29$; *I. monticola*: $n = 21$). Four 1-m transects were laid out radiating from this point along the 4 cardinal directions and records made at 5, 10, 15, 25, 75, and 100 cm. We noted the presence at substrate level of grass, leaf litter, bare sandy soil, small rocks (<25 cm), medium rocks (25–100 cm), large rocks (100–200 cm), or rocky outcrops and cliff walls (>200 cm). Plant contacts at 5, 10, 25, and 50 cm height were also noted, using a calibrated stick, for grasses or small herbaceous semi-perennial plants (<50 cm height), large woody bushes (*Cytisus oromediterraneus* and *Juniperus comunnis* in Guadarrama or *Cytisus scoparius* and *Ulex europaeus* in Galicia) or trees (*Pinus sylvestris*). We also noted whether the sample point was in a sunny or shaded location, the presence of canopy tree cover above each point, and the distance to the nearest potential refuge (rock crevice or protective vegetation cover). This procedure provided 24 sample points per lizard location and allowed us to calculate the percent cover values of each habitat variable (i.e., % contacts with each substratum, vegetation type and sunny spots, and the mean distance to the nearest refuge; for a similar sampling methodology see Martín and Salvador 1997). To estimate availability of microhabitats in a large area surrounding that actually used by lizards, we used a similar procedure to record the same variables as described above at 2, 3, and 4 m along the 4 cardinal directions from each sample point.

We used a principal component analysis (PCA) to reduce the microhabitat variables to a smaller number of independent components. Only principal components (PCs) with eigenvalues that explained more than 5% of the total variation and had biological significance were retained for further analysis. Original data (number of contacts) were normalized by means of

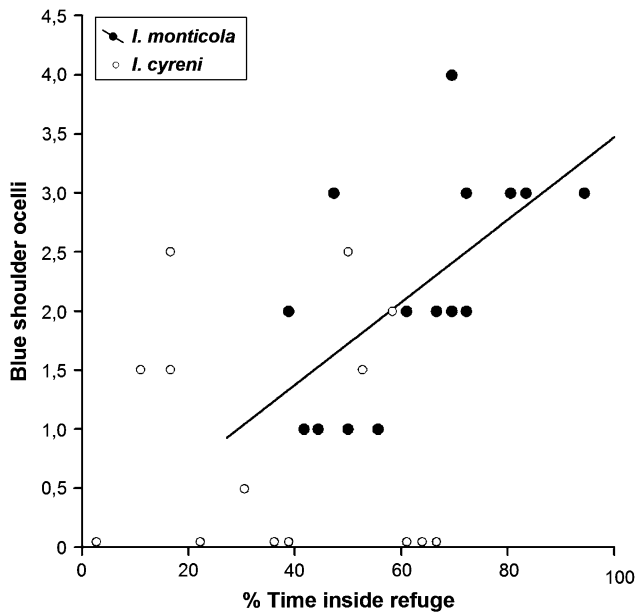


Figure 1
UV-blue shoulder ocelli (exposed sexual signal) versus time spent inside the refuge after simulated predatory threat for male *Iberolacerta monticola* (solid circles) and male *Iberolacerta cyreni* (open circles). Regression line is showed for male *I. monticola*; UV-blue shoulder ocelli did not correlate significantly with time inside refuge for male *I. cyreni*.

square-root transformation. Because of the large number of “zero” observations for many variables, some transformed data were not normally distributed, but otherwise met the assumptions of a PCA. Deviations from normality do not necessarily bias the analysis, as long as the distributions are reasonably unskewed (Legendre and Legendre 1998). Thus, we considered that our transformations reduced the skew sufficiently to minimize the risk of bias in the analysis. We used GLMs to compare PC scores describing microhabitat characteristics in relation to each species (*I. monticola* vs. *I. cyreni*) and the type of point (available vs. used by lizards) to determine whether lizards used available microhabitats in a nonrandom fashion. We included the interaction between species and type of point in the model to test for differences in microhabitat selection of lizards within each species. Post hoc pairwise comparisons

were planned using Tukey’s honestly significant difference tests (Sokal and Rohlf 1995).

RESULTS

Antipredator behavior

Separated analyses within each species showed that positive conspicuousness-dependent regulation of antipredatory behavior may occur in male *I. monticola* but not in male *I. cyreni* (Figure 1; Table 1). Thus, in male *I. monticola*, the best model based on AIC for time spent inside the refuge included blue shoulder ocelli, dull shoulder ocelli, and body condition. A stepwise multiple regression analysis (GLM: adjusted $R^2 = 0.47$, $F_{3,12} = 5.46$, $P = 0.013$) confirmed that time spent inside the refuge was positively and significantly correlated with the number of blue shoulder ocelli (Table 1). For the number of false alarms, the best model based on AIC included blue ventral spots and body condition, and stepwise multiple regression analysis (GLM: adjusted $R^2 = 0.35$, $F_{2,13} = 5.18$, $P = 0.022$) showed that blue ventral spots were not significantly correlated, and the negative correlation with body condition approached significance (Table 1). Thus, male *I. monticola* with a higher number of conspicuous ocelli (shoulder ocelli) spent less time exposed to predator threats. Likewise, male *I. monticola* with worse body condition retreated early into refuges under a predator threat. Visual signals not exposed to predators (ventral spots) were not significantly correlated with any behavioral variable ($P > 0.12$ in all cases).

In contrast, visual signals exposed to predators (shoulder ocelli) of male *I. cyreni* did not significantly correlate with any behavioral variable (Spearman’s rank correlation: $-0.28 < r_s < 0.27$, $P > 0.30$ in all cases) (Figure 1). However, signals not exposed to predators (lateral ocelli) correlated with bolder behavior (Table 1). The best stepwise multiple regression model based on AIC for the number of false alarms included dull shoulder ocelli, blue ventral spots, dull ventral spots, and body condition (GLM: adjusted $R^2 = 0.80$, $F_{4,10} = 15.16$, $P < 0.001$) showing that the number of false alarms was negatively and significantly correlated with the number of blue ventral spots and positively and significantly correlated with the number of dull ventral spots and with body condition (Table 1). The best stepwise multiple regression model based on AIC for the proportion of times that male *I. cyreni* remained undisturbed included blue ventral spots, dull ventral spots, and body condition (GLM: adjusted $R^2 = 0.35$, $F_{3,11} = 3.59$, $P = 0.049$), showing that the proportion of times that male *I. cyreni*

Table 1
Relationships between antipredatory behavioral variables and visual sexual signals or body condition in male lizards

	Time inside refuge	Time outside	False alarms	Undisturbed
<i>Iberolacerta Monticola</i>	$F_{1,12}$, β , P		$F_{1,13}$, β , P	
Blue shoulder ocelli	10.12, 0.85, 0.007	ns	ns	ns
Dull shoulder ocelli	ns	ns	ns	ns
Blue ventral spot	ns	ns	2.35, 0.34, 0.15	ns
Dull ventral spot	ns	ns	ns	ns
Condition	ns	ns	4.38, 0.46, 0.056	ns
<i>Iberolacerta cyreni</i>			$F_{1,10}$, β , P	$F_{1,11}$, β , P
Blue shoulder ocelli	ns	ns	ns	Ns
Dull shoulder ocelli	ns	ns	ns	Ns
Blue ventral spot	ns	ns	58.56, 2.47, 0.001	6.91, 1.46, 0.023
Dull ventral spot	ns	ns	53.82, 2.36, 0.001	6.34, 1.45, 0.028
Condition	ns	ns	9.40, 0.40, 0.011	6.69, 0.60, 0.025

P and β values from univariate regressions. Significant correlations are showed in bold; ns = not significant.

Table 2
Antipredatory behavior variables of lizards

	<i>Iberolacerta monticola</i> (mean ± SE)	<i>Iberolacerta cyreni</i> (mean ± SE)	$F_{1,29}$	P
Inside the refuge (%)	63.0 ± 4.0	39.6 ± 5.7	11.80	0.001
Leaning out of the refuge (%)	26.0 ± 3.6	5.5 ± 1.2	0.25	0.61
Outside the refuge (%)	4.7 ± 1.0	49.4 ± 5.9	11.59	0.001
False alarms (%)	30.1 ± 3.7	13.8 ± 2.2	42.2	<0.001
Undisturbed (%)	2.3 ± 1.0	40.2 ± 4.7	52.75	<0.001

F and P values from protected 1-way ANOVA tests.

remained undisturbed was positively and significantly correlated with the number of blue ventral spots and negatively and significantly correlated with the number of dull ventral spots and with body condition (Table 1). Thus, male *I. cyreni* in better condition retreated more often into the refuge (i.e., higher number of false alarms) and remained less often undisturbed under a predator threat.

Multivariate analyses on the antipredatory behavioral variables showed that there were significant differences between the 2 lizard species (multivariate ANOVA, Wilks' $\lambda = 0.20$, $F_{5,25} = 18.89$, $P < 0.001$). Univariate protected ANOVAs showed that these were due to significant differences in all behavioral variables, except in "time spent leaning out of the refuge" (Table 2). Thus, male *I. monticola* spent more time inside the refuge, performed a higher number of false alarms, and remained less time undisturbed than male *I. cyreni*.

Between-species differences in UV signals

Male *I. monticola* had a significantly larger number of blue and dull shoulder ocelli (mean of right + left sides) than male *I. cyreni* (blue shoulder ocelli: mean ± SD = 2.2 ± 0.9 vs. 0.8 ± 1.0; Mann-Whitney U test, $Z = 3.20$, $n_1 = 16$, $n_2 = 15$, $P = 0.001$; dull shoulder ocelli: 1.2 ± 0.7 vs. 0.4 ± 0.5; $Z = 3.02$, $n_1 = 16$, $n_2 = 15$, $P = 0.002$). In contrast, male *I. monticola* had significantly less unexposed blue and dull ventral spots (mean of right + left sides) than male *I. cyreni* (blue ventral spots: 1.3 ± 1.6 vs. 8.1 ± 3.6; $Z = -4.13$, $n_1 = 16$, $n_2 = 15$, $P < 0.001$; dull ventral spots: 1.5 ± 1.6 vs. 3.7 ± 1.4; $Z = -3.24$, $n_1 = 16$, $n_2 = 15$, $P = 0.001$).

Between-species differences in sympatric avian predator species

The 2 species of Iberian rock lizards live in habitats that differ in the number of potential avian predators. In the lowland habitat of *I. monticola*, potential avian predators are 7 raptor species, 1 gull, 1 shrike, 3 thrushes, and 3 crows (Table 3). In contrast, at the highland locality of *I. cyreni*, potential avian predators are only 1 raptor, 2 thrushes, and 1 crow (Table 3). Moreover, the densities of regular avian predators are higher in the habitat of *I. monticola* (Table 3).

Between-species differences in microhabitat characteristics

The PCA for microhabitats available and those used by lizards produced 3 components that together accounted for the 56.62% of the variance. The first PC (PC-1, eigenvalue = 5.02, 26.43% of total variance) was negatively correlated with sunny locations ($r = -0.51$) and positively correlated with the presence at substrate level of leaf litter ($r = 0.64$) and contacts with large woody bushes at 5, 10, 25, 50, 75, 100 cm height ($0.76 < r < 0.84$). The second PC (PC-2, eigenvalue = 3.01,

Table 3
Potential predator species of lizards in both study sites and densities (individuals/km²) of avian species

	<i>Iberolacerta monticola</i>	<i>Iberolacerta Cyreni</i>
Raptors		
<i>Milvus migrans</i> ^a	0–1	0
<i>Accipiter gentilis</i>	0–1	0
<i>Accipiter nisus</i>	0–1	0
<i>Buteo buteo</i>	1–2	0
<i>Circus gallicus</i>	0–1	0
<i>Hieraeetus pennatus</i>	0	0–1
<i>Circus pygargus</i> ^a	0–1	0
<i>Falco tinnunculus</i>	1–2	0
Gulls		
<i>Larus michahellis</i>	20–200	0
Shrike		
<i>Lanius collurio</i>	1–2	0
Thrushes		
<i>Monticola saxatilis</i> ^a	0–1	1–2
<i>M. solitarius</i> ^a	0–1	1–2
<i>Turdus merula</i> ^a	20–200	0
Crows		
<i>Pica pica</i>	2–20	0
<i>Corvus corax</i>	0–1	1–2
<i>Corvus corone</i>	20–200	0

^a Occasional predator of lizards. Species that implies higher predation risk (regular predators of lizards with higher densities) are highlighted in bold.

15.89% of variance) was negatively correlated with cover of large rocks ($r = -0.49$), rocky outcrops ($r = -0.55$), and distance to the nearest potential refuge ($r = -0.79$) and positively correlated with cover of small ($r = 0.57$) and medium rocks ($r = 0.71$). The third PC (PC-3, eigenvalue = 2.71, 14.29% of total variance) was negatively correlated with cover of bare sandy soil ($r = -0.47$); grass contacts at 5, 10, 25 cm height ($-0.85 < r < -0.69$); and tree cover ($r = -0.58$).

There were significant differences in relation to all PCs between the 2 lizard species (GLM, Wilks' $\lambda = 0.25$, $F_{3,94} = 92.24$, $P < 0.0001$) and between types of microhabitat points (available vs. used by lizards; Wilks' $\lambda = 0.63$, $F_{3,94} = 18.30$, $P < 0.0001$) (Figure 2). The interaction between species and type of point was significant (Wilks' $\lambda = 0.68$, $F_{3,94} = 14.33$, $P < 0.0001$). The general model showed significant overall differences for all PCs (PC-1: adjusted $R^2 = 0.24$, $F_{3,96} = 11.61$, $P < 0.0001$; PC-2: adjusted $R^2 = 0.58$, $F_{3,96} = 49.50$, $P = 0.0001$; PC-3: adjusted $R^2 = 0.06$, $F_{3,96} = 3.40$, $P = 0.02$). There were significant differences between populations in characteristics of available microhabitats defined by PC-1 and PC-2 scores (Tukey's tests, $P < 0.001$ in both cases) but not in those defined by PC-3 ($P = 0.91$). Thus, in the habitat of *I. monticola*, there was a higher cover of large woody bushes with presence at substrate level of leaf litter and large rocks or rocky outcrops, whereas in the habitat of *I. cyreni* there was a higher cover of small and medium rocks, with many crevices, and refuges were closer. Regardless of these differences in availability, there were not significant differences between species in the PC-1 and PC-3 scores of microhabitat used by lizards (Tukey's tests, $P > 0.60$ in both cases), but there were significant differences between species in the PC-2 ($P < 0.001$). Thus, males of both species used microhabitats with more sunny locations and less cover of small woody bushes, trees, and grasses, but *I. cyreni* used microhabitats with more small and medium rocks and closer to refuges than *I. monticola*. In sum, microhabitats available to the 2 species did not differ in

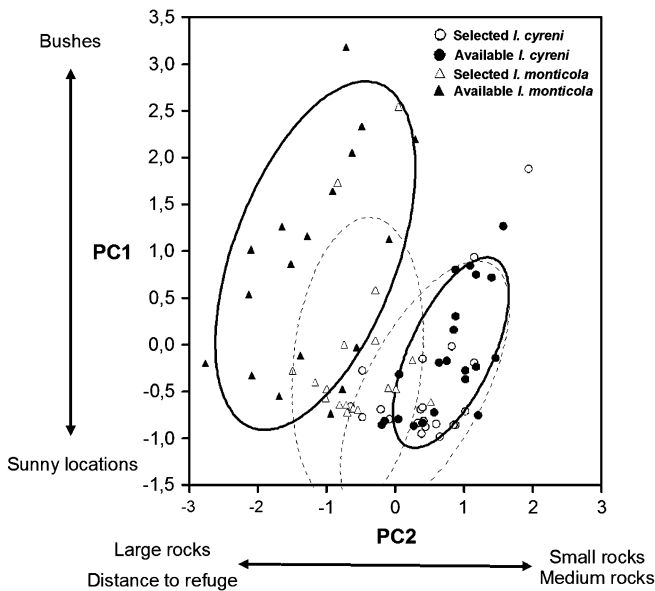


Figure 2
Microhabitat selected and available by male *Iberolacerta monticola* and male *Iberolacerta cyreni*, based on the 2 first PC scores representing 24 microhabitat characteristics; 95% confidence ellipses are shown.

characteristics such as the extent of vegetation or substrate cover, which may affect the visual background. The species selected microhabitats that differed in refuge availability or distance to the nearest refuge; however, neither of these factors are likely to affect the visual background and therefore should not affect relative conspicuousness.

There were not significant differences between microhabitats available and used by *I. cyreni* in all PC scores (Tukey's tests, $P > 0.10$ in all cases), but there were significant differences between microhabitat used by *I. monticola* and microhabitat availability in PC-1 and PC-2 scores ($P < 0.001$ in both cases) but not in PC-3 ($P = 0.91$). Thus, microhabitat availability and microhabitat preferences corresponded in *I. cyreni*, whereas *I. monticola* selected microhabitats with more sunny locations and less cover of small woody bushes (PC-1) and with more small and medium rocks and closer to refuges (PC-2) than those available in their habitat.

DISCUSSION

Increased predation pressure may shape the evolution of sexual traits favoring less conspicuous males (Endler 1982; Candolin 1998) or with colors biased against the spectral sensitivity of the most dangerous predator (Endler 1991). However, our results suggested that male lizards may compensate for negative effects of conspicuous sexual coloration on predation risk by modulating antipredatory behavior. This conspicuous-dependent antipredatory behavior may also function as a condition dependent cost promoting costly (honest) sexual signaling in some species but not in others.

Conspicuousness-dependent regulation of antipredatory behavior

Behavioral compensation has been reported in displaying males (Ryan et al. 1982; Hedrick 2000; Lewkiewicz and Zuk 2004; Lindström et al. 2007) but, to our knowledge, whether brighter coloration may be behaviorally compensated has been scarcely studied in vertebrates (but see Martín and

López 1999b; Cuadrado et al. 2001). We found that more conspicuous individual male *I. monticola* behave more cautiously, hiding for longer in refuges when they were threatened by a potential predator. Predation pressure may act differentially for exposed or unexposed signals. For example, body regions of lizards hidden from predators are more chromatically contrasting against the background than body regions exposed to predators (Stuart-Fox et al. 2004). Thus, we predicted that lizards should compensate for the negative effects of signals that increase conspicuousness to predators (lateral ocelli) but not for unexposed signals (ventral spots). In accordance, we found that male *I. monticola* with more shoulder ocelli, but not ventral spots, behaved shyer to compensate for their increased conspicuousness. Previous studies have shown that refuge use of Iberian rock lizards may vary as a function of predation risk level, physiological costs, and foraging or mating expectations outside refuges (Martín and López 1999a; Martín et al. 2003a,b). The compensation for conspicuousness could alter the trade-off between sexual and natural selection, thereby changing the dynamics of evolutionary models that assume that conspicuous male characters carry a cost in terms of natural selection. Thus, males with conspicuous colorations might not always experience as greater actual predation rates as suggested by some studies that used artificial static replica models of lizards (e.g., Stuart-Fox et al. 2003; Husak et al. 2006).

We did not find any correlation between antipredatory behavior and exposed signals in male *I. cyreni*, but a higher number of UV-blue ventral spots predicted bolder antipredator behavior. Most studies show that visual conspicuousness of male coloration correlates positively with shyness (Forsman and Appelqvist 1998; Martín and López 1999b; Hedrick 2000; Cuadrado et al. 2001; Lindström et al. 2007), but there are some exceptions (Godin and Dugatkin 1996). The non-adaptive or weaker value of conspicuousness-dependent regulation of antipredatory behavior when cost of signaling is low (because of reduced predation risk and low signal conspicuousness) may explain the lack of conspicuousness-dependent regulation of antipredatory behavior in some species. The UV-blue ventral spots of *I. cyreni* are hidden to predators, so they should not increase predation exposure (Stuart-Fox et al. 2004).

Moreover, our results of microhabitat selection suggested lower predation risk on *I. cyreni*, which is expected to occur in montane lizards (Van Damme et al. 1989; Fox et al. 1994). Differences in protective cover or the number of predator species affect predation risk (Snell et al. 1988; McLaughlin and Roughgarden 1989), and we found that the number and densities of avian predators were higher in the habitat of *I. monticola* that also showed a higher number of exposed UV-blue shoulder ocelli. Ornaments with bright and UV coloration may increase predation risk because diurnal raptors (Viitala et al. 1995, Honkavaara et al. 2002), and shrikes (Probst et al. 2002) use UV wavelengths as a hunting cue, so between-species differences in avian predators are especially important. Therefore, more conspicuous male *I. monticola* may spent more time inside refuges because their risk of be detected by a predator was higher than for more conspicuous male *I. cyreni*. We also found that in the habitat of *I. monticola* refuges were far and scarce, which may implicate high risk of predation and force lizards to select specific microhabitats where refuges are close. In contrast, male *I. cyreni* did not choose particular microhabitats because the high availability of small to medium rocks in their habitat provided abundant, evenly distributed and close refuges. Moreover, both species selected microhabitats with the same cover of vegetation (grasses or small woody bushes) and used the same class of granite rocks for thermoregulation and refuge (personal

observation), so we may expect that both species have similar visual backgrounds and visibility and that the number of UV-blue shoulder ocelli may be correlated with actual conspicuousness of Iberian rock lizards in their native habitats.

Although our study clearly suffers from the potential problems of inferring adaptation from 2-species comparisons (Garland and Adolph 1991), our within-species comparisons suggest that differences in antipredator behavior may be causally related to differences in predation costs of signals. Moreover, both lizard species are closely related and until recently were considered as belonging to the same species (Mayer and Arribas 2003; Carranza et al. 2004), so that any effect due to phylogenetic divergence should be very weak. Thus, our results may support the hypothesis about the adaptive value of conspicuousness-dependent regulation of antipredatory behavior only when cost of signaling was high (Kotiaho 2001), which may occur in *I. monticola* but not *I. cyreni*. The habitat of *I. monticola* has greater predation risk and fewer available shelters. Despite this, *I. monticola* is more conspicuous, potentially indicating stronger sexual selection on coloration in this species. These factors combined are likely to explain shyer behaviour as well as behavioural compensation in *I. monticola* but not in *I. cyreni*. Similarly, male lacertid lizards *Gallotia galloti* have more exposed UV blotches in habitats where they are more vulnerable to predation (Thorpe and Richard 2001).

In addition, for male *I. cyreni*, antipredatory behavior suppose to lose relatively more mating and thermoregulatory opportunities (see Martín et al 2003a) than for male *I. monticola* due to overall differences in mating season duration. Activity level has a consistent effect on reproductive success in *I. cyreni* (Salvador et al. 2008) and bolder behavior may be correlated with higher activity level. In *I. cyreni*, activity of individual males was correlated with their social rank (Martín and López 2000). More active males gained access to more females by overlapping not only home ranges of a larger number of females but also those of a larger number of male competitors, which increased the frequency of agonistic interactions (Aragón et al 2001). Then, the bolder behavior of male *I. cyreni* might be an attempt to balance predation risk with mate searching and thermoregulation (Martín et al 2003a). UV-blue ventral spots may be used to signal size or body condition and during agonistic encounters the presence of blue spots may elicit aggressiveness (López et al 2004). Both activity and sexual signals seem to be subject to hormonal regulation, probably mediated by testosterone, and may have an important effect on reproductive success. Then, if these unexposed signals do not need to be behaviorally compensated to reduce predatory costs, this may explain the positively correlation with bolder behavior.

Condition dependence of antipredatory behavior

Both the energetic and conspicuousness costs of signals have been suggested that may be important to consider in other lizards (Simon 2007), and our data also suggest that conspicuousness-dependent regulation of antipredatory behavior may also function as a condition dependent cost promoting honest sexual signaling in *I. monticola* but not in *I. cyreni*. One prominent model of sexual selection, the handicap model, assume that the marginal costs of signaling must be lower for males in good condition than for males in poor condition (Grafen 1990). If individuals in better condition are better at escaping predation, the condition dependent escape rate would reduce costs of signaling. Male *I. cyreni* with worse body condition were bolder, i.e., had less false alarms, and were more often undisturbed. On the contrary, male *I. monticola* with better body condition performed less "false alarms". This suggests that both species might experience different costs

associated to antipredatory behavior. Individuals should optimize their antipredatory responses by balancing antipredator demands with other requirements (Lima and Dill 1990). Between-species differences in mating system or mating season duration may promote differences in the trade-off between predation risk and social behavior (Lima and Dill 1990; Martín et al 2003a).

Due to the alpine environment of *I. cyreni* (high local population densities, extensive home range overlap, and a short breeding season), both body condition and activity level, which may enable males to search more intensively for females, are significant predictors of reproductive success (Salvador et al. 2008). This mating system would allow the coexistence of alternative mating strategies, as suggested by the successful matings obtained by putative "transients" and by the fact that large males did not monopolize females (Salvador et al. 2008). Thus, males in worse condition may gain opportunities to mate by increasing their activity level when predation risk was high and males in better condition were hidden. Concurrently, males with higher reproductive success, presumably males with high activity levels and better body condition, have higher survivorship (Salvador et al. 2008). Thus, although male *I. cyreni* with better body condition may be able to afford the energetic costs of higher activity, their shyer antipredatory behavior may result in higher survivorship without compromising their reproductive success (Abell 2000). Interestingly, this result contrasts with the data available for other lacertids from lower altitudes, such as *Psammodromus algirus*, in which more active males courted females more frequently, but at the cost of decreased survivorship (Díaz 1993; Salvador et al. 1996). Similar relationships might be found in *I. monticola*. Male *I. monticola* may be more territorial than male *I. cyreni* because we found that some microhabitat resources (refuge and sunny locations) differ between selected and available microhabitat in the former species. Moreover, overlapping among male home ranges is lower in *I. monticola* (Moreira et al. 1998) than in *I. cyreni* (Aragón et al. 2004). Our results showed that male *I. monticola* with better body condition, which may be more territorial, performed less "false alarms" which might allow them to remain more time defending their territories against other males. Thus, condition dependent escape behavior might allow male *I. monticola* to remain more time exposed to predators before hiding. Alternatively, bolder individuals may be in better condition simply because they can spend more time foraging.

Conclusions

A recent study (Oufiero and Garland 2007) illustrates the perils of ignoring potential compensatory mechanisms when studying the costs of sexually selected traits. However, most examples found that lizard populations that experience higher rates of predation exhibit less conspicuous sexual coloration (Macedonia et al. 2002; Kwiatkowski 2003; Stuart-Fox et al. 2004) and that conspicuous males suffer higher predation risk (e.g., Stuart-Fox et al. 2003; Husak et al. 2006; but see Olsson 1993). Most studies on lizards examine predator attacks on static painted models and, therefore, ignore potential compensatory antipredatory behavior. However, our results suggest that conspicuousness-dependent regulation of antipredatory behavior may explain the persistence of brighter signals in species that suffer high predation risk.

By altering the predation cost of sexual signals, conspicuousness-dependent regulation of antipredatory behavior can differentially influence the evolution of honest sexual signalling in closely related species. Ignoring this may lead to erroneous conclusions about the cost of sexually selected traits.

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