

The Role of Lateral Blue Spots in Intrasexual Relationships Between Male Iberian Rock-Lizards, *Lacerta monticola*

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Abstract

Vertebrate males often show breeding colours that may function as reliable signals of status in intrasexual competition. In many lacertid lizards, males show a conspicuous row of small but distinctive blue spots that runs along their body side on the outer margin of the belly. However, no study has examined the role of these blue spots. We first analysed in a field population of the Iberian rock lizard, *Lacerta monticola*, the relationships between number of blue spots and some morphological traits, which are known to be related to males' fighting ability. The number of spots seems to be an character showing ontogenetic change as large (generally older) males showed more blue spots than small (generally younger) males. Males with a higher body condition also showed a higher number of blue spots. Thus, a higher number of blue spots may be used to signal size, age or body condition. Many contiguous blue spots would result in a visual artefact consisting of a continuous blue band, which might be a reliable size- or condition-dependent signal in some social contexts. We further examined in the laboratory whether male characteristics are related to dominance status. In males with similar body size or age, those with relatively larger heads were more dominant, whereas the number of blue spots was not important. Moreover, the number of blue spots in nature was not related to relative head size. Finally, we experimentally manipulated the presence and the number of blue spots of intruding males, and examined the aggressive response of resident males. Intruder individuals manipulated to cover all their blue spots received a lower amount of aggression. However, males with different numbers of manipulated blue spots received a similar number of aggressive responses. These results suggest that, during agonistic encounters, the presence of blue spots, but not their number, may elicit aggressiveness. Thus, blue spots may serve to identify an individual as an adult male, and to enhance body size of larger males.

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Introduction

In many vertebrates, such as fishes, birds or lizards, conspicuous patches of colour that may reliably signal fighting ability have evolved (Rohwer 1982; Whitfield 1987). For instance, males of many species of lizards show breeding colours during the mating season that may function as social releasers (review in Cooper & Greenberg 1992). These conspicuous badges may function as reliable signals of status in competition between males (Thompson & Moore 1991a; Olsson 1994a; Zucker 1994). Individuals may use these badges to judge status or relative fighting ability of their opponents, and to modify their own behaviour accordingly (Maynard Smith & Price 1973; Parker 1974; Enquist & Leimar 1983). Thereby, males may avoid the costs associated with escalated aggressive interactions (Rohwer & Ewald 1981; Marler & Moore 1988, 1989). However, if status signalling was based on features (e.g., coloration) which are not directly related to fighting ability, individuals might benefit from 'cheating', i.e. signalling at too high a level (Krebs & Dawkins 1983). Thus, only if the signal is costly or condition dependent can it be used by rivals as indicators of resource holding power. Competition between males and social control of deception can act to reinforce the honesty of the signal through repeated aggressive contests (Andersson 1982; Rohwer 1982; Martín & Forsman 1999).

In many lacertid lizards, males show a conspicuous row of small but distinctive blue spots that runs along their body side on the outer margin of the belly (see Fig. 1). For example, blue spots are present in several species of the genus *Lacerta* and *Podarcis* (see for example Barbadillo et al. 1999 for photographs of several Iberian species). However, at least to our knowledge, no study has examined experimentally or empirically the role of these blue spots in intraspecific relationships between males (but see Molina-Borja et al. 1997, 1998, for the effect on the outcome of male contests of the wider lateral blue patches of

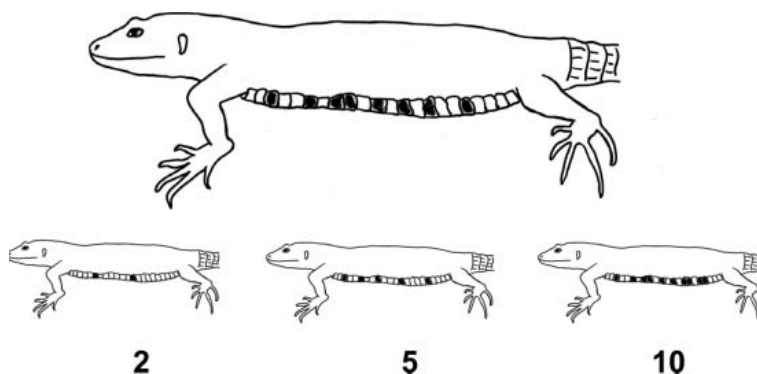


Fig. 1: Line diagram showing an example of the position of natural blue spots on the row of scales on the outer margin of the belly in a male *Lacerta monticola*. Below are manipulated males showing the position of different numbers of artificially painted blue spots after covering with paint the natural ones to match the background grey-olive coloration

some *Gallotia* lizards from the Canary Islands). Such colour spots might play an important role during sexual selection because this is a sexually dimorphic character. Thus, the colour pattern is markedly stronger during the mating season in males, whereas it is normally absent in females in all seasons. In addition, the number of blue spots varied among different individuals within the same population (see Results), suggesting that blue spots might be signalling 'some' intrinsic characteristic of each male related to its condition (e.g. age, fighting ability, or 'individual quality'). Therefore, the number of blue spots might be a signal of status or fighting ability that may be used in intrasexual encounters between males.

On the other hand, sex recognition is based on colour signals in many species of lizards, especially in sexual dichromatic species where one sex, often males display brighter colours than females (Cooper & Burns 1987; see Cooper & Greenberg 1992 for a review). The artificial manipulation of body colours by painting experiments has provided strong evidence that sex identification relies on visual cues in many lizards (Bauwens et al. 1987; Cooper & Greenberg 1992; Cuadrado 2000) at least at long distance (López & Martín 2001a; López et al. 2003). In addition, dull coloration in females presumably allows sexual recognition reducing the aggressive response of conspecific males. Furthermore, other studies show that some female lizards develop a male-like bright coloration during pregnancy as a way to avoid male harassment (Cooper & Greenberg 1992; Galán 2000). Therefore, the possibility remains that the presence of blue spots in many male lacertid lizards (or their absence in females) may be not related to fighting ability of individual males, but may be just a sex recognition cue during intersexual encounters. Alternatively, by using a female-like dull coloration, males with a low resource-holding potential might evade aggression from a dominant male, adopting a satellite-sneaking mating strategy (Kodrick-Brown 1998; Martín & Forsman 1999; López et al. 2003). In this context, dull coloration may be a reliable signal of subordination of younger males (Lyon & Montgomerie 1986).

In this paper, we analysed in a field population of the lacertid Iberian rock lizard, *Lacerta monticola*, the relationships between number of blue spots in males and some morphological traits (e.g. body and head size, body condition), which are known to be related to males' fighting ability (López et al. 2002b). We also examined in the laboratory whether male characteristics (especially head size or number of blue spots) are related to dominance status. Finally, we experimentally manipulated the presence and the number of blue spots of intruding males, and examined the consequences on the aggressive response of unmanipulated resident males.

Materials and Methods

Natural Variation

During May to July 2001 we made field observations of morphological characteristics of male *L. monticola* in 'Puerto de Navacerrada' (Guadarrama

Mountains, 1900 m a.s.l., Central Spain). Lizards were captured by noosing, measured in situ and released within 5 min at their capture sites. We measured their body size with a ruler (snout-to-vent length, SVL, to the nearest 1 mm) and their weight (to the nearest 0.1 g) with a digital balance. 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, an estimation of individual physical condition or nutritional status (Bonnet & Naulleau 1994, see Green 2000 for a review). We also noted the number of blue spots on each side of the lizards (see Fig. 1). For a human observer, it was possible to distinguish between spots of a dark blue colour and others of white colour (sometimes turning to very pale blue). We are aware of the possibility that lizards might respond to cues other than the spectrum visible for the human eye such as, for example, ultraviolet radiation (Fleishman et al. 1993). However, preliminary observations in this and other lacertid species indicate that several types of 'blue' marks had a similar reflectance in UV (with a peak around 360 nm), whereas the scales between blue marks did not show UV reflectance (Font & Molina-Borja 2001; Thorpe & Richard 2001; Arribas 2002). Thus, we are confident that our counts of spots actually reflect the number of spots that are also visible for lizards, independently of the possible differences in colour perception. In addition, we considered only the number of spots, but we did not measure the actual surface area occupied by these spots, because each spot coincides with a small scale, and all these scales have a similar surface area (see Fig. 1). Thus, the number of spots is highly correlated with the total surface occupied by these spots.

Lacerta monticola is a sexually dimorphic lizard with respect to head and body size (Braña 1996), with males having larger heads than females. Head size is known to play an important role in the outcome of intrasexual agonistic contests of many lizards including this species and this seems to be the evolutionary cause of sexual dimorphism in head size (Anderson & Vitt 1990; López et al. 2002b). We used a digital calliper to make morphological measurements (to the nearest 0.01 mm) of the head of males. Head height 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 was the greatest horizontal distance between the tip of the snout and the posterior side of the parietal scales. Head width was the greatest horizontal distance between the external sides of the parietal scales. We removed the influence of body size on head measurements by regressing each against SVL (all variables log-transformed) and used the residuals in further analyses. Given the high correlation between these measurements, we used principal component analysis (PCA) to reduce the nine morphological variables (see Table 1) to a smaller number of independent components. The initial factorial solutions were rotated by the Varimax procedure (Nie et al. 1975). Thereafter, we used Pearson's product-moment correlation to examine the possible relationships between the number of white and blue spots and the average values of the PC scores reflecting morphological characteristics of lizards (Sokal & Rohlf 1995).

Table 1: Principal components analysis for morphological measurements of lizards in the field. Residuals were derived from correlations with SVL. Bold values indicate correlations of variables with the principal components > 0.60

	PC-1	PC-2	PC-3
Snout-to-vent length	0.98	-0.05	-0.05
Body mass	0.86	0.07	0.47
Head height	0.66	0.50	-0.46
Head width	0.38	0.79	0.01
Head length	0.90	0.33	0.04
Body mass residuals	0.12	0.19	0.85
Head height residuals	0.08	0.65	-0.44
Head width residuals	-0.02	0.89	-0.04
Head length residuals	0.09	0.75	0.17
Eigenvalue	4.05	2.01	1.37
% Variance	45.0	22.3	15.2

Relationships Between Blue Spots and Social Status

To determine social status we staged agonistic encounters in the laboratory between pairs of males in all possible combinations within two groups of different males ($n = 12$ in the year 2000, and $n = 12$ in 2001). Different lizards were captured each year by noosing in different places of the study area (Guadarrama Mountains) to ensure that individuals had not been in previous contact, which may affect the outcome of the experiment (López & Martín 2001b). They were individually housed at 'El Ventorrillo' Field Station (Navacerrada, Madrid Province), 5 km from the capture site, in outdoor plastic cages (80×50 cm) containing rocks for cover. Lizards were weighed and their SVL was measured (body mass: $\bar{x} \pm \text{SE} = 8.4 \pm 0.3$ g, range: 6.7–10.0 g; SVL: $\bar{x} \pm \text{SE} = 76.1 \pm 0.6$ mm, range: 73–80 mm). We also measured head length, width and height (see above), and counted the number of white and blue spots on both body sides. Food (mealworms and crickets) dusted with a multi-vitamin powder and water were provided ad libitum. Lizards were captured 2 wk before the start of the mating season and held in their home cages for at least 1 wk to familiarize them with the novel environment prior to testing. The experiments were carried out during May and June, coinciding with the mating season of lizards in this population (Aragón et al. 2001). To avoid the effect of prior residence advantage (Cooper & Vitt 1987; López & Martín 2001b), we performed all experiments in a neutral, previously unoccupied arena, consisting of a 1×0.5 m terrarium divided into two equal compartments by the use of a plywood partition. Males were placed in separate compartments and given 15 min to habituate to the new environment before the partition was removed. Each male was used 11 times, in staged encounters with all the other males in a randomized sequence, but participated in only one interaction per day. Staged encounters were spaced sufficiently (at least 1 d) so that fatigue or stress resulting from one trial did not affect subsequent trials. All tests were made in outdoor conditions when lizards were fully active.

Multiple interactions between the two males could occur during each trial. In each interaction, responses were classified as 'aggressive' if a male approached another individual with aggressive display and made the other male retreat or run away either without contact, by touching him on the flanks, or, occasionally, by giving quick bites, specially on the snout or head. Approaching males employed threatening postures (i.e. strut towards an opponent on raised, stiff forelegs with their neck arched and the snout pointing slightly down). We recorded the outcome of each interaction by noting which male won (i.e. chased the other male at the end of an interaction) and which one was chased. Thereafter, we calculated a sum of aggressive interactions won, less interactions lost for each male of each pair, and defined the male with the highest positive sum as the dominant individual (Fox et al. 1981; Martín & Salvador 1993; Martín & López 2000). Typically, males considered as winners repeatedly dominated their opponents over a series of interactions in each encounter. Only in a few cases, it was not possible to determine which male was the dominant of the pair because both males won an equal number of times, or because there were not aggressive responses, and we considered it a neutral relationship. A trial was interrupted after 15 min.

A matrix of dominance was constructed for each group based on the results of agonistic staged encounters between males. For each pair of males, the dominant male was given a score of 1, and the subordinate a score of 0. For neutral or unknown relationships, each male was given a score of 0.5 (Martín & López 2000). Thus, males with higher sums of scores were considered to be the most dominant. This method allowed us to evaluate the potential role of coloration in signalling status or fighting ability in dominance relationships between unfamiliar males. We did not infer that coloration is used to uphold a dominance hierarchy in the wild, because in a group of familiar males coloration might be used for individual recognition rather than as a signal of status.

We used PCA as above to reduce the 11 morphological variables (see Table 2) to a smaller number of independent components. We used Pearson's product-moment correlation to examine the possible relationships between the social status of males (i.e. the score of each male), and the average values of the PC scores reflecting morphological characteristics of lizards (Sokal & Rohlf 1995).

Experimental Manipulation of the Blue Spots

During May 2001, we captured by noosing 20 adult male *L. monticola* in different places in the study area (Guadarrama Mountains). They were individually housed at 'El Ventorrillo' Field Station and maintained as above. After a week of acclimatization, we experimentally manipulated the number of blue spots of small males (SVL: $\bar{x} \pm \text{SE} = 70.2 \pm 0.2$ mm, range: 69–72 mm, $n = 10$) and staged agonistic encounters between pairs of males in the home cage (80 × 50 cm) of an unmanipulated responding large male (SVL: $\bar{x} \pm \text{SE} = 75.9 \pm 0.3$ mm, range: 75–77 mm, $n = 10$). These size categories also corresponded to two age categories of adult males (Moreira et al. 1998; Aragón 2001),

Table 2: Principal components analysis for morphological measurements of lizards in the social status experiment. Residuals were derived from correlations with SVL. Bold values indicate correlations of variables with the principal components > 0.60

	PC-1	PC-2	PC-3
Snout-to-vent length	0.93	-0.17	0.30
Body mass	0.78	0.16	0.18
Head height	0.79	0.22	0.45
Head width	0.80	0.43	0.10
Head length	0.97	0.17	-0.01
Body mass residuals	0.18	0.80	-0.05
Head height residuals	-0.02	0.74	0.36
Head width residuals	0.20	0.79	-0.15
Head length residuals	0.33	0.62	-0.42
Blue spots	0.24	-0.04	0.85
White spots	-0.28	-0.03	-0.84
Eigenvalue	5.11	2.46	1.28
% Variance	46.5	22.4	11.7

with large males being older than small males. The responding large male acted as the owner and the manipulated male acted as an intruder. With this design we tried to mimic a natural field situation where a resident large male found a conspecific in his home range. The responding male had the initial advantage of being resident and should fight aggressively for maintaining its owner condition (e.g. López & Martín 2001b). Large males are also usually dominant over smaller males in the field (Aragón 2001). However, if blue spots signal status or fighting ability, responses of the large resident male should be more aggressive against any intruding male signalling a higher status. Conversely, a responding male should be less aggressive and more neutral when finding males signalling low status, because these intruders will not pose a high threat for the maintenance of his territory. This behaviour is similar to that we have observed in the field in this and other lacertid species; fights were more intense and frequent when size or status differences were smaller (Olsson 1992; Martín & Salvador 1993; López, P. & Martín, J. 2001b; unpubl. data). In addition, if the status signal is incongruent with the actual status, as estimated by other traits, deception may be detected and punished by genuinely dominant individuals by increasing their aggressive responses (Martín & Forsman 1999).

Before the treatment, lizards were placed in a refrigerator for 10 min to immobilize them and facilitate the manipulations. Lizards were painted with flexible non-toxic Testor's paints for model aeroplanes mixing them to achieve good visual matches with the natural colours of *L. monticola* in our study area. The belly and lateral scales were first painted to match the background grey-olive coloration, covering the entire rows of lateral scales where blue spots appear. After drying at room temperature, we painted small blue spots along the edge of the belly, similar in size and colour to the natural ones (Fig. 1). Lizards were replaced in the refrigerator until the paint had dried before using them in

experiments. The paint of manipulated lizards was removed immediately with water after they had completed each trial. No damage or necrosis of tissue due to the paint were ever recorded.

We attempted to match natural male coloration. Lizards might, however, respond to cues that are not in the spectrum visible for the human eye, such as ultraviolet radiation (Fleishman et al. 1993), which might not be accurately imitated or concealed by the paint used. We are confident that this was not the case because we conducted preliminary observations in a randomized sequence of the responses of resident large males ($n = 8$) towards unmanipulated small males ($n = 8$) and manipulated small males ($n = 8$) that had been painted as above to cover their natural spots with grey-olive paint, and then painted with blue paint with the same number of spots that they had originally. The results showed that responding males did not change their normal expected behavioural responses (see below) as a result of this manipulation (Wilcoxon tests, aggressive response: $Z = 0.45$, $p = 0.65$; neutral response: $Z = 0.71$, $p = 0.48$). Thus, the experimental treatment seemed to be effective in resembling the natural colour of blue spots. In addition, other species of lizards seem to respond normally to artificially painted individuals that resemble natural coloration (e.g. Cooper & Vitt 1988; Thompson & Moore 1991a; Olsson 1994a; Martín & Forsman 1999; Cuadrado 2000).

In a first experiment, we analysed the effect of showing blue spots on the aggressive behaviour of responding males ($n = 10$). Thus, we compared the responses of the same resident males to an intruding male whose natural blue spots were artificially covered with paint to match the background grey-olive colour ('no spots' treatment), and to a different intruding male whose blue spots were covered to match the background grey-olive colour and then painted with blue paint (10 spots per side; 'with spots' treatment) (see Fig. 1). Although body size differences within manipulated intruding males were small, males were size-matched by SVL and assigned to each different treatment ($n = 10$, five in each treatment), such that average body size of males did not differ between treatments. Therefore, differences in the responses to the two groups could not be due to differences in body size. We planned a repeated measures design in which each responding male encountered in a randomized sequence one different manipulated male of each treatment that had a similar body size. Manipulated males within the same treatment participated in two different tests with two different responding males.

In a second experiment, we analysed the effect of different numbers of blue spots on the aggressive responses of males. Thus, we compared the responses of the same resident males ($n = 10$) to different intruding males whose natural blue spots were artificially covered to match the background grey-olive colour and then painted with two, five or 10 blue spots per side (see Fig. 1). Manipulated males were size-matched by SVL and assigned to each treatment as above. Each responding male encountered in a randomized sequence one different manipulated male of each treatment that had a similar body size.

In both experiments, males participated in only one interaction per day to avoid stress. We also spaced staged encounters sufficiently (at least 1 d) so that fatigue resulting from one test did not affect subsequent tests. To avoid the effects

of previous experience between individuals (Olsson 1994b; López & Martín 2001b), in each test the two lizards had never been together before the trials. All tests were made in outdoor sunny conditions between 09.00–12.00 hours GMT when lizards were fully active.

To begin a trial, we gently took one manipulated lizard from its cage and placed it gently in the middle of the responding male's cage. Observations were made from a blind. We considered an interaction to begin when two lizards approached to within 5 cm of each other and to end when they moved further than 5 cm apart. Multiple interactions between the two males could occur during each trial. In each interaction, responses were classified as 'neutral' if both individuals were close (< 5 cm) together but no agonistic response of the intruding male was observed. Aggressive responses included those in which the resident approached with head lowered, neck and throat inflated, back arched and the body raised, and chased or bit the intruder, usually on the snout or head. Approach without display was considered to be aggressive if the intruder fled. We noted the number and characteristics of the responses of the resident male ('aggressive' vs. 'neutral') during each trial, which lasted 15 min. We decided to stop observations if persistent attacks or desperate attempts to escape were recorded. This was, however, not necessary as interactions mostly consisted of threatened displays and short chases, and only very rarely escalated to single quick bites that did not cause observable injury. No individuals suffered physical injuries or showed physical stress due to experimental conditions or captivity. Although agonistic interactions between lizards were not very aggressive, we used a minimal number of animals over the minimum time necessary to test our hypothesis. All the animals were healthy during the trials and at the end of the experiments were released to their initial sighting location prior to the capture, and all of them had maintained or increased their original body mass.

To compare the number of aggressive interactions and the number of neutral interactions of the responding males observed in the 15 min of the trial across treatments, we used non-parametric Wilcoxon matched-pairs signed-ranks tests or Friedman's analyses of variance (ANOVA), examining the effects of the painting treatments of manipulated-intruder individuals on the responses of the same responding-resident male (Sokal & Rohlf 1995). Alpha level was 0.05 and all tests were two-tailed.

Results

Natural Variation

All males examined had lateral spots ($\bar{x} \pm \text{SE} = 7.8 \pm 0.3$ spots per side, range: 4–13, $n = 44$), whereas lateral spots were totally absent in all females examined. All males had some lateral dark blue spots ($\bar{x} \pm \text{SE} = 6.5 \pm 0.3$ spots per side, range: 1–13) (Fig. 1), but not every male had white spots ($\bar{x} \pm \text{SE} = 1.2 \pm 0.2$ spots per side, range: 0–7). Occasional recapture observations of 10 males indicate that the number of spots of each class was maintained constant during the same activity period (Apr. to Sep.).

The PCA for morphological measurements produced three components that together accounted for 82.5% of the variance (Table 1). The first PC was positively correlated with variables describing absolute body size. The second PC was positively correlated with variables describing relative head size. The third PC was positively correlated with residuals of body mass on SVL.

The total number of spots (dark blue + white) did not change significantly with PC1 (Pearson's correlation: $r = 0.18$, $F_{1,42} = 1.38$, $p = 0.25$). However, the number of blue spots increased significantly with PC1 ($r = 0.37$, $F_{1,42} = 6.58$, $p = 0.014$) (Fig. 2a), whereas the number of white spots decreased significantly with PC1 ($r = -0.41$, $F_{1,42} = 8.70$, $p = 0.005$) (Fig. 3a). Thus, larger/older, males had a higher number of blue spots and fewer white spots than smaller/younger males. White spots were often absent in larger individuals.

The total number of spots was not significantly correlated with PC2 ($r = 0.18$, $F_{1,42} = 1.38$, $p = 0.25$). Neither the number of blue ($r = -0.02$, $F_{1,42} = 0.01$, $p = 0.90$) (Fig. 2b) nor white spots ($r = 0.10$, $F_{1,42} = 0.47$, $p = 0.50$) (Fig. 3b) varied significantly with PC2. Thus, the number of spots was not related to relative head size.

The total number of spots did not change significantly with PC3 ($r = 0.09$, $F_{1,42} = 0.36$, $p = 0.55$). However, the number of blue spots increased significantly with PC3 ($r = 0.34$, $F_{1,42} = 5.65$, $p = 0.022$) (Fig. 2c), whereas the number of white spots decreased significantly with PC3 ($r = -0.48$, $F_{1,42} = 12.65$, $p < 0.001$) (Fig. 3c). Thus, lizards with higher body mass condition had a greater number of blue spots and fewer white spots.

Blue Spots and Social Status

The PCA for morphological measurements of males used in staged encounters produced three components that together accounted for 80.6% of the variance (Table 2). The first PC was positively correlated with variables describing body size. The second PC was positively correlated with variables describing relative head size and relative body weight (i.e. body condition). The third PC was positively correlated with the number of blue spots, and negatively correlated with the number of white spots.

Social status scores of lizards were not significantly correlated with either PC1 ($r = 0.14$, $F_{1,22} = 0.46$, $p = 0.50$) or PC3 ($r = 0.03$, $F_{1,22} = 0.02$, $p = 0.89$), but they were significantly and positively correlated with PC2 ($r = 0.51$, $F_{1,22} = 7.81$, $p = 0.01$) (Fig. 4). Thus, lizards with higher scores in staged encounters (i.e. dominants) were those that have relatively larger heads and a higher body condition, independently of their actual body size or number of spots.

Experimental Manipulations

In the first experiment, the total number of interactions did not significantly differ between treatments (Wilcoxon signed-ranks test: $Z = 0.36$, $p = 0.72$, $n = 10$). However, resident males responded to intruding males manipulated to cover

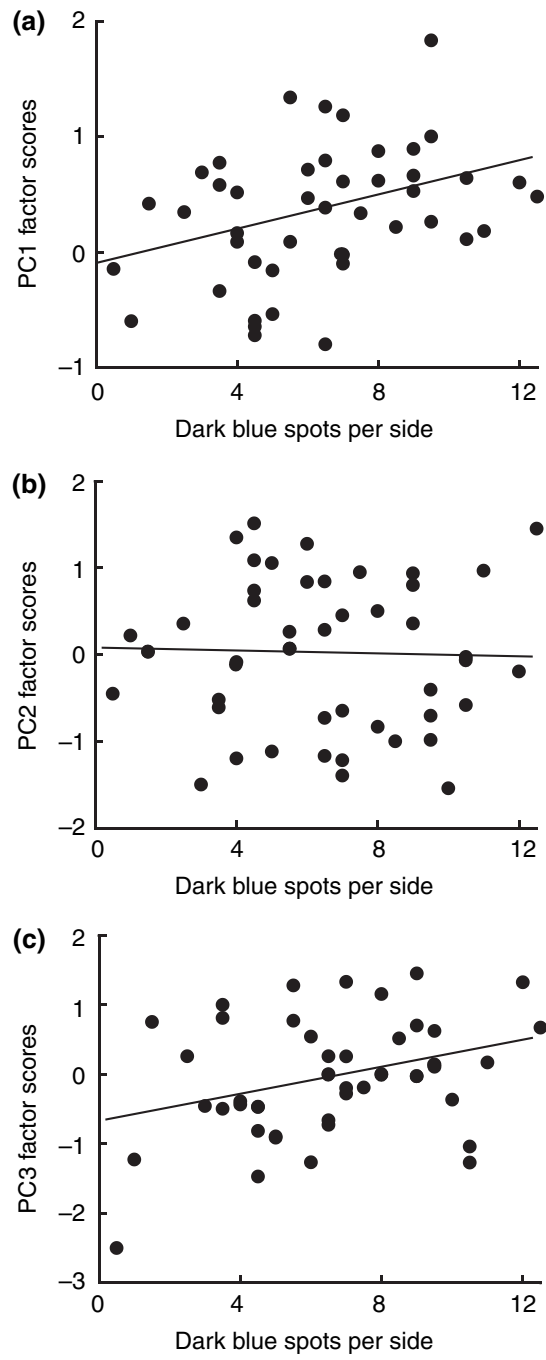


Fig. 2: Relationships between PC scores describing morphological characteristics and the average number of dark blue spots on each side of male *L. monticola*, measured within the same field population. The regression lines are shown

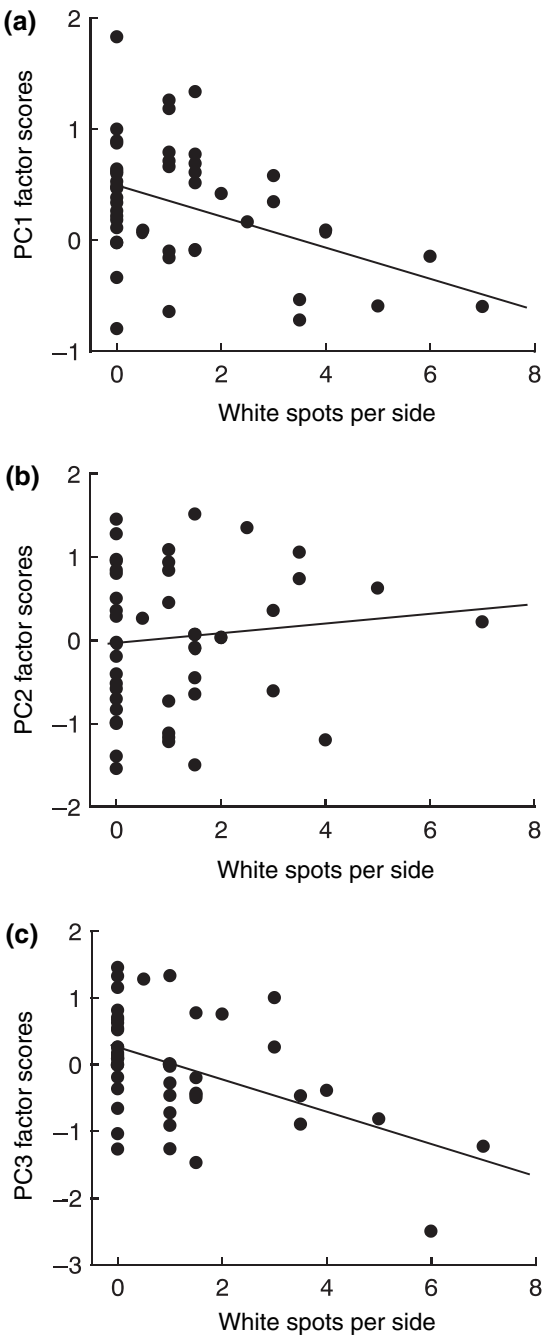


Fig. 3: Relationships between PC scores describing morphological characteristics and the average number of white spots on each side of male *L. monticola*, measured within the same field population. The regression lines are shown

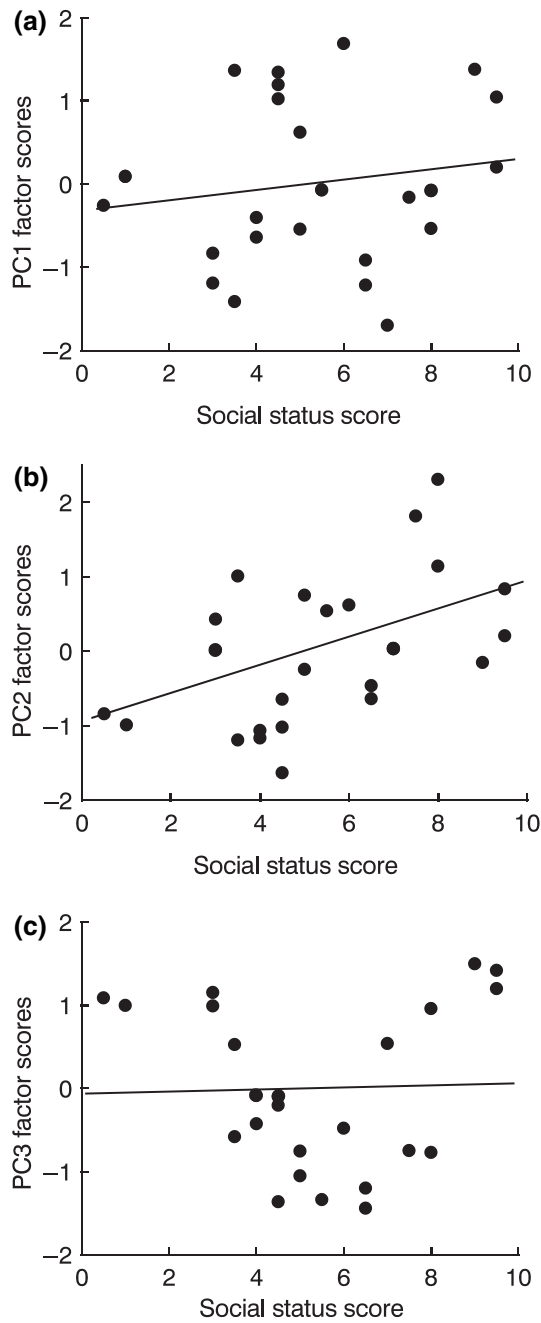


Fig. 4: Relationships between PC scores describing morphological characteristics and social status scores (increasing from 0 to 10) of male *L. monticola* based upon staged encounters between unfamiliar males in the laboratory. The regression lines are shown

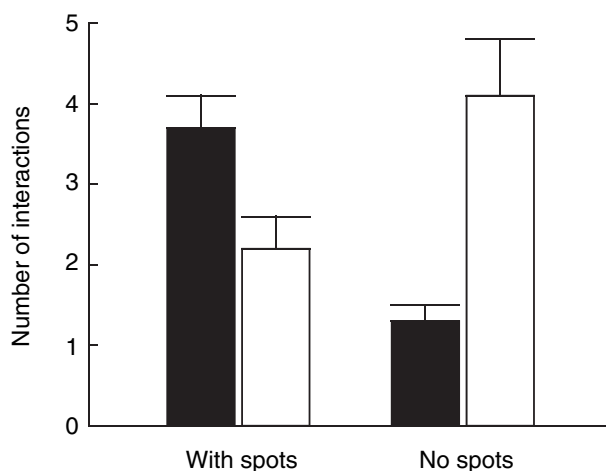


Fig. 5: Number ($\bar{x} + 1$ SE) of aggressive (black boxes) and neutral interactions (open boxes) in contests of the same resident unmanipulated males with an intruder manipulated male with artificially painted blue spots, or with a different intruder male painted to conceal their blue spots (no spots treatment). The order of presentation of these two conditions was counterbalanced

their blue spots with a significantly lower number of aggressive interactions ($Z = 2.20$, $p = 0.028$, $n = 10$) and a significantly higher number of neutral interactions ($Z = 2.19$, $p = 0.028$, $n = 10$) than to intruding males with artificially painted blue spots (Fig. 5).

In the second experiment, the total number of interactions did not significantly differ between treatments (Friedman's ANOVA: $\chi^2_2 = 2.52$, $p = 0.28$, $n = 10$). Responding resident males did not differ significantly in the number of aggressive interactions that they directed to intruding males with different number of manipulated blue spots ($\chi^2_2 = 1.39$, $p = 0.50$, $n = 10$) or in the number of neutral interactions that occurred ($\chi^2_2 = 1.12$, $p = 0.57$, $n = 10$) (Fig. 6). These results suggest that the presence of blue spots (but not the number of spots) may elicit aggressiveness of resident males.

Discussion

Data from the individual variation in the number of blue spots in nature suggest that the number of spots may be a character showing ontogenetic change as large (normally older) males exhibited more blue spots than small (normally younger) males. This suggests that spots may change from white to blue with age. Thus, a higher number of blue spots may be used to signal size or age. Furthermore, males are able to exhibit these spots clearly while using lateral displays, and these may function as signals enhancing the perception of a larger body size. Because when the number of blue spots increases most scales in the row are pigmented, the conjunction of many contiguous blue spots would probably

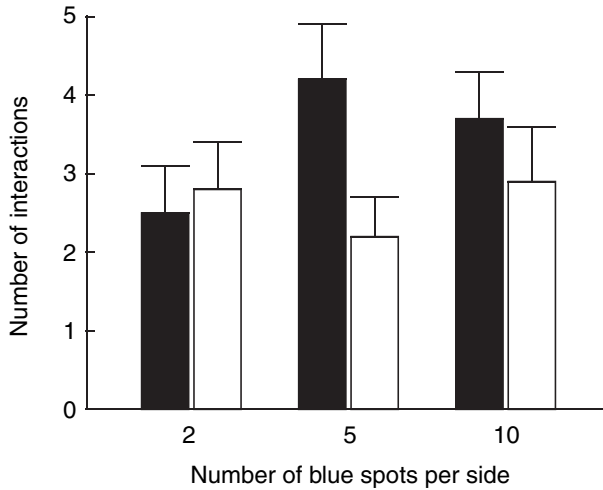


Fig. 6: Number ($\bar{x} + 1$ SE) of aggressive (black boxes) and neutral interactions (open boxes) in contests of the same resident unmanipulated males with different intruder manipulated males showing different numbers of artificially painted blue spots on each side. The order of presentation of the three treatments was counterbalanced

result in a visual artefact consisting of a continuous blue band, and probably also UV, along the flanks, which may be easily perceived at long distance (see Fig. 1). Indeed, this is a reliable signal of male size as the number of blue spots and SVL of individuals are correlated, and the actual length of this row of blue spots should be tightly correlated with the actual body size of an individual. On the contrary, smaller individuals with many blue spots only would enhance the impression of a small body size (i.e. a ‘short’ blue row). Thus, showing these blue spots would not be advantageous for smaller individuals. In this context, the smaller males show a greater number of apparently more inconspicuous white spots, that might turn to dark blue in subsequent seasons when the male has increased its body size. This ontogenetic change in blue coloration in these patches is correlated with corresponding changes in green dorsal coloration typical of old males, as opposed to brown dorsal coloration of younger individuals (Aragón 2001). Therefore, we hypothesize that blue spots in this species may function as a signal of age or as way to enhance the perception of a larger body size.

Males with a higher body mass condition also showed a higher number of blue spots, suggesting that showing a higher number of spots might be costly and only males in good condition may exhibit them. A possible explanation is that coloration might be correlated with plasma testosterone levels (Moore & Marler 1987; DeNardo & Sinervo 1994; Salvador et al. 1997). Therefore, further experiments should test whether the exhibition of this signal, or rather the physiological/hormonal state (e.g. testosterone levels) that correlates with the exhibition of blue spots might be costly for males. If so, the number of blue spots might be a reliable condition-dependent signal that may be useful in some social

contexts. This is a pattern common to many lizard species where certain male body coloration, under androgenic control, plays an important role in social relationships (Cooper & Vitt 1988; Thompson & Moore 1991a,b; Salvador et al. 1996; Martín & Forsman 1999).

With respect to the social status between unfamiliar males of similar body size, our results show that males with relatively larger heads and with a higher body condition were more dominant, whereas the number of blue spots was not important in determining status between males with similar body size or age. Males with relatively larger heads can bite harder (Herrel et al. 1999) and thus can have advantage in intrasexual agonistic contests if an escalation occurs. In contrast, body size per se did not convey status, within the range of sizes considered in this experiment (i.e. all males were large/old individuals). Previous results have shown that males fight each other to increase their dominance status because this increases their mating success (Martín & Salvador 1993). In the field, the number of agonistic interactions between males was high, suggesting intense competition for access to females. Dominant males had more exclusive home ranges that include several females, and could access easily to more females whereas subordinate males were immediately chased when detected by resident males acquiring a lower access to females (Martín & Salvador 1993, 1997; Aragón 2001). The evolution of social dominance requires phenotypic traits that convey honest information on an individual's status. Thus, most interactions consisted of displays where the dominant male approached with head lowered and the neck and throat inflated. This display would allow a male to judge in advance the fighting ability of the opponent from his relative head size, and to retreat before a fight (and possibly, some injuries) occurs. Although the presence of blue spots might also serve as a signal allowing smaller males to retreat from large males, the definitive status relationship between two individuals of similar absolute body size will probably depend mainly on their relative head size and fighting ability. Therefore, at a finer scale (i.e. between males with similar body size) the fighting ability did not seem to be directly signalled by the number of blue spots.

The manipulation of the number of blue spots also suggests that at close range, during agonistic interactions, male *L. monticola* use cues other than the number of blue spots (such as body and head size or certain behavioural postures) when judging social status or fighting ability of other males. Relative body size (or another trait correlated with fighting ability such as relative head size) may be the most important character when two individuals are close together, whereas coloration may be more important in long-distance communication, when body size may be difficult to assess accurately. A similar function of coloration has been suggested for the orange coloration in the heads of male skinks *Eumeces laticeps* (Cooper & Vitt 1988) and male *Psammodromus algirus* lizards (Martín & Forsman 1999). Thus, large males may be easily perceived at a distance and be able to expel competitors avoiding a potentially costly agonistic encounter for both contenders (Martín & Forsman 1999). Similarly, the dorsal badge of male *Urosaurus ornatus* may act to broadcast his status over a greater distance (Zucker 1994).

Nevertheless, the experimental manipulation of blue spots suggests that individuals without blue spots received a lower amount of aggression. Probably, these males were mistaken for females or immature males that do not exhibit blue spots and are not attacked by resident males. Thus, the presence of some blue spots may also serve to identify an individual as an adult male. Similarly, in the lacertid lizard *Podarcis hispanica*, males painted as females, which included the cover of their blue spots, did not elicit aggressive responses at long distances (López & Martín 2001a; López et al. 2002a). In this context, the lower number of blue spots showed by smaller/younger males might be an attempt to resemble female-like coloration to elude aggression by older males. Thus, younger males may adopt a sneaking mating strategy.

We conclude that blue spots may be a reliable signal of sex, body size/age and/or body condition in this lizard, and probably also in many other lacertid lizards that have very similar spots. Blue spots may be used by dominant/older males to advertise their age-related status, enhancing the impression of a large body size. When the outcome of costly agonistic encounters interactions is predictable, inferior competitor males may retreat before a fight occurs, which would be beneficial for both contenders to avoid costly interactions. Therefore, the use of blue spots as a signal may play an important role in intraspecific relationships of this lizard.

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