Female lizards ignore the sweet scent of success: Male characteristics implicated in female mate preference

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ABSTRACT

Sexual selection molds the morphology, physiology and behavior of males in many animals. At first glance, it seems reasonable to assume that females would use the same male traits and signals in mate choice as males do during male–male competition. However, intra- and intersexual competition may affect traits in the same or the opposite direction, with differing strength. We investigated which color, morphometric and performance traits are selected for through male–male competition and whether female mate preference is based on these same traits and/or dominance status in the three male color morphs of the lizard *Podarcis melisellensis*. Males with relatively bigger heads and relatively higher bite forces were more likely to win fights and orange males were always dominant over the other morphs. Females, however, preferred scents of bigger males that were in better body condition, and surprisingly had lower bite force capacities. They did not show a preference for scents of any particular color morph or for scents of the more dominant males. These results indicate that intra- and intersexual competition may result in selection for different secondary sexual traits in *P. melisellensis*.

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1. Introduction

Sexual selection molds the morphology, physiology and behavior of males in many animals (Andersson, 1994). Male competition over females typically selects for attributes related to fighting capacity and may result in males that are, for example, larger, heavier, stronger, faster and more aggressive than females (Andersson, 1994). In addition, males often bear sexual signals such as bright colors or exaggerated weapons that convey their fighting capacity to sexual opponents (Emlen, 2008). At first glance, it may seem reasonable to assume that females would use the same traits and signals in mate choice, because they should experience both direct (e.g., more or better resources) and indirect benefits (good genes/sexy sons) from associating with socially dominant males (Berglund et al., 1996; Kokko et al., 2003; Emlen, 2008). However, theoretical models (Holland and Rice, 1998; Kokko et al., 2003) and empirical evidence (e.g., Rice, 1992; Qvarnström and Forsgren, 1998; López et al., 2002a) indicate that at least in some animals, intra- and intersexual selection may work in different, or even opposing, directions. For instance, male dominance may not be a desired feature in females of polygynous species, if females have to

share the territory of a dominant male with many other females, or if males trade off efforts spent in male contests with parental care (Qvarnström and Forsgren, 1998). Trade-offs may occur between different fitness benefits if some are correlated with male competitive ability and others are not (see review in Wong and Candolin, 2005).

Studies of sexual selection in lizards have centered on male–male competition (Olsson and Madsen, 1998). A variety of morphological, physiological and performance characteristics are known to contribute to male fighting capacity and hence dominance. These include body size (e.g., Edsman, 1989; Wikelski and Trillmich, 1997), relative head size (e.g., López and Martín, 2002; Huyghe et al., 2005), testosterone levels (e.g., Tokarz, 1995; Husak et al., 2007), sprint speed (e.g., Perry et al., 2004; Husak et al., 2006), biting force (Huyghe et al., 2005; Husak et al., 2006) and calling frequency (Hibbitts et al., 2007), although results differ depending on the species considered. Males can often judge their opponents' fighting capacity from morphological attributes, such as dewlap size (Tokarz et al., 2003) and coloration (e.g., Thompson and Moore, 1991; Olsson, 1994) or behavioral displays (e.g., Lappin et al., 2006). Recently, a number of studies provided convincing evidence that chemical cues in femoral excretions deposited on the substrate may also provide males with important information on the dominance status of contending males (e.g., López et al., 2002b; Martín and López, 2007; Moreira et al., 2006; Carazo

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et al., 2007). Male color morphs can be associated with alternative reproductive strategies, and the color morph of the opponents may predict the contest outcome irrespective of other differences (Sinervo and Lively, 1996; Healey et al., 2007). However, in some species, the role of color signals in intra-sexual contests is less clear in determining dominance (Sacchi et al., 2009).

Until fairly recently, female choice was deemed unimportant or even non-existent in lizards (Olsson and Madsen, 1995). In recent years, however, it has been discovered that female lizards prefer to associate with males that have large body size (e.g., Karsten et al., 2009), relatively large heads (Karsten et al., 2009), particular colors or color patterns (e.g., Healey et al., 2008; Rosenblum, 2008; Lancaster et al., 2009) or that engage more in behavioral displays (e.g., Baird et al., 2007). In the context of female choice chemical senses may play an important role as well. Evidence has been accumulated that females can obtain information on the age (López et al., 2003), cell-mediated immune response (López and Martín, 2005; Martín and López, 2006), symmetry (Martín and López, 2000; López et al., 2002a), major histocompatibility complex (Olsson et al., 2003), color (López et al., 2009), and general health (López et al., 2006; Martín et al., 2006) of males by examining their femoral excretions.

It is less clear whether the same traits are implicated in intra- and intersexual selection. At least some of the traits that can be assessed and are preferred by females (e.g., body weight, health) may very well function in male–male combat, too (Karsten et al., 2009). However, the few studies that have addressed this issue suggest the reverse. In *Anolis carolinensis*, for instance, relative bite force and jumping capacity decide the outcome of male–male conflicts (Lailvaux et al., 2004), but do not function in female choice (Lailvaux and Irschick, 2006). Similarly, *Lacerta monticola* females were not particularly attracted by the scent of socially dominant males (López et al., 2002a).

In the present study, we examined which morphological and whole-animal performance attributes contribute to social dominance in males of the lizard species *Podarcis melisellensis*. We then let females of this species choose between areas labeled with the femoral excretions of two males, to test whether they preferred to associate with dominant males or with males with other characteristics. Since both males and females of *P. melisellensis* are polymorphic in ventral color (Huyghe et al., 2007), and since male color has been associated with traits such as body size, relative head size and biting capacity in this species (Huyghe et al., 2007, 2009), we also tested whether females preferred the scent of particular color morphs.

2. Materials and methods

2.1. Study species

P. melisellensis is a medium-sized heliothermic, insectivorous lacertid lizard (snout–vent length up to 70 mm) that occupies a variety of habitats along the Adriatic coast and on islands in the Adriatic Sea. At our study site on the island Lastovo (Croatia, 42°16′N, 16°54′E), males and females occur in three color morphs, with individuals having either a solid white, yellow or orange ventral color (Fig. 1).

Fifteen adult males of each color morph (white, yellow, and orange), 15 white and 15 yellow adult females (orange females are rare) were caught by noose in May 2007 and transported in individual cloth bags to the laboratory in Belgium. There, the lizards were housed individually in glass terraria (30 cm × 40 cm × 40 cm) and fed twice a week with calcium-dusted crickets and occasionally with field-caught insects and spiders. Water was available ad libitum. Lamps (40 W) provided light and heat for 14 h per day.

Upon completion of the experiments, all lizards were returned in seemingly good health to the study site in Croatia in September 2007. Of 75 lizards taken, only 3 (2 males + 1 female) died in captivity.

2.2. Morphometrics and performance measurements

The following morphometrical measurements (Table 1) were taken using digital calipers (precision 0.01 mm; Mitutoyo, Kawasaki, Japan): snout–vent length (SVL), head length, head height, head width, and lower jaw length. Body mass was determined using an Ohaus Scout Pro balance (precision 0.01 g; Ohaus Corp., Pine Brook, NJ, USA). Body condition was estimated as the residual of a linear regression of body mass on SVL.

Maximal sprint speed capacity was determined by chasing the lizards down a 2 m race track, following standard procedures for quantifying sprint performance (e.g., Vanhooydonck et al., 2001). Eight pairs of photocells, placed at 25 cm intervals, signaled passing lizards to a PC computer that calculated speed over the consecutive 25 cm intervals. The fastest speed over any 25 cm out of 3 trials was used as an estimate of maximal sprint speed.

Maximal bite force capacity was estimated by the highest of 5 recordings of a lizard biting on two metal plates connected to an isometric force transducer and a charge amplifier (see Herrel et al., 1999 for more details on the experimental set-up). Prior to every sprint and bite performance trial, males were kept individually in cloth bags and placed in an incubator set at 34 °C for at least 1 h. In

Fig. 1. Three male color morphs (orange, yellow, white) of the Dalmatian wall lizard, *Podarcis melisellensis*.

Table 1

Means ($\bar{X}$), standard errors of means (SEM) and range of body size (SVL), mass, head size, bite force capacity and maximal velocity (v) for the different color morphs. Head size is a new composite variable, obtained through a principal component analysis with head length, head height, head width and lower jaw length as input variables.

	Males			Females	
	Orange	Yellow	White	Yellow	White
SVL (mm)					
$\bar{X}$	64.01	61.42	64.74	55.94	55.59
SEM	0.55	0.82	0.73	0.78	0.40
Range	7.13	8.88	11.29	10.01	5.50
Mass (g)					
$\bar{X}$	6.71	5.74	6.45		
SEM	0.23	0.23	0.19		
Range	3.32	2.56	2.74		
Head size					
$\bar{X}$	0.50	−0.66	0.13		
SEM	0.22	0.28	0.20		
Range	2.67	3.05	2.32		
Bite force (N)					
$\bar{X}$	20.62	16.48	18.59		
SEM	0.59	0.79	0.68		
Range	7.94	9.83	7.31		
v (cm/s)					
$\bar{X}$	186.72	194.42	180.64		
SEM	8.70	12.02	6.56		
Range	118.42	180.92	69.44		

this way, all tests were done with lizards at or near their field-active body temperature (34 °C, unpublished data).

2.3. Male dominance

The 45 males were split into 21 pairs (3 males were not used in this experiment). Pairs consisted of males that differed less than 3 mm in SVL, but had different ventral coloration. Members of a pair were housed at either side of a terrarium (30 cm × 40 cm × 80 cm), divided equally by a removable partition. Lizards were kept under these conditions for two weeks before we started the behavioral observations. With this set-up, we could initiate encounters between competitors, which were both on home ground, simply by removing the partition. In this way, we aimed to circumvent the confounding effect of prior residence on the outcome of the interactions. After the removal of the partition, males could interact and we observed the lizards' behavior over a period of 30 min, starting from the moment when one of the focal lizards moved. During this time period, the number of attacks and flights were counted for each competitor, resulting in an 'aggressiveness' score for each individual (number of attacks minus number of flights). For each pair, the male with the highest score was considered the winner. This method has been proven effective in assigning dominance hierarchies to competing male lizards (Lailvaux et al., 2004; Perry et al., 2004; Huyghe et al., 2005).

2.4. Female-choice experiments

To examine whether adult females can and will discriminate between chemical clues left behind by the two males, we introduced them into the terrariums described above, with both males absent (identical pairs of males as in the male–male competition experiments) and the wooden partition removed. Two females (one yellow, one white) were confronted with the scents of the same pair of males, and each female was tested twice. At the onset of a trial, a female was introduced into the empty terrarium, and her position was recorded every 10 min during 5 h (from 10 a.m. to 3 p.m.). The number of times a female was observed in each male's

territory was considered this male's preference score. Each female was tested twice with the same pair of males, and preference scores were summed over these two tests. In one case the female was seen less than 6 times (less than 10% of the observations) in both her trials because she was hidden, and therefore this observation was disregarded.

2.5. Statistical analyses

When normality assumptions were not fulfilled, data were transformed accordingly or appropriate non-parametric tests were used. A principal component analysis (PCA) was performed on the head dimensions (head length, head height, head width and lower jaw length), resulting in one new variable, hereafter called "head size". Paired samples t-test (univariate) analyses were used to compare traits of winners vs. losers of agonistic interactions. To decouple head size and bite force capacity traits from body size, we calculated residual values of these traits from regressions on SVL and tested the residuals. To determine which male traits determined preference scores (dependent variable), a backward linear regression was used with SVL, mass, body condition, head size and bite force capacity as dependents. Spearman's rank correlation was used to test the relationship between preference score and sprint speed capacity. Multinomial tests were used to assess whether males of specific colors won fights more often, or were preferred by females.

3. Results

3.1. Male dominance

In 17 out of 21 cases, the male–male confrontations ended in a clear hierarchy; the dominant male typically remained active, while the subdominant male hid under a stone or retreated to the edge of the terrarium. The four experiments for which no winner could be assigned were removed from further analyses. Orange males typically won fights against the other morphs (Table 2). White and yellow males did not differ in their chances of winning when confronted with one another (Table 2).

A PCA on the four head dimensions (absolute measures of head length, width and height, and lower jaw length) resulted in one new variable that explained 86.07% (eigen value 3.44) of the total observed variation. This new variable, termed "head size", was positively correlated with head length ($r = 0.90$), head width ($r = 0.96$), head height ($r = 0.88$) and lower jaw length ($r = 0.97$). Winners tended to have relatively larger heads (residual head size, $t = 3.78$, $p = 0.006$), better body condition ($t = 2.40$, $p = 0.029$) and higher relative maximal bite forces (residual bite force, $t = 2.42$, $p = 0.028$) than losers. However, when controlling for multiple comparisons (Bonferroni correction, adjusted p-value = 0.013), only residual head size remained a significant predictor of the outcome of male–male fights. Maximal sprint speed capacity did not predict the probability of winning a fight ($t = -1.32$, $p = 0.21$).

### 3.2. Female-choice experiments

We assumed that a female prefers the scent of a male when she was observed more often at this male's side of the terrarium. We found no evidence for assortative preference with regard to ventral color. In the cases in which females could choose between a male with a color similar to her own vs. a male with a different color, the females chose the similarly colored male as often as the other one (multinomial test, $p = 0.50$). There was also no indication that females prefer males of a particular color (Table 2). Female preference was unaffected by male dominance: winners and losers were preferred at the same rate (multinomial test, $p = 0.18$).

Table 2
Multinomial probabilities of winning fights or being preferred by a female for the three color morphs of *P. melisellensis*.

Color		% Fights won		Probability fights	% Chosen preferred		Probability preference
Male 1	Male 2	Male 1	Male 2		Male 1	Male 2	
White	Orange	0	100	0.016[*]	20	80	0.20
White	Yellow	67	33	0.23	71	29	0.16
Orange	Yellow	100	0	0.031[*]	50	50	0.65

[*] Significant probabilities (<0.05).
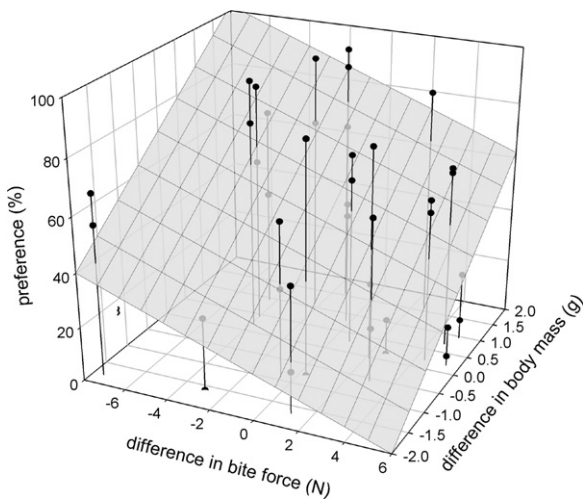
Fig. 2. The relationships among male preference score (% of female presence on the male's territory) and the differences with its competitor in bite force (N) and mass (g). The grid represents the predicted values generated from a multiple regression model (preference score = 15.5 × difference in mass − 2.9 × difference in bite force + 48.16).

A backward linear regression analysis with preference score as the dependent variable and SVL, mass, body condition, head size and bite force capacity as independent factors resulted in a significant model ($F_{3,38} = 5.55$, $p = 0.003$). The predicting factors were SVL, body condition, and bite force capacity, although in different directions. Preference scores were positively determined by SVL ($B = 5.13$, $p = 0.043$) and body condition ($B = 14.08$, $p = 0.005$), but negatively by bite force capacity ($B = -3.11$, $p = 0.011$) (Fig. 2). In other words, females preferred bigger males that were in better condition and had a lower maximal bite force capacity. Maximal sprint speed capacity was not correlated with male preference scores (Spearman's $\sigma = 0.20$, $p = 0.12$).

4. Discussion

In our experiments, *P. melisellensis* females showed a preference for chemicals deposited by bigger males with a better body condition. Unexpectedly, females also tended to be attracted by males with relatively low bite forces. Females did not prefer the scents of faster or more dominant males. Nor did females tend to associate with males of their own or a particular color morph. Orange males and males with big heads prevailed in agonistic interactions.

The fact that males with red (orange) pigmentation had a higher probability of winning contests is in agreement with a large number of studies. A red or orange coloration is often associated with aggression and dominance in a wide variety of animal taxa (see review in Pryke, 2009), including humans (Hill and Barton, 2005). These studies show that red coloration is an intrasexually selected signal in males, awarding a general intimidation value and thus a distinct dominance status to red coloration in agonistic encounters (Pryke, 2009). The color orange in *P. melisellensis* is a signal for fighting capacity through its association with head size and

bite force capacity: orange males have relatively bigger heads and can bite relatively harder than white and yellow males (Huyghe et al., 2007, 2009). Indeed, males with bigger heads and higher bite force capacity than their rivals tended to win fights. In lizards, there is growing evidence for the importance of whole-animal performance capacities during agonistic encounters between males. Locomotor performance can determine dominance (Garland et al., 1990; Robson and Miles, 2000; Perry et al., 2004), but more recently higher bite force capacity has been found to increase chances of winning a fight (Lailvaux et al., 2004; Huyghe et al., 2005; Husak et al., 2006) and the number of offspring sired (Husak et al., 2009). How this dominance advantage of orange males in *P. melisellensis* translates into relative morph fitness or the maintenance of the polymorphism is still unclear. As males do not change color throughout life (unpubl. data) and as the white and yellow morphs continue to persist in our study species, it seems that this orange dominance also has its drawbacks.

We did not find any evidence for a possible disadvantage of orange coloration through female mate choice, but orange dominance during fights was not accompanied by female preference for orange males. Instead, the three morphs were equally preferred by females. Alternatively, females may not have preferred a particular morph because they were not able to distinguish the color morphs by scent only. However, in the lizard *Iberolacerta monticola*, it has been demonstrated that females can and do distinguish color morphs by chemical secretions (López et al., 2009), making it likely that female *P. melisellensis* are also able to do so. Moreover, preliminary results of a study testing female choice based on visual and chemical signals show an equal outcome (Rotsaert et al., unpublished results). Interestingly, previous authors have argued that in lizards females rarely, if ever, choose their mates (Olsson and Madsen, 1995; Lebas and Marshall, 2001; Lailvaux and Irschick, 2006). There are several reasons why female choice in lizards is not expected, for example, the absence of parental care, the unreliability of male phenotypic traits as cues to heritable fitness and the many risks associated with mate choice, such as increased exposure to predators or time investment. On the other hand, when good genes are signaled by elaborate and/or showy secondary sexual characters in males, such as coloration in *P. melisellensis*, female choice should be evolutionary beneficial. Although color did not determine female preference, our data confirm the existence of female preference for bigger males in good body condition. Although body size differed by less than 3 mm within a pair of males, females seemed to be able to distinguish this difference and preferred the slightly bigger male. Body size and condition might thus be indexes for male quality, independent of color. In the Iberian rock lizard (*L. monticola*) females also showed strong chemosensory responses and preferred the scent of males of presumed high quality (López et al., 2003; Martín and López, 2006) and with a greater body mass (López et al., 2002a), and in the common lizard (*Lacerta vivipara*) males in better body condition were more likely to mate and father offspring (Fitze et al., 2008). The indication that low male bite forces were preferred by females might also mean that possibly there is selection against bite force to avoid male harassment (Rankin and Kokko, 2006). Male harassment has been associated with an increase in female mortality (Réale et al., 1996; Le Galliard

et al., 2006; Heubel and Plath, 2008) and this might be the case in *P. melisellensis* as males bite females during mating, which may cause injuries. In a similar vein, female *L. monticola* lizards show a preference for the scent of older over younger males, possibly to avoid harassment by sneaking young males (López et al., 2003).

Our results indicate that traits used in assessing male dominance hierarchies and traits determining females' preferences do not completely overlap. Even though the ultimate result of sexual selection, i.e. the number of offspring sired by each color morph, is yet unknown, these results indicate a possible differential impact of intra- vs. intersexual selection on male traits.

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References

Andersson, M., 1994. Sexual Selection. Princeton University Press, Princeton.
Baird, T.A., Fox, S.F., McCoy, J., 2007. Behavioral attributes influence annual mating success more than morphological traits in male collared lizards. Behav. Ecol. 18, 1146–1154.
Berglund, A., Bisazza, A., Pilastro, A., 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biol. J. Linn. Soc. 58, 385–399.
Carazo, P., Font, E., Desfilis, E., 2007. Chemosensory assessment of rival competitive ability and scent-mark function in a lizard, *Podarcis hispanica*. Anim. Behav. 74, 895–902.
Edsman, L., 1989. Territoriality and competition in wall lizards. Ph.D. Thesis, University of Stockholm.
Emlen, D.J., 2008. The evolution of animal weapons. Annu. Rev. Ecol. Evol. Syst. 39, 387–413.
Fitze, P.S., Cote, J., Martínez-Rica, J.P., Clobert, J., 2008. Determinants of male fitness: disentangling intra- and intersexual selection. J. Evol. Biol. 21, 246–255.
Garland Jr., T., Hankins, E., Huey, R.B., 1990. Locomotor capacity and social dominance in male lizards. Funct. Ecol. 4, 243–250.
Healey, M., Uller, T., Olsson, T., 2007. Seeing red: morph-specific contest success and survival rates in a colour-polymorphic agamid lizard. Anim. Behav. 74, 337–341.
Healey, M., Uller, T., Olsson, T., 2008. Variety is the spice of life: female lizards choose to associate with colour-polymorphic male dyads. Ethology 114, 231–237.
Herrel, A., Spithoven, L., Van Damme, R., De Vree, F., 1999. Sexual dimorphism of head size in *Gallotia galloti*, testing the niche divergence hypothesis by functional analyses. Funct. Ecol. 13, 289–297.
Heubel, K.U., Plath, M., 2008. Influence of male harassment and female competition on female feeding behavior in a sexual–asexual mating complex of mollies (*Poecilia mexicana, P. formosa*). Behav. Ecol. Sociobiol. 62, 1689–1699.
Hibbitts, T.J., Whiting, M.J., Stuart-Fox, D., 2007. Shouting the odds: vocalization signals status in a lizard. Behav. Ecol. Sociobiol. 61, 1169–1176.
Hill, R.A., Barton, R.A., 2005. Red enhances human performance in contests. Nature 435, 293.
Holland, B., Rice, W.R., 1998. Perspective: chase-away sexual selection: antagonistic seduction versus resistance. Evolution 52, 1–7.
Husak, J.F., Lappin, A.K., Fox, S.F., Lemos-Espinal, J.A., 2006. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). Copeia 2006, 301–306.
Husak, J.F., Irschick, D.J., Meyers, J.J., Lailvaux, S.P., Moore, I.T., 2007. Hormones, sexual signals, and performance of green anole lizards (*Anolis carolinensis*). Horm. Behav. 52, 360–367.
Husak, J.F., Lappin, A.K., Van Den Bussche, R.A., 2009. The fitness advantage of a high-performance weapon. Biol. J. Linn. Soc. 96, 840–845.
Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., Van Damme, R., 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. Funct. Ecol. 19, 800–807.
Huyghe, K., Vanhooydonck, B., Herrel, A., Tadić, Z., Van Damme, R., 2007. Morphology, performance, behaviour and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. Integr. Comp. Biol. 47, 211–220.
Huyghe, K., Herrel, A., Adriaens, D., Tadić, Z., Van Damme, R., 2009. It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard. Biol. J. Linn. Soc. 96, 13–22.
Karsten, K.B., Andriamandimbiarisoa, L.N., Fox, S.F., Raxworthy, C.J., 2009. Sexual selection on body size and secondary sexual characters in two closely related, sympatric chameleons in Madagascar. Behav. Ecol. Sociobiol. 20, 1079–1088.
Kokko, H., Brooks, R., Jennions, M.D., Morley, J., 2003. The evolution of mate choice and mating biases. Proc. R. Soc. Lond. B 270, 653–664.
Lailvaux, S.P., Irschick, D.J., 2006. No evidence for female association with high-performance males in the green anole lizard, *Anolis carolinensis*. Ethology 112, 707–715.
Lailvaux, S.P., Herrel, A., Vanhooydonck, B., Meyers, J.J., Irschick, D.J., 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). Proc. R. Soc. Lond. B 271, 2501–2508.
Lancaster, L.T., Hipsley, C.A., Sinervo, B., 2009. Female choice for optimal combinations of multiple male display traits increases offspring survival. Behav. Ecol. 20, 993–999.
Lappin, A.K., Brandt, Y., Husak, J.F., Macedonia, J.M., Kemp, D.J., 2006. Gaping displays reveal and amplify a mechanically based index of weapon performance. Am. Nat. 168, 100–113.
Lebas, N.R., Marshall, N.J., 2001. No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. Behaviour 138, 965–980.
Le Galliard, J.-F., Fitze, P.S., Ferrière, R., Clobert, J., 2006. Sex ratio bias, male aggression, and population collapse in lizards. Proc. Natl. Acad. Sci. U.S.A. 102, 18231–18236.
López, P., Martín, J., 2002. Locomotor capacity and dominance in male lizards *Lacerta monticola*: a trade-off between survival and reproductive success? Biol. J. Linn. Soc. 77, 201–209.
López, P., Martín, J., 2005. Female Iberian wall lizards prefer male scents that signal a better cell-mediated immune response. Biol. Lett. 1, 404–406.
López, P., Muñoz, A., Martín, J., 2002a. Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. Behav. Ecol. Sociobiol. 52, 342–347.
López, P., Martín, J., Cuadrado, M., 2002b. Pheromone-mediated intrasexual aggression in male lizards, *Podarcis hispanicus*. Aggr. Behav. 28, 154–163.
López, P., Aragon, P., Martín, J., 2003. Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males. Behav. Ecol. Sociobiol. 55, 73–79.
López, P., Amo, L., Martín, J., 2006. Reliable signalling by chemical cues of male traits and health state in male lizards. J. Chem. Ecol. 32, 473–488.
López, P., Moreira, P.L., Martín, J., 2009. Chemical polymorphism and chemosensory recognition between *Iberolacerta monticola* lizard color morphs. Chem. Senses 34, 723–731.
Martín, J., López, P., 2000. Chemoreception, symmetry and mate choice in lizards. Proc. R. Soc. Lond. B 267, 1265–1269.
Martín, J., López, P., 2006. Links between male quality, male chemical signals, and female mate choice in Iberian rock lizards. Funct. Ecol. 20, 1087–1096.
Martín, J., López, P., 2007. Scent may signal fighting ability in male Iberian rock lizards. Biol. Lett. 3, 125–127.
Martín, J., Civantos, E., Amo, L., López, P., 2006. Chemical ornaments of male lizards *Psammodromus algirus* may reveal their parasite load and health state to females. Behav. Ecol. Sociobiol. 62, 173–179.
Moreira, P.L., López, P., Martín, J., 2006. Femoral secretions and copulatory plugs convey chemical information about male identity and dominance status in Iberian rock lizards (*Lacerta monticola*). Behav. Ecol. Sociobiol. 60, 166–174.
Olsson, M., 1994. Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. Anim. Behav. 48, 607–613.
Olsson, M., Madsen, T., 1995. Female choice on male quantitative traits in lizards–why is it so rare? Behav. Ecol. Sociobiol. 36, 179–184.
Olsson, M., Madsen, T., 1998. Sexual selection and sperm competition in reptiles. In: Birkhead, T., Møller, A. (Eds.), Sexual Selection and Sperm Competition. Academic Press, London, pp. 503–564.
Olsson, M., Madsen, T., Nordby, J., Wapstra, E., Ujavri, B., Wittsell, H., 2003. Major histocompatibility complex and mate choice in sand lizards. Proc. R. Soc. Lond. B 270, S254–S256.
Perry, G., Levering, K., Girard, I., Garland Jr., T., 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. Anim. Behav. 67, 37–47.
Pryke, S.R., 2009. Is red an innate or learned signal of aggression and intimidation? Anim. Behav. 78, 393–398.
Qvarnström, A., Forsgren, E., 1998. Should females prefer dominant males? Trends Ecol. Evol. 13, 498–501.
Rankin, D.J., Kokko, H., 2006. Sex, death and tragedy. Trends Ecol. Evol. 21, 225–226.
Réale, D., Boussès, P., Chapuis, J.-L., 1996. Female-biased mortality induced by male sexual harassment in a feral sheep population. Can. J. Zool. 74, 1812–1818.
Rice, W.R., 1992. Sexually antagonistic genes: experimental evidence. Science 256, 1436–1439.
Robson, M.A., Miles, D.B., 2000. Locomotor performance and dominance in male tree lizards. Funct. Ecol. 14, 338–344.
Rosenblum, E.B., 2008. Preference for local mates in a recently diverged population of the lesser earless lizard (*Holbrookia maculata*) at White Sands. J. Herpetol. 42, 572–583.
Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M., Galeotti, P., 2009. Male–male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. Aggr. Behav. 35, 274–283.
Sinervo, B., Lively, C., 1996. The rock–paper–scissors game and the evolution of alternative male strategies. Nature 380, 240–243.
Thompson, C.W., Moore, M.C., 1991. Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. Anim. Behav. 42, 745–753.
Tokarz, R.R., 1995. Importance of androgens in male territorial acquisition in the lizard *Naolis sagrei*: an experimental test. Anim. Behav. 49, 661–669.

Tokarz, R.R., Paterson, A.V., McMann, S., 2003. Laboratory and field test of the functional significance of the male's dewlap in the lizard *Anolis sagrei*. Copeia 2003, 502–511.

Vanhooydonck, B., Van Damme, R., Aerts, P., 2001. Speed and stamina trade-off in lacertid lizards. Evolution 55, 1040–1048.

Wikelski, M., Trillmich, F., 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution 51, 922–936.

Wong, B.B.M., Candolin, U., 2005. How is female choice affected by male competition? Biol. Rev. 80, 559–571.