Behav Ecol Sociobiol (2003) 55:73–79
DOI 10.1007/s00265-003-0675-3

ORIGINAL ARTICLE

Pilar López · Pedro Aragón · José Martín

Responses of female lizards, *Lacerta monticola*, to males' chemical cues reflect their mating preference for older males

Received: 29 April 2003 / Revised: 11 July 2003 / Accepted: 13 July 2003 / Published online: 2 September 2003

Abstract Female mate choice based on visual traits appears to be rare in lizards. Field observations suggest that females of the lizard *Lacerta monticola* preferred to mate with larger/older males. Although older males are usually green and larger, and younger males brown and smaller, there is some overlap in size and coloration between age classes. Thus, visual cues may not always be reliable indicators of a male's age. We hypothesized that female mate-choice preferences may be based on males' pheromones, which might transmit information about characteristics such as age. In a laboratory experiment, we analyzed the effect of age of males on attractiveness of their scents to females. When we offered scents of two males of different age, females associated preferentially with scents of older males. This suggested that females were able to assess the age of males by chemical signals alone, and that females preferred to be in areas scent-marked by older males. Thus, females may increase their opportunities to mate with males of high quality, or may avoid harassment by sneaking young males. This result agreed with field observations on females mating with old males, and rejection of advances by young males. Our results also suggested that female preference for older males may depend on their own body size. Large females showed a strong preference for older males, whereas smaller females were not so selective. This, together with males' preference for large females, might lead to size-assortative matings. We suggest that the quality and/or quantity of male pheromones could communicate to the female heritable male genetic quality (i.e. age) and thereby serve as the basis of adaptive female choice in lizards.

Communicated by W.E. Cooper

P. López (✉) · P. Aragón · J. Martín
Departamento de Ecología Evolutiva,
Museo Nacional de Ciencias Naturales, CSIC,
José Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: Pilar.Lopez@mncn.csic.es
Fax: +34-91-5645078

Keywords Chemoreception · Lizards · Female mate choice · Femoral glands · Male mating success

Introduction

Female choice based on visual quantitative traits such as coloration has rarely been demonstrated in reptiles (Olsson and Madsen 1995, 1998; Tokarz 1995; Baird et al. 1997; McCoy et al. 2003). However, female choice based on male body size has been demonstrated in some lizard species (Cooper and Vitt 1993; Wikelski et al. 1996; Censky 1997; Martín and Forsman 1999). Females might choose larger/older males based on male quality reflecting superior genes (Cooper and Vitt 1993), or on the quality of the resource that the male holds (Hews 1990) because these resources affect the female's survival or fecundity. Alternatively, females may choose large males to avoid harassment from other males, which would allow females to increase foraging time (Censky 1997).

In species, such as lizards, in which males provide only sperm to females, it is widely held that females should prefer to mate with older males because viability selection leads to older males of higher genotypic quality than younger males (Kirkpatrick 1987; Andersson 1994; Brooks and Kemp 2001). However, age and body size may be poorly correlated in some lizards, and thus size would be a poor indicator of male longevity (Olsson and Shine 1996). Even though bright male colors might be important in social interactions between males, they do not always vary consistently with age (Olsson 1994; Olsson and Madsen 1995; Smith and Zucker 1997; Martín and Forsman 1999). Thus, female choice of older males might be rare because visual cues of male age are poor or inaccurate (Olsson and Madsen 1995, 1998).

Although communication by chemical signals is widespread (Stoddart 1980), research on sexual selection and mate choice has focused mainly on visual signals, ignoring chemical communication (Bateson 1983; Møller and Thornhill 1998). However, many species rely on chemical signals to attract mates, and male odors convey a great amount of information in many animals, such as a male's age, dominance status, health, parasite load, or genetic quality (e.g., Moore et al. 1997; Penn and Potts 1998; Osada et al. 2003). Chemical cues also play an important role in intraspecific communication of lizards (Halpern 1992; Mason 1992; Cooper 1994; Fox and Shipman 2003). Pheromonal detection has been demonstrated in several different species, and is often based on precloacal and femoral-gland secretions (e.g., Cooper and Vitt 1984; Alberts 1989; López et al. 1998; Aragón et al. 2000, 2001a, 2001b). The presence and relative concentration of pheromone components in the gland secretions vary, not only between sexes, but also consistently among individuals, which may convey information on individual identity and serve a variety of functions (Alberts 1990, 1992, 1993; Aragón et al. 2001a, 2001b). Males' secretions might transmit chemical information about an individual's quality, and this information may be used by females in their mate-choice process. For example, when scents from two males of similar body size were offered, female *Lacerta monticola* associated preferentially with scents of males with low asymmetry in their femoral pores (Martín and López 2000) or with better body condition (López et al. 2002). This suggests that females were able to discriminate the quality and condition of males by chemical signals alone, and that females preferred to be in areas marked by these males, thus increasing their opportunities to mate with males of high quality.

The Iberian rock-lizard (*L. monticola*) is a small, diurnal lacertid lizard found mainly in rocky habitats of some high mountains of the Iberian Peninsula (Martín and Salvador 1992; Pérez-Mellado 1998). Within sexually mature male *L. monticola*, there are distinct ontogenetic classes. Recapture observations and skeletochronology data indicate that most, but not all, older males show dorsal green coloration (4–5 years old; snout-to-vent length, SVL: $\bar{X}$+SE=73+1 mm, range=67–78 mm, *n*=30), and are on average larger, although the body-size ranges overlap with younger males, which always show dorsal brown coloration (3 years old; SVL: $\bar{X}$+SE=67+1 mm, range=61–79, *n*=28) (see also Moreira et al. 1998; Pérez-Mellado 1998; Aragón 2001). Therefore, body size and coloration do not always reliably signal age in males. Young males are sexually mature, based on observations of spermatogenic activity (Elvira and Vigal 1985), courting behavior, and attempted copulation (Aragón 2001; unpublished data, see Results). Males are aggressive and defend their territories, which can contain several female home ranges, although overlap between males' home ranges is extensive (Martín and Salvador 1993, 1997; Aragón 2001). Agonistic encounters between males of both types are frequent during the mating season, suggesting intense competition for access to females (Aragón et al. 2001d).

Male *L. monticola* deposit fecal pellets and femoral secretions on specific sites, and are able to detect and discriminate individuals based on chemical cues alone (López et al. 1998; Aragón et al. 2001a, 2001b). Substrates marked with feces and femoral-gland secretions may serve as scent marks in the field and probably function also in home-range advertisement (Alberts 1992; López et al. 1998; Aragón et al. 2001c). They might be used by females to estimate mate quality (Martín and López 2000; López et al. 2002). We hypothesized that if females preferred to mate with older males, nonvisual cues to male age should be important due to the unreliability of body size and color. Females might be able to assess the age of males by chemical signals, associate preferentially with scent marks of older males, and use this information to allow or reject matings by courting males.

We present field observations on differences between old and young male *L. monticola* in mating success with females, as indicated by the propensity of females to accept courtship and copulations from males, and by the frequency of observations of females allowing males to guard them. Also, we conducted a laboratory experiment to analyze the effect of age of male *L. monticola* on attractiveness of their scent marks to females.

Methods

Male mating success in the field

We performed the study from May to June 1998–2001 in the Guadarrama Mountains (Madrid Province, central Spain) at an elevation of 1,900 m. Granite rock boulders and scree interspersed with shrubs (*Cytisus oromediterraneus* and *Juniperus communis*) predominated at the study site, together with meadows of *Festuca* and other grasses (Martín and Salvador 1992). The field study was conducted on a 0.2-ha plot (50×40 m) located in this area at "Alto del Telégrafo". Lizards were captured by noosing, weighed with a Pesola spring scale, their SVL measured with a ruler, and their sex and coloration (green vs brown) were noted. Lizards were individually marked permanently by toe-clipping and temporarily with small dots of acrylic paint on the dorsum. They were released at the capture site within 5 min. Additional field work was done in the subsequent mating seasons to study survival, growth, and changes of coloration of individuals studied in previous years (Aragón 2001; unpublished data). Age estimation was possible by using previously marked lizards from earlier years (i.e. 1st-year juveniles of known age identified by their blue tails).

We searched for lizards by walking the area between 0700 and 1200 hours (G.M.T.) each day during May and June, which coincided with the mating season (Aragón et al. 2001d). All observed sexual interactions between marked males and females were noted. We used binoculars to identify marked lizards at long distances. To avoid pseudoreplication, only the first observation of each individual male was considered for analyses. During courtship displays, the male approached the female slowly and began to tongue-flick her body or tail, or the surrounding substrate. He next gripped and shook the female's tail with a gentle bite, and then attempted mounting. If the female was receptive, she allowed this courtship and posterior copulation. However, females sometimes tried to escape from the male, even by biting him. Some males were able to force the copulation, anyway. Female rejection behaviors are easy to identify in many lizards and can be used to test mate-choice preferences of females. Thus, we noted for each attempt whether the male was successful and completed a copulation, or was unsuccessful, either because the female escaped from the male or because another older male appeared and chased the male that was courting the female, thus preventing copulation. We also noted those males found close to females and following female movements closely (<0.1 m apart continuously during more than 5 min), which were defined as mate guardings (Olsson and Shine 1998).

To compare the number of copulation attempts and mate guardings performed by old and young males, we conducted two-tailed binomial tests (Siegel and Castellan 1988), assuming frequencies to be equally probable for each male category because the proportion of males in each category in the population did not differ from a 1:1 ratio (Aragón 2001; unpublished data).

Scent-choice experiments

During May 2001, we captured by noosing 20 adult males marked in the study plot in previous years. Eighteen adult females were captured in different places over a large area ("Puerto de Navacerrada", Guadarrama Mountains, central Spain) to ensure that females had not been in previous contact with males, which might affect the outcome of the experiment. Lizards were captured before the start of the mating season. We confirmed that females had not mated yet by their lack of characteristic mating scars on the belly (unpublished data). The experiments were carried out during May and June, which coincided with the mating season of lizards in their original natural population (Aragón et al. 2001d).Lizards were weighed and their SVL was measured (males: SVL: $\bar{X}$+SE=72+1 mm, range=69–77 mm; body mass: 7.8+0.2 g, range=6.5–9.5 g; females: SVL: $\bar{X}$+SE=75+1 mm, range=68–86 mm; body mass: 6.3+0.3 g, range=4.5–9 g). Based on recapture observations, we classified the males into two age classes (young males: $\bar{X}$+SE=70+1 mm, range=69–71 mm, *n*=12; old males: $\bar{X}$+SE=76+1 mm, range=75–77 mm, *n*=8). Lizards 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 set in different places to ensure no contact between sexes. Food (mealworms and crickets dusted with a multivitamin powder) and water were provided ad libitum. Lizards were held in their home 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 locations.

To obtain the scents and secretions from the femoral and cloacal glands of lizards, 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. Males were often observed depositing feces and rubbing the cloaca and the femoral pores on this paper substrate. Papers were removed to be placed in females' cages immediately before each experiment began. Paper strips were manipulated with fresh rubber gloves to avoid contaminating them with human odors.

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 center. At the beginning of each experiment (0700 hours GMT), when females were still inactive and hidden in the refuge, we fixed on one tile one paper strip from one young male, and another from an old male on the other tile. The individual male tested within each age category and the position of the tiles in the cages were randomly determined. Each female was tested on two different days, with papers from four different males (two different pairs of a young and an old male). Each paper strip was used only in one test to avoid contamination by females. We used the instantaneous scan sampling method: females were monitored each 30 min from a hidden point, and their locations in the cages were recorded. Each trial lasted 8 h (between 0800 and 1600 hours GMT, when lizards hid again in the refuge). At the conclusion of each trial, the papers were removed and the cage was thoroughly rinsed with clean water. Female *L. monticola* have limited movement rates, spending long time periods stationary, and use more often a sit-and-wait foraging strategy than males (Martín and Salvador 1997). Thus, the locations observed on each of the 17 scans were considered to be representative of females' space use of the cages.

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 or inside the refuge she was designated as having made no choice. To ensure that females were exposed to both males' tiles and were aware of both males' stimuli, at least one recording in each male's section was considered necessary for a trial to be valid. This presumption was fulfilled in all tests.

We determined a female choice to be the side on which she was on the tile in greater than 50% of scans. Differences between treatments were assessed for significance using binomial tests, assuming frequencies to be equiprobable on each side. We also used Wilcoxon matched-pairs tests to compare the number of times that females were recorded on each side. We used Pearson's correlation to analyze the relationship between body size of females and number of times that they were recorded on the side containing scents from the old male (Sokal and Rohlf 1995).

Results

Male mating success in the field

In spite of a similar proportion of old and young males in the population (see Methods), more old than young males were observed attempting to copulate with females (24 old vs 10 young; two-tailed binomial test, *P*=0.026). Moreover, old and young males were not equally successful at obtaining matings. Of the successful copulations observed, old males performed 14 (58.3% success) and young males only 2 (20% success) (χ^2=4.16, 1 *df*, *P*=0.04). Unsuccessful copulations were due to female rejection (36.4% in unsuccessful copulation attempts of old males vs 62.5% in young males), or to interference by another old male (63.6% in large males vs 37.5% in young males). In addition, in two cases an old male tried to interrupt copulation by another old male without success. Thus, young males had significantly lower mating success than old males (restricting the analysis to those cases in which females rejected a male: χ^2=4.41, 1 *df*, *P*=0.036), whereas males of the two age groups did not significantly differ in mating success when the analysis is restricted to those cases unsuccessful due to male interference (χ^2=0.87, 1 *df*, *P*=0.35). Additionally, old males were observed performing a significantly higher number of mate guardings than young males (16 old vs 4 young; two-tailed binomial test, *P*=0.011).

Scent-choice experiments

Females clearly selected the paper strips scent-marked by old males. In the first test, 12 females selected the side with the scent of old males, whereas the other 6 females did not select either side (two-tailed binomial test, *P*=0.0005). In the second test, 14 females selected the side with the scent of old males, 2 selected the side with the scent of young males, and the other 2 females did not select either side (two-tailed binomial test, *P*=0.004). Moreover, females were observed significantly more frequently on the side with scents of old males in both tests (Wilcoxon matched-pairs test, first test: *z*=3.06,

Table 1 Number of times that female *Lacerta monticola* were observed on the sides with scent of the older or the younger male, or in the non-choice area in two different tests

Female	1st test			2nd test		
	Old	Young	Neither	Old	Young	Neither
1	4	1	12	8	4	5
2	8	8	1	16	1	0
3	1	1	15	7	4	6
4	4	4	9	4	1	12
5	1	1	15	11	4	2
6	8	1	8	4	1	12
7	4	1	12	8	4	5
8	5	5	7	15	1	1
9	4	1	12	8	4	5
10	8	1	8	4	1	12
11	3	1	13	1	1	15
12	11	1	5	1	8	8
13	4	1	12	8	4	5
14	5	4	8	11	4	2
15	12	1	4	16	1	0
16	1	1	15	3	1	13
17	4	1	12	4	4	9
18	8	1	8	4	5	8

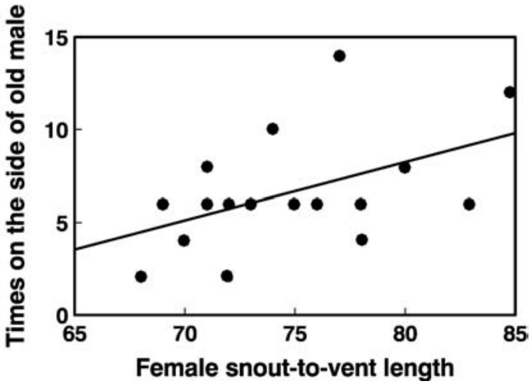

Fig. 1 Time spent by female *Lacerta monticola* on the side containing chemicals from the older male (the average number of times that females were recorded on that side in the two trials) as a function of female snout-to-vent length

df=17, *P*=0.002; second test: *z*=2.84, *df*=17, *P*=0.004) (Table 1).

One piece of evidence suggests that although females preferred the scent of old males, females may also tend to associate assortatively with males' scents according to their own body size. The average number of times that females were recorded on the side with chemicals from the old male in the two trials was significantly correlated with SVL of females (Pearson correlation, *r*=0.50, *F*=5.29, *P*=0.03) (Fig. 1). Thus, large females spent more time on the side scent-marked by old males, whereas smaller females did not show such a pattern. The relationship between time spent on the side of old males and body mass of females was also positive, but not significant (*r*=0.43, *F*=3.56, *P*=0.08).

Discussion

Previous field observations indicated that in agonistic interactions, larger/older males were dominant over smaller/young males and had a higher access to mates (Martín and Salvador 1993; Aragón 2001). The present results show that males use two different mating strategies. More old than young males were observed guarding or at least staying close to females, who later usually accepted copulations from these old males without apparent resistance. In contrast, young males used alternative reproductive tactics, and obtained access to some unguarded females by sneaking. In many animals, including other lizards, sneak matings are typically an ontogenetic alternative to guarding, performed by younger or subordinate phenotypes (Koprowski 1993; Olsson 1994; Baird and Timanus 1998; Martín and Forsman 1999). Males of many species exhibit alternative mating strategies depending upon age and/or local social conditions (Dominey 1984; Caro and Bateson 1986; Moore 1991). These age-related differences may be selected because some behavior patterns may be adaptive at one life stage, or under one set of local conditions, but disadvantageous during others (Baird and Timanus 1998). Dominant old males may exclude subordinate young males from access to females by guarding these females, and by interfering with attempts at copulation by young males (Baird and Timanus 1998; Martín and Forsman 1999). However, the chance of successful copulation by young male *L. monticola* was low even in the absence of other males because females rejected copulation attempts by young males, which were only successful in getting forced copulations if they were able to subdue the females (see also Cooper and Vitt 1987; Martín and Salvador 1993; Martín and Forsman 1999). Nevertheless, old males also attempted forced copulations with females other than those that they courted and guarded. This strategy may enhance their reproductive success if the risk of cuckoldry is small because males may devote less time to guarding and more time to seeking copulations with other females.

These field observations suggest that female *L. monticola* prefer to mate with older males. Body size and coloration may be the first indication of a male's age for a female, especially at long distance. In many cases, these visual signals would be enough and reliable (i.e., a large green male is always an old male). However, the laboratory experiment suggests that females are also able to discriminate between old and young males by chemical cues alone. Pheromonal identification may be the most important and confirmatory cue when two individuals are close together, or when a conflict between the meaning of the visual and scent signals arises (i.e., a large brown male can be either an old or a young male). A similar identification procedure is used by other lizards when visual and chemical signals conflict (López and Martín 2001; López et al. 2003).

The properties of lizard pheromones are propitious for use in identification by females. Femoral-gland secretions are composed of both lipids and proteins (Alberts 1990).

Lipids have a high degree of molecular diversity, which increases the potential information content of a pheromone, and individual differences in protein secretion chemistry are consistent over time (Alberts 1992). Thus, femoral-gland secretions could potentially function in individual recognition (Glinsky and Krekorian 1985; Aragón et al. 2001a, 2001b), but also indicate the characteristics, age, and quality of the male.

Moreover, the quantity or concentration of pheromonal secretion also might vary with age or body size in the scent marks of a male. As in insects (Breed et al. 1980; Thornhill 1992) and mammals (Drickamer 1992; Osada et al. 2003), the quality or quantity of male pheromone could communicate to the female heritable male genetic quality. Thus, it could serve as the basis of adaptive female choice. This agrees with the preference by female *L. monticola* for scents of old males. This preference suggests that female *L. monticola* may increase their opportunities to mate with males of high quality by selecting areas scent-marked by these males (see also Martín and López 2000; López et al. 2002). Alternatively, even if females did not intend to mate with these males, they could use males' chemical signals to select high-quality territories if larger/older males maintain territories of high quality in terms of food availability and thermoregulatory opportunities (Hews 1990), or to avoid costly harassment from males seeking forced copulations (Censky 1997).

Costs associated with female mate choice may reduce the likelihood that female preferences are expressed (Beck and Powell 2000). Thus, it has been proposed that female insectivorous lizards do not exercise mate choice very often because it will be costly in terms of time and energy to assess multiple males as potential mates (Stamps 1983). However, in *L. monticola* density of males is high, their home ranges have a high degree of overlap, and males seem to scent-mark their home ranges with feces and femoral secretions (López et al. 1998; Aragón et al. 2000, 2001a, 2001b, 2001c). Thus, females may have the opportunity to sample the scent markings of several males within a short enough period to recall differences. Pheromone components in scent marks may provide detailed and reliable information on the male about traits such as age, body size, or competitive ability (Alberts 1992; Aragón et al. 2000, 2001a, 2001c). Therefore, this and previous studies suggest that mate choice in at least some species of lizards may be based on, or complemented by, chemical cues (Martín and López 2000; López et al. 2002). However, this possibility has been largely ignored in studies of mate choice in lizards (Tokarz 1995), despite pheromonal recognition being widespread among lizards (Halpern 1992; Mason 1992).

Our results also suggest that female preference for old males may also depend on the female's own body size. Large females showed a strong preference for large/old males, whereas smaller, often younger, females were not as selective. Younger females might be inexperienced in discriminating or selecting scents of old males. Alternatively, these differences could result from males' preference for large females, as female body size may be a correlate of fecundity (Olsson 1993; Whiting and Bateman 1999). In fact, clutch size is correlated with female *L. monticola* body size (Pérez-Mellado 1982; Braña 1996). Although further studies on male preferences are needed, it is possible that smaller females are not courted often by old males, and these females might have to accept copulations from young males to ensure being fertilized. Both female and male preferences for older individuals (or for a larger body size) might lead to size-assortative mating in this lizard.

We conclude that, because most species of lizards seem able to detect pheromones from conspecifics (Mason 1992), female mate choice based on chemosensory cues may be more widespread than previously expected among lizards. Our findings point out the need for further studies of mate choice in lizards, taking into account the different roles and relative importance of morphological, color, and chemical cues.

Acknowledgements We thank W.E. Cooper and an anonymous reviewer for helpful comments, and "El Ventorrillo" MNCN Field Station for use of their facilities. Lizards were captured under license from the "Consejería del Medio Ambiente de la Comunidad de Madrid" (Spain). Financial support was provided by the MCYT projects BOS2002-00598 and BOS2002-00547.

References

Alberts AC (1989) Ultraviolet visual sensitivity in desert iguanas: implications for pheromone detection. Anim Behav 38:129–137

Alberts AC (1990) Chemical properties of femoral gland secretions in the desert iguana *Dipsosaurus dorsalis*. J Chem Ecol 16:13–25

Alberts AC (1992) Pheromone self-recognition in desert iguanas. Copeia 1992:229–232

Alberts AC (1993) Chemical and behavioral studies of femoral gland secretions in iguanid lizards. Brain Behav Evol 41:255–260

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Aragón P (2001) Mecanismos para reducir los costes derivados de los encuentros agresivos en los machos de la lagartija serrana (*Lacerta monticola*). PhD Thesis, University Complutense, Madrid

Aragón P, López P, Martín J (2000) Size-dependent chemosensory responses to familiar and unfamiliar conspecific faecal pellets by the iberian rock-lizard, *Lacerta monticola*. Ethology 106:1115–1128

Aragón P, López P, Martín J (2001a) Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards: implications of field spatial relationships between males. Behav Ecol Sociobiol 50:128–133

Aragón P, López P, Martín J (2001b) Discrimination of femoral gland secretions from familiar and unfamiliar conspecifics by male iberian rock-lizards, *Lacerta monticola*. J Herpetol 35:346–350

Aragón P, López P, Martín J (2001c) Effects of conspecific chemical cues on settlement and retreat-site selection of male lizards, *Lacerta monticola*. J Herpetol 35:681–684

Aragón P, López P, Martín J (2001d) Seasonal changes in activity and spatial and social relationships of the Iberian rock-lizard *Lacerta monticola*. Can J Zool 79:1965–1971

Baird TA, Timanus DK (1998) Social inhibition of territorial behaviour in yearling male collared lizards, *Crotaphytus collaris*. Anim Behav 56:989–994

Baird TA, Fox SF, McCoy JK (1997) Population differences in the roles of size and coloration in intra- and intersexual selection in the collared lizard, *Crotaphytus collaris*: influence of habitat and social organization. Behav Ecol 8:506–517

Bateson P (1983) Mate choice. Cambridge University Press, Cambridge

Beck CW, Powell LA (2000) Evolution of female mate choice based on male age: are older males better males? Evol Ecol Res 2:107–118

Braña F (1996) Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase. Oikos 75:511–523

Breed MD, Smith SK, Gall BG (1980) Systems of mate selection in a cockroach species with male dominance hierarchies. Anim Behav 28:130–134

Brooks R, Kemp DJ (2001) Can older males deliver the good genes? Trends Ecol Evol 6:308–313

Caro TM, Bateson P (1986) Organization and ontogeny of alternative tactics. Anim Behav 34:1483–1499

Censky EJ (1997) Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae). Behav Ecol Sociobiol 40:221–225

Cooper WE Jr (1994) Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. J Chem Ecol 20:439–487

Cooper WE Jr, Vitt LJ (1984) Conspecific odor detection by the male broad-headed skink, *Eumeces laticeps*: effects of sex and site of odor source and of male reproductive condition. J Exp Zool 230:199–209

Cooper WE Jr, Vitt LJ (1987) Deferred agonistic behavior in a long-lived sicincid lizard *Eumeces laticeps*. Oecologia 72:321–326

Cooper WE Jr, Vitt LJ (1993) Female choice of large male broad-headed skinks. Anim Behav 45:683–693

Dominey WI (1984) Alternative mating tactics and evolutionary stable strategies. Am Zool 24:385–396

Drickamer LC (1992) Oestous female house mice discriminate dominant from subordinant males and sons of dominant from sons of subordinate males by odour cues. Anim Behav 43:868–870

Elvira B, Vigal CR (1985) Further data on the reproduction of *Lacerta monticola cyreni* (Sauria, Lacertidae) in Central Spain. Amphib Rept 6:173–179

Fox SF, Shipman PA (2003) Social behavior at high and low elevations: environmental release and phylogenetic effects in *Liolaemus*. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behavior. Johns Hopkins University Press, Baltimore, pp 310–355

Glinsky TH, Krekorian CO'N (1985) Individual recognition in free-living adult male desert iguanas, *Dipsosaurus dorsalis*. J Herpetol 19:541–544

Halpern M (1992) Nasal chemical senses in reptiles: structure and function. In: Gans C, Crews D (eds) Biology of the Reptilia, vol 18. Brain, hormones, and behavior. University of Chicago Press, Chicago, pp 423–522

Hews DK (1990) Examining hypotheses generated by field measures of sexual selection on male lizards, *Uta palmeri*. Evolution 44:1956–1966

Kirkpatrick M (1987) Sexual selection by female choice in polygynous animals. Annu Rev Ecol Syst 18:43–70

Koprowski JL (1993) Alternative reproductive tactics in male eastern grey squirrels: "making the best of a bad job". Behav Ecol 4:165–171

López P, Martín J (2001) Pheromonal recognition of females takes precedence over the chromatic cue in male iberian wall lizards, *Podarcis hispanica*. Ethology 107:901–912

López P, Aragón P, Martín J (1998) Iberian rock lizards (*Lacerta monticola cyreni*) assess conspecific information using composite signals from faecal pellets. Ethology 104:809–820

López P, Muñoz A, Martín J (2002) 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 (2003) Chemosensory cues allow male lizards *Psammodromus algirus* to override visual concealment of sexual identity by satellite males. Behav Ecol Sociobiol 54:218–224

Martín J, Forsman A (1999) Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards: an experiment. Behav Ecol 10:396–400

Martín J, López P (2000) Chemoreception, symmetry and mate choice in lizards. Proc R Soc Lond B 267:1265–1269

Martín J, Salvador A (1992) Tail loss consequences on habitat use by the Iberian rock-lizard, *Lacerta monticola*. Oikos 65:318–324

Martín J, Salvador A (1993) Tail loss reduces mating success in the Iberian rock-lizard. Behav Ecol Sociobiol 32:185–189

Martín J, Salvador A (1997) Effects of tail loss on the time budgets, movements, and spacing patterns of Iberian rock lizards, *Lacerta monticola*. Herpetologica 53:117–125

Mason RT (1992) Reptilian pheromones. In: Gans C, Crews D (eds) Biology of the Reptilia, vol 18. Brain, hormones, and behavior. University of Chicago Press, Chicago, pp 114–228

McCoy JK, Baird TA, Fox SF (2003) Sexual selection, social behavior, and the environmental potential for polygyny. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behavior. Johns Hopkins University Press, Baltimore, pp 149–171

Møller AP, Thornhill R (1998) Bilateral symmetry and sexual selection: a meta-analysis. Am Nat 151:174–192

Moore MC (1991) Application of organizational-activation theory to alternative male reproductive strategies: a review. Horm Behav 25:154–179

Moore PJ, Reagan-Wallin NL, Haynes KF, Moore AJ (1997) Odour conveys status on cockroaches. Nature 389:25

Moreira PL, Almeida AP, Delgado H, Salgueiro O, Crespo EG (1998) Bases para a Conservação da Lagartixa-da-montanha (*Lacerta monticola*). Estudos de Biologia e Conservação da Natureza, nº 25. Instituto da Conservação da Natureza, Ministerio do Ambiente, Lisbon

Olsson M (1993) Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). Behav Ecol Sociobiol 32:337–341

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 TR, Møller AP (eds) Sperm competition and sexual selection. Academic, San Diego, pp 503–578

Olsson M, Shine R (1996) How and why does reproductive success increase with age? A case study using sand lizards (*Lacerta agilis*). Oecologia 105:175–178

Olsson M, Shine R (1998) Chemosensory recognition may facilitate prolonged mate guarding by snow skinks, *Niveoscincus microlepidotus*. Behav Ecol Sociobiol 43:359–363

Osada K, Yamazaki K, Curran M, Bard J, Smith BPC, Beauchamp GK (2003) The scent of age. Proc R Soc Lond B 270:929–933

Penn D, Potts WK (1998) Chemical signals and parasite-mediated sexual selection. Trends Ecol Evol 13:391–396

Pérez-Mellado V (1982) Datos sobre *Lacerta monticola* Boulenger, 1905 (Sauria: Lacertidae) en el oeste del Sistema Central. Doñana Acta Vert 9:107–129

Pérez-Mellado V (1998) *Lacerta monticola* Boulenger, 1905. In: Salvador A. (ed) Fauna Ibérica, vol 10. Reptiles. Museo Nacional de Ciencias Naturales, Madrid, pp 207–215

Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York

Smith JM, Zucker N (1997) Do female tree lizards, *Urosaurus ornatus*, exhibit mate choice? J Herpetol 31:179–186

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Stamps JA (1983) Sexual selection, sexual dimorphism and territoriality. In: Huey RB, Pianka ER, Schoener TW (eds)

Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Mass, pp 169–204

Stoddart MD (1980) The ecology of vertebrate olfaction. Chapman & Hall, London

Thornhill R (1992) Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*: Mecoptera). Behav Ecol 3:277–283

Tokarz RR (1995) Mate choice in lizards: a review. Herpetol Monogr 9:17–40

Whiting MJ, Bateman, PW (1999) Male preference for large females in the lizard *Platysaurus broadleyi*. J Herpetol 33:309–312

Wikelski M, Carbone C, Trillmich F (1996) Lekking in marine iguanas: female grouping and male strategies. Anim Behav 52:581–596