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ORIGINAL ARTICLE

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Chemosensory cues allow male lizards *Psammodromus algirus* to override visual concealment of sexual identity by satellite males

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Abstract Males of many species of lizards show conspicuous breeding colors but, in some species, young competitively inferior males conceal their sexual identity by a female-like dull coloration that allows them to evade aggression from dominant males and to adopt an alternative satellite-sneaking mating tactic. However, large males of the lizard *Psammodromus algirus* reacted aggressively to young intruder males despite their female-like coloration, suggesting that they might have the ability to recognize competitor males by chemosensory cues. We experimentally manipulated the head coloration (brown vs orange) and scents (male vs female) of small young males. For staged agonistic encounters, we compared the response of resident unmanipulated large males to the different manipulated small males. When we manipulated only the color of small males, the response of resident large males was independent of the paint manipulation; brown and orange males elicited a similar aggressive response. However, when we also manipulated the scent, small males painted orange or brown, but bearing the scent of males, received a significantly higher number of aggressive responses than small males painted orange or brown, but bearing the scent of females. The results showed that, at close range, the reaction of large males to manipulated individuals was dependent on the scent, whereas color seemed to be less important. Coloration may be, however, more important in long-distance communication as shown by the outcome of the first encounters. Also, orange coloration may increase the intensity of the aggressive response. Effective sex recognition by territorial large males is important in natural situations to avoid sneak matings by young male competitors. Thus, even if small males visually conceal their sexual identity, chemosensory cues allow large males to identify them at close range.

Keywords Chemoreception · Lizards · Male-male competition · Ontogenetic conditional tactic · Social signals

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Introduction

In many lizards, home ranges overlap greatly between the sexes and males defend non-overlapping breeding territories (e.g. Stamps 1977; M'Closkey et al. 1990; Baird et al. 1996). However, other species have a more complex social system in which the territories of dominant males include the home ranges of one or more females (see Stamps 1977 for a review), and subordinate (often younger) males have home ranges that overlap extensively with those of dominant (older) males. By adopting inconspicuous behaviors, subordinate males may exhibit a satellite-sneaking mating tactic (e.g. Zucker 1989).

Males of many lizard species show conspicuous breeding colors during the mating season that may function as social releasers (review in Cooper and Greenberg 1992). However, in many species young, but sexually mature, males delay the development of nuptial coloration until a later breeding season. When males of different age classes exhibit different status badges, individuals might use these badges to judge relative fighting ability (related to body size). In the lizard *Psammodromus algirus*, two age categories of sexually mature males occur; larger, older ones with orange coloration on most of the head during the breeding season, and smaller, younger (albeit sexually mature) males lacking orange coloration. The coloration of young males resembles female coloration except on a few infralabial scales at each side of the mouth, which usually are only visible when the mouth is open (for more detailed descriptions of coloration and behavior, see Díaz 1993; Díaz et al. 1994; Salvador et al. 1995, 1996, 1997; Martín and Forsman 1999). In this species, large males are territorial and direct their aggressive behavior to conspecific males, but not towards females, suggesting that female-like dull coloration may reduce the aggressive response by territorial males (Salvador et al. 1995, 1997). Concealment of sexual identity by a female-like dull coloration might allow a young, competitively inferior, male to avoid aggression by a dominant male (Cooper and Vitt 1987a; Martín and Forsman 1999). Hence, subordinate males might adopt a satellite-sneaking mating tactic (Zucker 1989; Salvador et al. 1995, 1997). However, field data and laboratory experiments indicate that resident (large) male *P. algirus* reacted aggressively to intruder young males independently of their actual coloration (Salvador et al. 1995; Martín and Forsman 1999). Social costs may contribute to natural selection against the appearance of nuptial coloration in young lizards (Martín and Forsman 1999).

In many cases, physiological constraints and biases of sensory organs may be important causal factors of the observed behavior, and can be underlying mechanisms of sexual selection (Sherman et al. 1997; Wehner 1997). Together with body colors, chemical cues play an important role in the intraspecific communication of lizards (Halpern 1992; Mason 1992; Cooper 1994), and several studies have shown pheromonal detection in different species (e.g. Cooper and Vitt 1984; Alberts 1989). The presence and relative concentration of pheromonal components vary not only between sexes, but also among individuals, which may convey information on the individual identity and serve a variety of functions (Alberts 1992; Aragón et al. 2001; López and Martín 2002). Therefore, in lizards, discriminations based on pheromonal components may provide more reliable information about the conspecific than body colors alone. We suggest that, in lizards, coloration is probably more important in long-distance intraspecific communication, whereas pheromone identification is the most important and confirmatory cue when two individuals are close together (López and Martín 2001; López et al. 2002). Agonistic responses of large males towards intruder young males with female-like coloration could be interpreted in terms of ability to recognize competitor males by chemosensory cues.

In this paper, we examine whether color patterns, scents, or a combination of both factors, are used by large male *P. algirus* to discriminate between females and small, young males with female-like dull coloration. We experimentally manipulated the head coloration and scent of small, young males, thereby creating groups of experimental small males with or without orange coloration on the sides of the mouth and/or bearing the scent of other small males or females. Using data from staged agonistic encounters, we compared the responses of large, unmanipulated resident males to the different groups of manipulated small males. Males should respond to manipulated individuals that they recognize as males as if they were intruders in their home ranges, and display aggressive behaviors towards them. Individuals recognized as females should not elicit aggressive behaviors. The outcome of aggressive versus neutral behaviors should indicate whether visual or olfactory cues, or both, are used in sex discrimination and recognition of intruding small males by large male *P. algirus*.

Methods

Study animals

We captured adult *P. algirus* (large males snout-to-vent length, SVL: $\bar{X}$±SE=83.2±9.8 mm; small males SVL: 75.3±9.9 mm; females SVL: 80.2±11.2 mm) in an oak forest near Cercedilla (40°44′N, 4°02′W; Madrid province, Spain). To ensure that individuals had not been in previous contact, which may affect the outcome of the interactions (Olsson 1992), we captured lizards in different places over a large area. Lizards were housed individually at "El Ventorrillo" Field Station (5 km from the capture site) in outdoor plastic cages (60×50×50 cm) containing sand substrate, leaf litter and rocks for cover. Cages were placed so that exposure to sunlight was very similar for all individuals. We provided mealworms dusted with a multivitamin powder as food and water ad libitum. The experiments were carried out during April 1999, which coincided with the mating season of lizards in their original natural population (Salvador et al. 1995, 1996). All lizards were healthy during the trials and were released at their capture sites at the end of the experiment. No damage due to experimental conditions or treatments was recorded.

Experimental procedure

We experimentally manipulated color and/or scent of small male *P. algirus*. In a first experiment, we compared the response of resident large males to unmanipulated small males and females, and to small males painted to match (orange treatment) or eliminate (brown treatment) the orange natural coloration on the sides of the mouth. In a second experiment, we manipulated both the color (orange vs brown) and the scent (male vs female) of small males in a 2×2 factorial design. Small males were swabbed with either small male or female scents (taken from other individuals, see below). In each experiment, manipulated small males (*n*=12) were size-matched by SVL and randomly assigned to treatments. Other individuals were used as unmanipulated controls (four small males and four females). Each manipulated or control individual was used in different experiments, but never more than once with a given individual.

Before the treatment, lizards were cold anaesthetized in a refrigerator. For the color manipulations, we employed flexible non-toxic Testor's paints for model airplanes, mixing them to achieve good visual matches with the natural color of the lizards. We painted the scales of the sides of the mouth of small males with either orange (to match their natural orange coloration) or brown colors (to eliminate their orange coloration and match the normal color of all other dull scales). Lizards were replaced in the refrigerator until the paint had dried before they were used in experiments. We are aware that lizards might respond to visual cues outside the spectrum visible to the human eye. For example, ultraviolet patches (Fleishman et al. 1993) might not be accurately imitated or concealed by the paint used. However, the results of a previous experiment suggested that lizards did not change their behavior as a result of this manipulation (Martín and Forsman 1999). Also, other lizard species seem to respond normally to individuals painted to resemble natural colorations (e.g. Cooper and Vitt 1988; Thompson and Moore 1991; Olsson 1994; López et al. 2002).

For the manipulations of scent, we first attempted to eliminate olfactory skin secretions. To achieve this, we washed the bodies of lizards with cotton swabs moistened with 96% alcohol, devoting special attention to removing scents from the more odorous areas such as the cloacal and femoral regions. This treatment has been effective in removing sexual pheromones of snakes (Noble 1937; Ross and Crews 1978) and lizards (Ferguson 1966; Bauwens et al. 1987; López et al. 2002). We then painted individuals as above, and thereafter coated them with a thin layer of non-odoriferous vaseline to eliminate scents. The vaseline treatment did not alter the visual appearance of the lizards. During the trials, there was no indication that vaseline may have affected lizards' normal behavior. Male or female scents were transferred to the experimental individuals immediately preceding each trial. A cotton swab moistened in distilled water was rubbed on the head, neck, trunk and tail skin and the cloacal area and femoral pores of a donor lizard, and then rubbed against the corresponding skin areas of the experimental individual. We made an effort to ensure scent transfer in those areas more frequently and intensely investigated by tongue-flicking during social encounters. This technique has been successfully employed to transfer scents between individuals in other lizard species (Cooper and Vitt 1987b; López and Martín 2002; López et al. 2002).

Staged agonistic interactions

We staged encounters between pairs of lizards by introducing a new male (intruder, hereafter) into the home-cage of the responding large male (owner, hereafter). With this design, we tried to mimic a natural field situation in which a resident large male finds a conspecific in his home range. The owner had been maintained and fed in his cage for at least 10 days prior to staged encounters. Resident males fight aggressively to maintain owner status against any intruding male, but do not respond aggressively to females. We planned a repeated measures design in which each responding large male (n=12) encountered either a manipulated individual of each treatment or an unmanipulated individual in a randomized sequence in each experiment. Owners participated in only one interaction per day to avoid stress associated with manipulation or fatigue due to multiple contests. To avoid the effects of previous experience between individuals (Olsson 1992; López and Martín 2001), in each test the two contestant lizards had never been together before the trials. All tests were made in outdoor conditions when lizards were fully active.

To begin a trial, we took a manipulated lizard from its cage, placed it gently in the responding male's cage at least 25 cm away from the resident male's location. We recorded lizards' behavior from a blind. We considered an interaction to begin when two lizards approached to within 5 cm of each other and to end when they moved further than 5 cm apart. Multiple interactions between the two males could occur during each trial. In each interaction, responses by the owners were classified as "neutral" if both individuals were close (less than 5 cm) together but no response or a non-agonistic interaction was observed. Aggressive responses included those in which the resident approached with head lowered, neck and throat inflated, back arched and the body raised, and chased or bit the intruder, usually on the snout or head. Approach without display was considered to be aggressive if the intruder fled. Aggressive interactions were considered to be of high intensity if one male bit or attempted to bite the other, or both males simultaneously interlocked jaws by reciprocal biting and clasping.

A trial was ended after 15 min. We stopped observations sooner if persistent attacks or desperate attempts to escape occurred. This was, however, not necessary in most trials because most interactions did not escalate beyond threat displays and short chases. None of the individuals suffered physical injuries or showed physical stress during or after the trials, and all lizards had maintained or increased their original body mass at the end of the trials. The paint of experimental lizards was removed with water once they had completed all the trials. No damage or necrosis of tissue due to the paint was observed.

Data analysis

We analysed the outcome of the first encounter (neutral vs aggressive) in each trial as an indication of a long-distance response by the owner, because males responded first to the intruding individual from a relatively long distance, presumably before any direct chemical testing could occur. We employed McNemar's χ^2 tests for the significance of changes (Siegel and Castellan 1988) to test whether the first response by owners changed significantly among the different types of manipulations of intruders.

To compare the number of aggressive responses in the trials of the same responding individual across treatments, we used a one-way repeated measures analysis of variance (ANOVA) in the first experiment, or a 2×2 repeated measures ANOVA with color (brown vs orange) and scent (male vs female) as factors, both with repeated measures, in the second experiment. Data were previously log-transformed to achieve normality. Differences between treatments were assessed a posteriori using Tukey's honestly significant difference (HSD) tests. Significance level was 0.05 and all tests were two-tailed.

Results

Response of large males to unmanipulated intruders of both sexes, and to small male intruders painted brown or painted orange

Large male owners responded differently to unmanipulated male and female intruders. In the first encounters, owners were always neutral towards females, but many showed aggressive responses towards small males (McNemar test; χ^2=5.14, P<0.025) (Fig. 1a). The first response of large resident males was independent of the painted manipulation of small males and hence brown males elicited aggressive responses similar to those of orange males. Although orange small males received a higher number of aggressive responses than brown ones, the difference was not significant (χ^2=2.29, P<0.10) (Fig. 1a).

The total number of aggressive interactions differed significantly between treatments (one-way repeated measures ANOVA; F=7.58, df=3,33, P=0.0005) (Fig. 2a). Unmanipulated females received a significantly lower number of aggressive responses than unmanipulated and brown or orange color-manipulated small males (Tukey tests, P<0.003 in all cases). Small males received a similar high number of aggressive responses, independent of being unmanipulated or of their color treatment (Tukey tests, P>0.95 in all comparisons).

Effects of scent and color treatments on the response of large males

The analyses of the first encounters showed that small males painted orange and with the scent of males received a significantly higher number of aggressive responses than small males painted brown and with scent of males (McNemar test; χ^2=3.20, P<0.05) (Fig. 1b). In contrast, small males with the scent of females received similar

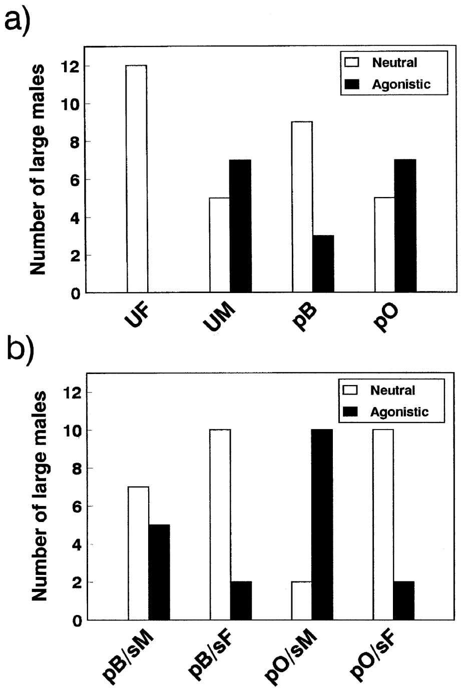

Fig. 1a, b Number of resident large male *Psammodromus algirus* (*n*=12) that showed neutral (*unfilled boxes*) or agonistic (*filled boxes*) responses as **a** the first response to an unmanipulated female (*UF*) or small male (*UM*), or manipulated small male painted brown (*pB*) or orange (*pO*), or **b** as the first response to an intruding manipulated small male painted brown (*pB*) or orange (*pO*) and then impregnated with scents from another small male (*sM*) or from a female (*sF*)

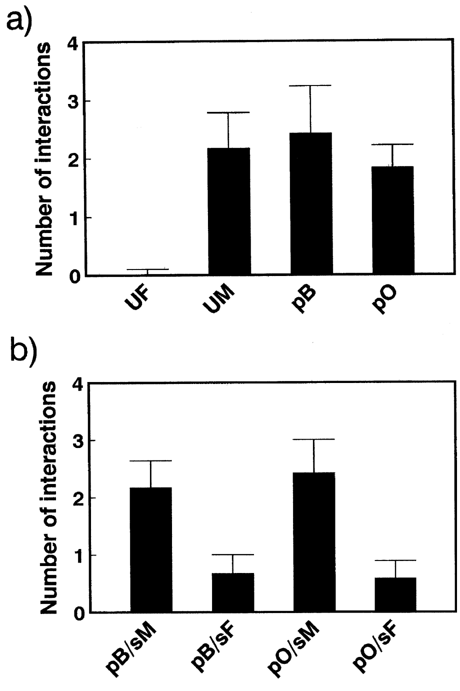

Fig. 2a, b Number ($\bar{X}$+1 SE) of aggressive interactions in 15-min staged encounters of a resident large male *Psammodromus algirus* (*n*=12) with **a** an unmanipulated female (*UF*) or small male (*UM*), or an intruding manipulated small male painted brown (*pB*) or orange (*pO*), or **b** with an intruding manipulated small male painted brown (*pB*) or orange (*pO*) and then impregnated with scents from another small male (*sM*) or from a female (*sF*)

low numbers of aggressive responses regardless of color treatment (χ^2=0.01, *P*=0.45) (Fig. 1b).

Scent greatly influenced the overall response by large males during an encounter; the number of aggressive interactions was significantly higher in the male scent treatments (two-way repeated measures ANOVA; scent effect: *F*=90.20, *df*=1,11, *P*<0.0001), but did not vary significantly between color treatments (color effect: *F*=0.02, *df*=1,11, *P*=0.88), and the interaction was not significant (*F*=0.43, *df*=1,11, *P*=0.52) (Fig. 2b). Small males painted orange and with the scent of males received a significantly higher number of aggressive responses than small males painted orange but with the scent of females (Tukey test, *P*<0.001). Similarly, small males painted brown and with scent of males received a significantly higher number of aggressive responses than small males painted brown but with the scent of females (*P*=0.003). Small males bearing the scent of males received a similar high number of aggressive responses regardless of their coloration (*P*=0.93), and small males bearing the scent of females received a similar low number of aggressive responses regardless of their coloration (*P*=0.98) (Fig. 2b).

However, orange color linked to a male scent seemed to increase the intensity of the aggressive responses of resident males. Thus, a further analysis showed that small males with scent of males and painted orange received a significantly higher number of high-intensity aggressive interactions (i.e. those involving bites or scaling) than small males painted orange but with the scent of females (male scent: 0.50±0.15 high-intensity responses, female scent: 0.17±0.11; Wilcoxon signed-ranks test, *Z*=2.01, *P*=0.04), and than small males painted brown with either scent of males or females, which did not receive any high-intensity aggressive response (*Z*=2.01, *P*=0.02 in both cases). However, small males bearing the scent of females received a similar low number of high-intensity aggressive responses independent of their coloration (brown: 0, orange: 0.17±0.11; *Z*=1.79, *P*=0.07), and small males painted brown received no high-intensity aggressive response independent of their scent manipulation.

Discussion

Conspecific discrimination

Our experiment indicated that large males were able to identify unmanipulated small males even at a long distance and to respond aggressively, which is similar to the behavior in the field (Salvador et al. 1995, 1997). This could be explained by either the orange coloration on infralabial scales at each side of the mouth of some small males, or by the ability to discriminate scents even at a relatively long distance. Thus, the color manipulation results suggested that when the small amount of orange coloration is concealed, large males might not be able to identify some small males at a long distance, thus reducing their aggressive response.

In contrast, the results showed that at close range the reaction of large males to manipulated individuals was dependent on the scent, whereas color seemed to be less important, and most small males were positively identified when bearing male scent independent of their coloration. Moreover, when a conflict between the meaning of the visual and scent signals arose, male recognition seemed to rely on scent (i.e. pheromones) rather than on color (infralabial scales) cues. Therefore, at close range, pheromonal identification of potential small male competitors seems to take precedence over the chromatic cue in the lizard *P. algirus*. Thus, even if small males visually conceal their sexual identity, large males would be able to identify them at close range. Similarly, male *Eumeces laticeps* directed agonistic behavior primarily to conspecific males, whereas heterospecific males of the same genus, although visually quite similar, were ignored following chemosensory investigation (Cooper and Vitt 1987b).

Responding males were less aggressive towards males bearing the scent of females, suggesting that female-like scent reduces the agonistic response of territorial males. Moreover, in the first encounters with large males, small males with the scent of females received a low number of aggressive responses regardless of coloration, whereas the first response to small males with scent of males was dependent on coloration. These results suggest that female scent might be detected at relatively longer distances than male scent, perhaps enabling females to avoid unnecessary chases by large males. Females' scent may inhibit aggression, allowing females to remain in male territories. Chemosensory cues to female sex are reliable and they are probably dependent on female-specific hormones as in *E. laticeps* (Cooper et al. 1986). Similar results were found after experimental manipulations of color and scent of males and females of the lacertid *Podarcis hispanica* (López and Martín 2001; López et al. 2002).

Our experiments suggest that discriminations based on pheromone components may provide more detailed and reliable information regarding an intruder than might be obtained from color patterns alone. Nevertheless, the analysis of the first responses of male *Psammodromus algirus* to manipulated individuals suggests that although pheromone identification may be the more important and confirmatory cue when two individuals are close together, coloration may be more important in long-distance communication. Moreover, large male *Psammodromus algirus* responded with a higher level of aggressivenes to small males with heads showing some orange coloration than to those painted brown. Bright-orange head coloration has been found to be an important releaser of aggressive behavior in males in other lizards (Madsen and Loman 1987; Cooper and Vitt 1988). This result reinforces the conclusion of a previous experiment that small male *Psammodromus algirus* showing nuptial coloration would pay a cost in that they would elicit aggressive behavior and be punished by larger dominant males (Martín and Forsman 1999).

Our study, then, raises the question of why small males maintain traces of orange coloration that are only visible when the mouth is open. In many lizards, males display morphological changes in pattern and coloration during social interactions to convey information about their social status (e.g. Madsen and Loman 1987; see Cooper and Greenberg 1992 for a review). The selective advantage of this system could be that the subdominant dull body coloration might reduce aggressive behavior from dominant males (Kodric-Brown 1986; Andrews and Summers 1996). However, by opening the mouth, small male *Psammodromus algirus* are able to show this visual signal in encounters with other small males (personal observation), which clearly identifies them as males. This supports the coverable badge hypothesis (Hansen and Rohwer 1986), as this signal can be facultatively exhibited or concealed depending on variable social factors (Veiga 1996). The facultative exhibition of the signal (by opening the mouth) at long distance might reduce the chances of sexual harassment by other small males.

Consequences for the mating system

By having a female-like dull coloration, a small male that does not allow close approach by large males might evade aggression from a dominant male, facilitating a satellite-sneaking mating tactic (Martín and Forsman 1999). Similarly, in passerine birds, delayed plumage maturation in subadult dull-colored males reduces attacks from dominant males and increases breeding opportunities (Rohwer et al. 1980). Nevertheless, concealment of the sexual identity by small male *Psammodromus algirus* is not entirely successful. Our field observations showed that the number of agonistic interactions between large and small males was high, suggesting intense competition for access to females (Salvador et al. 1995, 1996, 1997). Agonistic interactions were always initiated by the large male, which chased the small male whenever it approached a female or the large male closely. Stimuli other than color or scent could also influence the response of large males. For instance, small males might be identified by morphological traits or behavioral cues associated with sex. This might explain aggressive responses of large males to some small males with color and scent of females.

Small males of *Psammodromus algirus* are always located within the territories of large males, and continuously try to sneak matings instead of defending their own territories (Salvador et al. 1995; P. López, personal observations). Sneak matings are typically an ontogenetic alternative to guarding performed by competitively inferior individuals (e.g. younger males or subordinate phenotypes) in situations of intense competition. However, the chance of successful copulation by small male

Psammodromus algirus is low because large males interrupted all copulation attempts of small males when they noticed them (P. López, unpublished data). Similarly, in the collared lizard, *Crotaphytus collaris*, young males were prevented from mating because they could not compete effectively with older males (Baird and Timanus 1998). These findings suggest that effective sex discrimination by territorial large males is important in natural situations to avoid losses of matings to young males. Thus, in *Psammodromus algirus*, it would be an advantageous tactic to rely on chemosensory cues to identify young males that visually conceal their sexual identity.

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References

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

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

Andrews TJ, Summers CH (1996) Aggression, and the acquisition and function of social dominance in female *Anolis carolinensis*. Behaviour 133:1265–1279

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

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

Baird TA, Acree MA, Sloan CL (1996) Age and gender-related differences in the social behaviour and mating success of free-living collared lizards, *Crotaphytus collaris*. Copeia 1998:336–347

Bauwens D, Nuitjen K, Van Wezel H, Verheyen RF (1987) Sex recognition by males of the lizard *Lacerta vivipara*: an introductory study. Amphibia-Reptilia 8:49–57

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, Greenberg N (1992) Reptilian coloration and behavior. In: Gans C, Crews D (eds) Biology of the Reptilia, vol 18. Brain, hormones, and behavior. University of Chicago Press, Chicago, pp 298–422

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 (1987a) Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*. Oecologia 72:321–326

Cooper WE Jr, Vitt LJ (1987b) Intraspecific and interspecific aggression in lizards of the scincid genus *Eumeces*: chemical detection of conspecific sexual competitors. Herpetologica 43:7–14

Cooper WE Jr, Vitt LJ (1988) Orange head coloration of the male broad-headed skink (*Eumeces laticeps*), a sexually selected social cue. Copeia 1988:1–6

Cooper WE Jr, Garstka WR, Vitt LJ (1986) Female sex pheromone in the lizard *Eumeces laticeps*. Herpetologica 42:361–366

Díaz JA (1993) Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammodromus algirus*. Can J Zool 71:1104–1110

Díaz JA, Alonso-Gómez AL, Delgado MJ (1994) Seasonal variation of gonadal development, sexual steroids, and lipid reserves in a population of the lizard *Psammodromus algirus*. J Herpetol 28:199–205

Ferguson GW (1966) Releases of courtship and territorial behaviour in the side blotched lizard, *Uta stansburiana*. Anim Behav 14:89–92

Fleishman LJ, Loew ER, Leal M (1993) Ultraviolet vision in lizards. Nature 365:397

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

Hansen AJ, Rohwer S (1986) Coverable badges and resource defence in birds. Anim Behav 34:69–76

Kodric-Brown A (1986) Satellites and sneakers: opportunistic male breeding tactics in pupfish (*Cyprinodon pecosensis*). Behav Ecol Sociobiol 19:425–432

López P, Martín J (2001) Fighting rules and rival recognition reduce costs of aggression in male lizards, *Podarcis hispanica*. Behav Ecol Sociobiol 49:111–116

López P, Martín J (2002) Chemical rival recognition decreases aggression levels in male Iberian wall lizards, *Podarcis hispanica*. Behav Ecol Sociobiol 51:461–465

López P, Martín J, Cuadrado M (2002) Pheromone mediated intrasexual aggression in male lizards, *Podarcis hispanica*. Aggr Behav 28:154–163

Madsen T, Loman J (1987) On the role of colour display in the social and spatial organization of male rainbow lizards (*Agama agama*). Amphibia-Reptilia 8:365–372

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

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

M'Closkey RT, Deslippe RJ, Szpak CP, Baia KA (1990) Ecological correlates of the variable mating system of an iguanid lizard. Oikos 59:63–69

Noble GK (1937) Sense organs involved in the courtship of *Storeria*, *Thamnophis* and other snakes. Bull Am Mus Nat Hist 73:673–725

Olsson M (1992) Contest success in relation to size and residence in male sand lizards, *Lacerta agilis*. Anim Behav 44:386–388

Olsson M (1994) Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. Anim Behav 48:607–613

Rohwer S, Fretwell SD, Niles DM (1980) Delayed maturation in passerine plumages and the deceptive aquisition of resources. Am Nat 115:400–437

Ross P, Crews D (1978) Stimuli influencing mating behavior in the garter snake, *Thamnophis radix*. Behav Ecol Sociobiol 4:133–142

Salvador A, Martín J, López P (1995) Tail loss reduces home range size and access to females in male lizards, *Psammodromus algirus*. Behav Ecol 6:382–387

Salvador A, Veiga P, Martín J, López P, Abelenda M, Puerta M (1996) The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. Behav Ecol 7:145–150

Salvador A, Veiga P, Martín J, López P (1997) Testosterone supplementation in subordinate small male lizards: consequences for aggressiveness, colour development, and parasite load. Behav Ecol 8:135–139

Sherman PW, Reeve HK, Pfennig DW (1997) Recognition systems. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 4th edn. Blackwell, Cambridge, pp 69–98

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

Sokal RR, Rohlf FJ (1995) Biometry, 3rd ed. W. H. Freeman, New York

Stamps JA (1977) Social behavior and spacing patterns in lizards. In: Gans C, Tinkle DW (eds) Biology of the Reptilia, vol 7. Academic, New York, pp 265–334

Thompson CW, Moore MC (1991) Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus*. Anim Behav 42:745–753

Veiga JP (1996) Permanent exposure versus facultative concealment of sexual traits: an experimental study in the house sparrow. Behav Ecol Sociobiol 39:345–352

Wehner R (1997) Sensory systems and behaviour. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 4th edn. Blackwell, Cambridge, pp 42–68

Zucker N (1989) Dorsal darkening and territoriality in a wild population of the tree lizard (*Urosaurus ornatus*). J Herpetol 23:389–398