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ORIGINAL ARTICLE

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Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*

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Abstract Female preference for dominant males is widespread and it is generally assumed that success in male-male competition reflects high quality. However, male dominance is not always attractive to females. Alternatively, relatively symmetric individuals may experience fitness advantages, but it remains to be determined whether males with more symmetrical secondary sexual traits experience advantages in both intra- and intersexual selection. We analysed the factors that determine dominance status in males of the lizard *Lacerta monticola*, and their relationship to female mate preference, estimated by the attractiveness of males' scents to females. Sexually dimorphic traits of this lizard (head size and femoral pores) appear to be advanced by different selection pressures. Males with relatively higher heads, which give them advantage in intrasexual contests, were more dominant. However, head size was unimportant to females, which preferred to be in areas marked by relatively heavier males, but also by males more symmetric in their counts of left and right femoral pores. Chemicals arising from the femoral pores and other glands might honestly indicate quality (i.e. related to the symmetry levels) of a male to females and may result from intersexual selection. Females may use this information because the only benefit of mate choice to female lizards may be genetic quality. Chemical signals may be more reliable and have a greater importance in sexual selection processes of lizards than has previously been considered.

Keywords Female mate preference · Fluctuating asymmetry · Lizards · Male-male competition · Social dominance

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Introduction

It is generally assumed that success in male-male competition reflects high quality and that female preference for dominant males should be widespread (Quarnström and Forsgren 1998). Thus, traits reflecting dominance, such as large body size or badges of status, are expected to be selected by females. However, recent studies suggest that male dominance is not always attractive to females (Quarnström and Forsgren 1998; Moore and Moore 1999). Success in male contests probably depends on male condition, but dominance might not be a reliable indicator of better paternal care or genetic quality for females. Thus, in many cases, the interaction between intrasexual selection (i.e. male-male competition) and intersexual selection (i.e. mate choice) on the evolution of secondary sexual traits remains to be determined.

Fluctuating asymmetry (FA) is random deviation from perfect symmetry that arises due to the inability of individuals to undergo identical development of bilaterally symmetrical traits on both sides of the body (Van Valen 1962). There is evidence that relatively symmetric individuals of some taxa experience fitness advantages (Møller 1997), which might be explained by the two processes of sexual selection. First, it has been suggested that symmetric males might outcompete asymmetric males during intrasexual agonistic contests (Thornhill 1992a; Sneddon and Swaddle 1999). However, low levels of asymmetry are preferred by females in a potential mate in many species (Thornhill 1992b; Møller and Thornhill 1998; Martín and López 2000a) because they presumably indicate the developmental stability of an individual and, thus, its ability to cope with genetic and environmental perturbations during development (Møller and Swaddle 1997). However, it is unknown whether males with more symmetrical secondary sexual traits experience advantages in both intra- and intersexual selection.

Many lizard species exhibit social dominance systems. The Iberian rock lizard (*Lacerta monticola*) is a small diurnal lacertid found mainly in rocky habitats of some high mountains of the Iberian Peninsula. Field studies of this species have shown that males defend territories including several females against other males. However, overlap between home ranges is extensive because male density is very high. Fights between males are frequent and dominance hierarchies among neighbours of similar age or size often emerge (Martín and Salvador 1993, 1997; Martín and López 2000b). Pheromones are one of the most commonly used social signals among animals, including lizards (Mason 1992). Male *L. monticola* can detect and discriminate between femoral gland secretions of familiar and unfamiliar conspecific males (Aragón et al. 2001a, b). Chemical secretions from various sources are used in the field as scent marks and may contribute to stabilization of their social system by lowering the costs of aggressive interactions (Alberts 1992; López et al. 1998; Aragón et al. 2001a). Thus, dominant males have more exclusive home ranges and access to a higher number of potential mates (Martín and Salvador 1993, 1997; Aragón et al. 2001c). However, in a previous experiment, we demonstrated that female *L. monticola* are able to discriminate the symmetry of males using chemical signals from males' glands, and that females prefer to be in areas marked by symmetric males, thus increasing their opportunities to mate with these males (Martín and López 2000a). It remains to be determined whether traits determining social status in males are also those preferred by females, and whether symmetric males also have an advantage in intrasexual contests.

We designed a laboratory experiment to analyse the factors that determine dominance status in male *L. monticola*, and their relationship to female mate preferences, estimated by the attractiveness of males' scent to females. We hypothesized that sexually dimorphic traits of this lizard may be advanced by different selection pressures. Relatively larger heads may give advantage to males in intrasexual contests, but they may be unimportant for females, which may prefer other traits in their potential mates. Chemicals arising from the femoral pores and other males' glands might honestly indicate quality (i.e. related to levels of symmetry) of an individual male and may be used by females in the mate-choice process.

Methods

Study animals

During May 2000, we captured by noosing 12 adult male and 12 adult female *L. monticola* in different places over a large area ("Puerto de Navacerrada", Guadarrama Mountains, central Spain) to ensure that individuals had not been in previous contact, which might affect the outcome of the experiment. 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. Cages of males and females were in different places to ensure that there was no previous contact between them. Food (mealworms and crickets) dusted with a multivitamin powder and water were provided ad libitum. Lizards were housed in these cages for at least 1 week to familiarize them with the novel environment prior to testing. All the animals were healthy during the trials, and at the end of the experiments were released to their initial sighting location prior to capture. Lizards were captured before the start of the mating season. We confirmed that females had not mated yet because of their lack of characteristic mating scars on the belly (unpublished data). The experiments were carried out during May and June 2000, which coincided with the mating season of lizards in their original, natural population (Aragón et al. 2001c).

Measurement of morphological variables

Lizards were weighed and their snout-vent length (SVL) was measured (males: SVL mean±SE=76.1±0.6 mm, range=73–80 mm; body mass: 8.4±0.3 g, range=6.7–10.0 g; females: SVL mean±SE=77.0±0.8 mm, range=73–82 mm; body mass: 7.2±0.4 g, range=5.4–9.8 g). Individual values of body condition were calculated as the residuals from the regression equation of ln mass (grammes) on ln SVL (millimetres), which may represent an index of the relative amount of fat stored and, hence, an estimation of individual physical condition or nutritional status (Bonnet and Naulleau 1994).

L. monticola is a sexually dimorphic lizard with respect to head and body size (Braña 1996). Head size has been identified as an important component in intrasexual agonistic contests of lizards, and this seems to be the cause of sexual dimorphism in head size in this and other species of lizards (Vitt and Cooper 1985; Anderson and Vitt 1990; unpublished data). We used digital calipers to make morphological measurements (to the nearest 0.01 mm) of the heads 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 ln-transformed) and used the residuals in subsequent analyses.

We considered that femoral pores may be a secondary sexual trait, as their symmetry seems to be related to the quality of the pheromone output upon which females base their choice (Martín and López 2000a). Individuals with symmetric femoral pores are also more symmetric in several other meristic characters (unpublished data). We counted under a magnifying glass the number of femoral pores on the right and left hindlimbs of males (right limb: 18.2±0.5 pores, range=16–20; left limb: 18.7±0.5 pores, range=16–22; *n*=12 males). We have previously shown that counts of femoral pores are highly repeatable, and that the absolute value of asymmetry of the femoral pores, calculated as the unsigned right-minus-left number of pores, exhibits the properties of FA (Møller and Swaddle 1997; see Martín and López 2000a for statistical analysis of asymmetry of femoral pores in this lizard).

Social status

To determine social status of males, we staged paired encounters between males. To avoid the effect of prior residence advantage (Cooper and Vitt 1987), we performed all experiments in a neutral, previously unoccupied arena, consisting of a 1×0.5 m terrarium divided into two equal compartments by 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, facing all the other males in randomized sequence, but participated in only 1 test per day to avoid stress. A trial was interrupted after 15 min. Staged encounters were spaced sufficiently (at least 1 day) so that fatigue resulting from one trial did not affect subsequent trials. All tests were made in outdoor conditions when lizards were fully active.

We considered a response to be aggressive if a male approached another individual with an 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, especially to the snout or head. We noted which male won the 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 and Salvador 1993). Typically, males considered as winners repeatedly dominated their opponents over a series of interactions in each encounter. In some cases (17 out of 66, 25.8%), it was not possible to determine which male was the dominant of the pair, and we considered it an unknown relationship. A matrix of dominance was constructed, based on the results of agonistic staged encounters between males. The probability of linearity within hierarchies was calculated according to Appleby (1983). To demonstrate linearity of a hierarchy in a group, it is necessary to show that dominance tends to be transitive. Thus, we calculated the number of circular triads in the group (*d*), and the degree of linearity of a hierarchy (i.e. the coefficient *K*, which has values from 0, indicating complete absence of linearity, to 1, indicating a linear hierarchy) (see Appleby 1983).

Table 2 Models obtained by means of stepwise multiple regression analysis on factors that explained the variation of social status and attractiveness indices (dependent variables) of male *Lacerta monticola*. The independent variables were SVL, symmetry of the femoral pores, body mass, body condition and head height, head length and head width residuals. Standardized (*β*) and non-standardized (*B*) regression coefficients and their standard errors are shown. The table provides results from *t*-tests (*t*) and associated probability (*P*) levels

Independent variable	β±SE	B±SE	*t*	*P*
Social status				
Intercept		6.83±0.83	8.28	<0.0001
Head height residuals	0.52±0.22	81.06±33.30	2.43	0.038
Symmetry	–0.43±0.22	–1.33±0.67	–2.00	0.076
Attractiveness index				
Intercept		0.57±0.09	12.76	<0.0001
Body condition	0.50±0.21	0.93±0.39	2.39	0.04
Symmetry	–0.49±0.21	–0.09±0.04	–2.35	0.04

Choice of scent experiments

We placed in each male's cage several absorbent paper strips (35×10 cm) fixed to the floor of the cage, and left them there for 10 days, to obtain the scents and secretions from the femoral and cloacal glands of lizards. Papers were removed and placed in females' cages immediately before each experiment began. All tests were conducted in outdoor conditions. Females' cages (80×50 cm) had two basking platforms (two identical flat tiles) placed symmetrically at each end of the cage, and rocks for cover in the centre. At the beginning of each experiment (0700 hours GMT), when females were still inactive, we took a paper strip from each of two males and fixed each strip on alternate tiles. Each female was tested on four different days, with papers from eight different males (four pairs). The pair of males tested and the position of the papers in the cages were randomly determined. Paper strips were manipulated with fresh gloves to avoid contaminating them with human odours. We used the instantaneous scan sampling method; females were monitored each 30 min from a concealed view point and their locations in the cages were recorded. If a female was located on either of the two tiles with the paper strip, she was designated as having chosen that particular paper, whereas if she was located off the tiles she was designated as having made no choice (Martín and López 2000a). To ensure that females were aware of both males' stimuli, at least two recordings in each male's section were considered necessary for a trial to be valid. We determined the female's preference by calculating near which paper the female spent greater than 50% of her time (excluding time spent in the no-choice area). Each trial lasted 8 h (between 0800 hours and 1600 hours GMT), at which time the papers were removed and the cage was thoroughly rinsed with water. Different paper strips from each individual male were used in eight odour choice tests against the papers of other males, with different individual females. Each individual male was assigned an "attractiveness index" score, calculated as the proportion of trials in which a paper impregnated with his scent was preferred by a female.

We used forward stepwise multiple regression analysis to determine how symmetry of the femoral pores, snout-to-vent length, body mass, body condition or head height, head length and head width residuals (independent variables) influenced social status or attractiveness of males (Sokal and Rohlf 1995).

Results

The staged agonistic encounters showed that males developed a dominance hierarchy (*d*=33.25, *n*=12, *P*<0.01, *K*=0.54) (Table 1). Stepwise multiple regression (R^2=0.66, *F*=8.94, 2,9 *df*, *P*=0.007) showed that social status of males was significantly and positively correlated with head height residuals, whereas the relationship between status and asymmetry in the femoral pores was not significant (Table 2; Fig. 1). Thus, males with relatively higher heads reached superior status in the dominance hierarchy. Other body measures, such as SVL, body mass, body condition, or head length and head width residuals were not included in the model and, thus,

Table 1 Matrix of dominance relationships between male *Lacerta monticola* (*M1* to *M12*) based upon staged encounters. A score of *1*=row individual dominant to column individual; *0*=column individual dominant to row individual; *1/2*=relationship unknown

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	Total
M1	–	1/2	1/2	1	1	1	1	1/2	1	1	1	1	9.5
M2	1/2	–	1	0	1	1	1/2	1	1	1	1	1	9
M3	1/2	0	–	1/2	1/2	1/2	1	1	1	1	1	1	8
M4	0	1	1/2	–	1/2	1/2	1	0	1/2	1	1	1	7
M5	0	0	1/2	1/2	–	1/2	1/2	1	1/2	1	1	1	6.5
M6	0	0	1/2	1/2	1/2	–	0	1	1	0	1	1	5.5
M7	0	1/2	0	0	1/2	1	–	1/2	1/2	0	1	1	5
M8	1/2	0	0	1	0	0	1/2	–	1	1	0	1/2	4.5
M9	0	0	0	1/2	1/2	0	1/2	0	–	1/2	1	1	4
M10	0	0	0	0	0	1	1	0	1/2	–	0	1	3.5
M11	0	0	0	0	0	0	0	1	0	1	–	1	3
M12	0	0	0	0	0	0	0	1/2	0	0	0	–	0.5

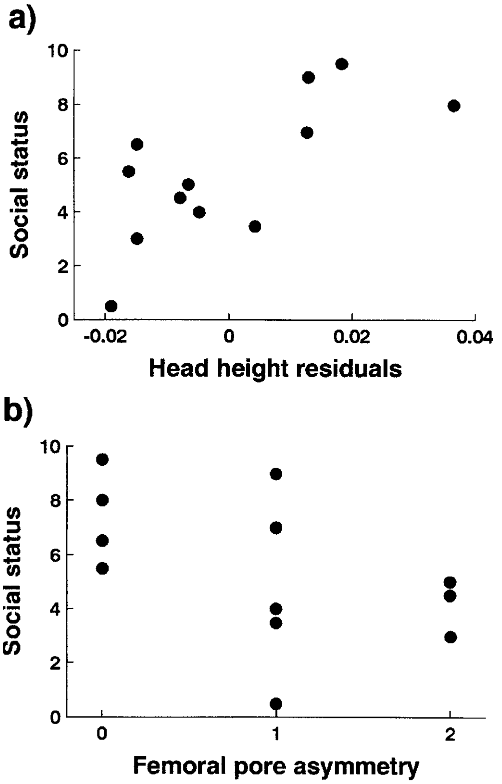

Fig. 1 Relationship between males' social status (increasing from 1 to 12) and **a** head height residuals of males, or **b** asymmetry of femoral pores of males (the unsigned right-minus-left number of pores)

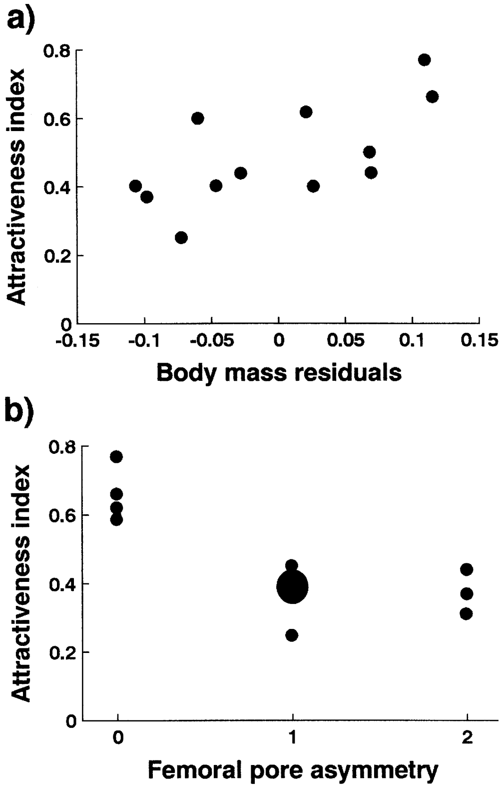

Fig. 2 Relationship between the index of attractiveness of males' scent to females and **a** body condition of males (residuals from the regression equation of ln mass on ln SVL), or **b** asymmetry of femoral pores of males (the unsigned right-minus-left number of pores). *Circles* of increasing size represent one or three observations, respectively

did not significantly affect social status of a male independently of their correlations with head height.

Stepwise multiple regression (R^2=0.66, F=8.71, 2,9 *df*, P=0.008) showed that attractiveness indices were significantly and positively correlated with the body condition of males (Table 2; Fig. 2). Additionally, females associated preferentially with the scent of males with low levels of asymmetry in the femoral pores. However, attractiveness indices were not significantly related to social status of males, head height residuals, or any of the other body measures that were not included in the regression model.

Discussion

Our results show that males with relatively higher heads reached a more dominant status. Males with 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 and body condition per se did not convey status within the range of sizes considered in this experiment (i.e. all males were large and old individuals). The results of previous studies suggest that males fought between themselves to establish a dominance hierarchy system, because this had a clear relationship with subsequent mating success (Martín and 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 included several females, and could easily access more females. Subordinate males were expelled when located and, as a consequence, had lower access to females (Martín and Salvador 1993, 1997; unpublished data). The evolution of social dominance requires phenotypic traits that convey honest information about an individual's status. Thus, most interactions consisted of displays in which 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 an opponent from his head size, and to retreat before a fight occurred.

Our experiment failed to find a significant relationship between male status and symmetry in the femoral pores. Nevertheless, it remains possible that chemical gland secretions of lizards may also indicate the status or competitive ability of a male to other males. Similarly, in male cockroaches (*Nauphoeta cinerea*), a social pheromone determines rather than reflects status, acting as a badge of status (Moore et al. 1997). The ability to discriminate between chemical secretions of different individuals might help male lizards quickly to determine status in an agonistic encounter or when encountering a scent mark, lowering the costs of aggressive interactions (Aragón et al. 2001a,b; López and Martín 2002). If the quality of chemical secretions is related to dominance, males might avoid entering areas scent-marked by competitively superior individuals or retreat from agonistic contests before escalation occurs. Supporting this, in other experiments, we found that competitively inferior small males (López et al. 1998) and also more asymmetrical males (Aragón et al. 2001d) significantly more often avoided entering areas scent-marked by dominant males.

The scent-choice experiments indicated that female *L. monticola* were able to assess the body condition of males by chemical signals alone and that they preferred to be in areas marked by relatively heavier males. Female choice based on visual quantitative traits has rarely been found in reptiles (Olsson and Madsen 1995, 1998; Tokarz 1995; Baird et al. 1997), although female choice based on male body size has been demonstrated in some lizard species (Cooper and Vitt 1993; Censky 1997). Females might prefer males in better body condition based on a presumed relation between male quality and superior genes (Cooper and Vitt 1993) or to avoid harassment from other males, which would allow females to increase foraging time (Censky 1997). Additionally, as occurred in a previous experiment, female *L. monticola* were also able to discriminate the symmetry of males by chemical signals alone, and preferred to be in areas marked by symmetric males (Martín and López 2000a). The quality of male pheromones could communicate to the female heritable male genetic quality and serve as the basis of adaptive female choice. One advantage of chemical signals is that they can be used to obtain information on an individual even when other sensory cues are absent. Thus, females might select where to establish their home ranges by relying on information from chemical signals left by males. We found that body condition of males per se did not convey status. Moreover, the attractiveness of the scent of a male to a female was not dependent on his social status. Therefore, female *L. monticola* did not prefer to be in areas marked by dominant males.

Our experiment indicates that sexually dimorphic traits in this lizard may be selected differently. Larger heads may give advantage to males in intrasexual contests, but are unimportant to females. In contrast, females prefer relatively heavier and more symmetrical males as potential mates. Chemicals arising from the femoral pores (a secondary sexual trait) and from other glands might honestly indicate quality (i.e. related to the symmetry) of an individual. Females may use this information because the only benefit of mate choice to female lizards may be genetic quality. These results suggest that chemical signals may be more reliable and have a greater importance in sexual selection of lizards than has been previously considered.

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