ORIGINAL ARTICLE

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Chemical rival recognition decreases aggression levels in male Iberian wall lizards, *Podarcis hispanica*

Abstract In an agonistic interaction, the assessment of the probable outcome of future encounters with the same individuals may be the best way of decreasing costs of fighting, but this may only be accomplished if animals are able to recognize individual conspecifics. We staged encounters between male lizards, *Podarcis hispanica*, to examine whether odoriferous cues are involved in rival recognition during agonistic interactions. We experimentally manipulated the odour of intruding males, creating familiar males with their own odour or bearing odours of unfamiliar males, and unfamiliar males bearing unfamiliar odours or odours of familiar males. The results showed that when familiar males were impregnated with scents from unfamiliar males, they elicited an aggressive response by resident unmanipulated males similar to that observed for a new unfamiliar male with unfamiliar odour. This suggests that resident males were unable to recognize familiar males when their own scents were removed. In contrast, responding males were less aggressive towards familiar males impregnated with their own odour and towards unfamiliar males impregnated with scents of familiar males, suggesting that when two males have already interacted, their scents become familiar for both males, and that the detection in successive encounters of the familiar scent suffices to reduce the aggressive response of territorial males. Therefore, recognition mechanisms based on chemical cues during agonistic encounters may contribute to reducing the intensity and the costs of fighting in *P. hispanica* and may play an important role in the organization of their social system.

Keywords Agonistic behavior · Chemoreception · Dear enemy recognition · Fighting strategies · Lizards

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Introduction

The ultimate goal of a fight is that the winner takes sole possession of the resource, but since fighting entails costs such as time and energy expenditure and risk of injury, it would be beneficial for both opponents to settle disputes as cheaply as possible (Huntingford and Turner 1987; Archer 1988). Thus, different fighting strategies have evolved for resolving conflicts (Maynard Smith and Price 1973; Maynard Smith 1982). In dominance hierarchies or territorial systems with extensive overlap between home ranges, the probability of agonistic interactions between neighbours is very high. However, individuals with higher agonistic interaction levels may incur greater energetic and survival costs (Marler and Moore 1988, 1989). Therefore, mechanisms for reducing the frequency of aggressive encounters and aggression levels would be advantageous.

The assessment of the probable outcome of future encounters with the same individuals is likely the best way of economizing energy and risk of injury (Barnard and Burk 1979). When two individuals have fought each other before, this prior experience may influence their fighting behaviour when they meet again. This can be achieved only if animals are able to recognize familiar neighbour individuals based on, for example, distinctive dermal or plumage patterns (Whitfield 1987; Olsson 1994) or chemosensory cues (Halpin 1986; Alberts and Werner 1993). This "dear enemy" recognition would be adaptive because it minimizes the energy expended on aggressive acts and may prevent escalated contests between neighbours (Jaeger 1981; Glinsky and Krekorian 1985; Qualls and Jaeger 1991). Individual recognition can be combined with the ability to learn the status of individual conspecifics through repeated encounters (Gosling 1982), which would help to stabilize the social systems by reducing the frequency and intensity of aggressive encounters (Glinsky and Krekorian 1985).

Several examples of rival recognition during agonistic interactions have been described in lizards. In staged en-

counters of male lizards, *Podarcis hispanica*, the second fight by the same pair of males had a lower aggression level (López and Martín 2001a). This result suggests that male *P. hispanica* were able to recognize individual opponents and that they used this information to determine the outcome of a contest more quickly. Similarly, the duration of contests was shorter when the same pair of males of *Lacerta agilis* had a previous agonistic experience (Olsson 1994). Also, other animals such as lobsters (Karavanich and Atema 1998), crayfish (Zulandt Schneider et al. 2001) or trout (Johnsson 1997; Höjesjö et al. 1998) reduce their aggressiveness in second contests with familiar individuals. Other field studies showed that territorial male desert iguanas, *Dipsosaurus dorsalis* (Glinsky and Krekorian 1985), and resident males of *Platysaurus broadleyi* lizards (Whiting 1999) were less aggressive towards neighbours than non-neighbours. However, the mechanisms that might be used for individual recognition by lizards during agonistic interactions remain unknown.

Chemical cues are known to play an important role in the intraspecific communication of lizards. Several studies have shown pheromonal detection in different species (Mason 1992), and individual recognition through chemosensory cues has been suggested in some species (e.g. Alberts and Werner 1993; Cooper 1996; Aragón et al. 2001). In some species of lizards, the presence and relative concentration of pheromone components vary not only between sexes, but also among individuals, and may convey information about an individual's identity (Alberts 1992).

The diversity of color patterns is limited in *Podarcis hispanica* whereas chemosensory abilities are well developed. This lizard can discriminate between cotton swabs impregnated with prey and non-prey chemicals (Cooper 1990), between conspecifics and heterospecifics (Gómez et al. 1993) and between sexes (López and Martín 2001b; López et al. 2001) by chemical cues alone. Moreover, the aggressive response of male *P. hispanica* to intruding individuals depends on pheromonally mediated sex recognition; males impregnated with scent of females did not elicit aggressive responses (López et al. 2001), whereas females with male odours were attacked (López and Martín 2001b). Similarly, males of the skink, *Eumeces laticeps*, directed aggressive behaviour to conspecific males, whereas heterospecific males of the same genus, although visually quite similar, were ignored following chemosensory investigation (Cooper and Vitt 1987).

In this paper, we analyse whether chemical cues are involved in rival recognition during agonistic interactions between males of *P. hispanica*. We experimentally manipulated the odour of individual males, thereby creating groups of familiar males with their own odour or bearing odours of unfamiliar males, and groups of unfamiliar males bearing unfamiliar odours or odours of familiar males. Using data from staged encounters, we compared the responses of resident unmanipulated males with the different groups of manipulated males. A previous agonistic experience with a male affects the outcome and characteristics of a subsequent encounter, decreasing aggression levels (López and Martín 2001a). Thus, we hypothesized that males should respond in a second encounter less aggressively to manipulated individuals that they recognize as familiar males (i.e. with which they have a previous agonistic experience) than to males identified as new or unfamiliar. The comparison of aggressive responses to the different manipulated individuals should indicate whether pheromonal cues are used in individual recognition.

Methods

Study animals

The Iberian wall lizard, *Podarcis hispanica*, is a small (50- to 70-mm adult snout-to-vent length, SVL) diurnal lacertid lizard of the Iberian Peninsula, common at rocky habitats or artificial walls (Martín-Vallejo et al. 1995). Males are aggressive and, although they are not strictly territorial, a male defends some area around himself and his females (Gil et al. 1988). Population densities are high although highly variable (between 50 and 500 ind./ha) (Pérez-Mellado 1998) and individuals aggregate around favourable areas with rock crevices. Overlap between male home ranges is extensive, and agonistic encounters are frequent during the mating season (López and Martín 2001a; P. López and J. Martín, unpublished data).

During May 2001, we captured adult male *P. hispanica* on rocky outcrops in an oak forest near Cercedilla (40°44′N, 4°02′W; Madrid province, Spain). We captured lizards in different places over a large area (10 km²) to ensure that individuals had not been in previous contact, which might affect the outcome of the interactions (Olsson 1994; López and Martín 2001a). 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 and rocks for cover. We provided mealworms dusted with a multivitamin powder as food and water ad libitum. The experiments were carried out during June, which coincided with the mating season of lizards in their original natural population. All lizards were healthy during the trials and, at the end of the experiment, were released at their capture sites.

Experimental procedure

We experimentally manipulated the odour of males by impregnating them with their own odours or with odours taken from other individuals. We first attempted to eliminate odoriferous secretions with a treatment that has been effective in removing sexual pheromones of snakes (Noble 1937; Ross and Crews 1978) and lizards (Ferguson 1966; Bauwens et al. 1987; López and Martín 2001b; López et al. 2001). Lizards were first washed with cottons swabs moistened with 96% alcohol, devoting special attention to removing scents from the more odorous areas such as the cloacal and femoral regions. We then coated the lizards with a thin layer of non-odoriferous vaseline to eliminate scents. The vaseline treatment did not alter the visible appearance of the lizards. During the trials there was no indication that vaseline may have affected lizards' normal behaviour. Odours were transferred to the experimental individuals preceding each trial by rubbing with cotton swabs moistened with distilled water on the head, neck, trunk, tail, cloacal area and femoral pores of the same male (taken before washing him as a control of the manipulation) or of a different individual. We made an effort to ensure odour transfer in those areas most frequently and intensely investigated by tongue-flicking during social encounters. This technique has been successfully employed to transfer odours between individuals in this and other

lizard species (Cooper and Vitt 1987; López and Martín 2001b; López et al. 2001).

Staged agonistic interactions

We staged encounters between pairs of lizards in the home cage of the responding male and, thus, the responding male acted as the "owner" and the manipulated male acted as an "intruder". With this design, we tried to mimic a natural field situation in which a resident male found a conspecific male in his home range. The responding male has the initial advantage of being resident and should fight aggressively to maintain its owner status against any intruding male (López and Martín 2001a). However, the intensity of the aggressive response should be lower in the second encounter with a given individual male recognized as familiar (López and Martín 2001a). The pairs of males were chosen randomly, but all individuals had similar body sizes (SVL: $\bar{X}+SE=62.9+0.4$ mm; range 60–65 mm; body mass: $\bar{X}+SE=3.8+0.1$ g; range 3.0–4.5 g). However, to minimize the effects of body-size differences on the outcome of the contests, we never paired males that differed by >2 mm and/or 0.5 g.

We planned a repeated-measures design in which each responding male ($n=16$) encountered different manipulated individuals. The first day, the responding male encountered a manipulated male impregnated with his own odour that acted as an intruder. The next day, we conducted four trials in a counterbalanced order, in which the resident responding male encountered: (1) his familiar former partner bearing its own odour (familiar male with familiar odour treatment: Fm/Fo); (2) his familiar former partner but bearing odour from an unfamiliar male (familiar male with unfamiliar odour treatment: Fm/Uo); (3) a different unfamiliar new partner bearing odour of the familiar male (unfamiliar male with familiar odour treatment; Um/Fo); (4) a different unfamiliar new partner bearing odour from another unfamiliar male (unfamiliar male with unfamiliar odour treatment; Um/Uo). Unfamiliar male odours were taken from individuals not used in the tests. Males used as unfamiliar were also used as familiar males with other new resident males on different days. Males participated in a maximum of five contests in two consecutive days. All tests were made in sunny conditions outdoors between 0900 and 1200 hours GMT when lizards were fully active.

To begin a trial, we gently took one manipulated lizard from its cage, placed it carefully in the middle of the responding male's cage and, from a blind, recorded behaviours. In agonistic contests, we recorded a "neutral response" when the two individuals were together but no response or non-aggressive interaction was observed, or an "aggressive response" if the responding male approached the intruding male with aggressive display. Responding males employ threatening postures, strut toward an opponent on raised, stiff forelegs with their neck arched and the snout pointing slightly down. With this display, the responding male made the intruding male retreat or run away either without contact, by touching him on the flanks or, occasionally, by giving quick bites, especially on the snout or head (López and Martín 2001a; López et al. 2001). Multiple interactions could occur during each trial.

A trial was terminated after 15 min. Most interactions consisted of threat displays and short chases, and only very rarely escalated to single quick bites, which did not cause observable injury. No individual suffered physical injuries or showed physical stress during or after the trials, and all animals had maintained or increased their original body mass at the end of the trials.

To compare the number of neutral and aggressive responses of the same responding individual across treatments, we used 2×2 repeated-measures analyses of variance (ANOVA) with intruder male (Fm vs Um) and odour (Fm vs Uo) as factors, both with repeated measures. Data were previously log-transformed. To compare changes in the responses from day 1, we used one-way repeated-measures analyses of variance (ANOVA) with log-transformed data (Sokal and Rohlf 1995). Differences between treatments were assessed a posteriori using Tukey's honestly significant difference (HSD) tests. Significance level was set at 0.05 and all tests were two-tailed.
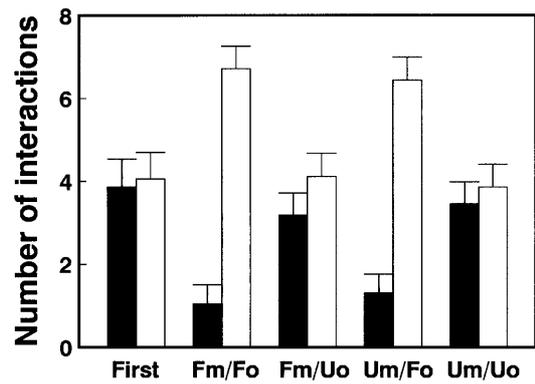
Fig. 1 Number ($\bar{X}+1SE$) of aggressive (*black bars*) and neutral (*white bars*) interactions in the first contest of a resident male with an intruder male impregnated with his own odour, in posterior contests with the same familiar male bearing his own odour (*Fm/Fo*) or impregnated with odour of an unfamiliar male (*Fm/Uo*), and in posterior contests with unfamiliar males impregnated with odour of a familiar male (*Um/Fo*) or bearing their own odour (*Um/Uo*). The order of presentation of the last four conditions was counterbalanced

Results

The total number of interactions between males did not vary significantly between treatments (two-way repeated measures ANOVA; Odour effect: $F=1.34$, $df=1.15$, $P=0.26$; Male effect: $F=0.20$, $df=1.15$, $P=0.66$; Interaction: $F=1.29$, $df=1.15$, $P=0.27$). However, the number of aggressive interactions was significantly higher in the unfamiliar odor treatments (Odor effect: $F=38.05$, $df=1.15$, $P<0.0001$), but did not vary significantly in relation to the familiarity with the intruder male (Male effect: $F=2.97$, $df=1.15$, $P=0.10$), and the interaction was not significant ($F=0.02$, $df=1.15$, $P=0.88$) (Fig. 1). Conversely, the number of neutral interactions was significantly lower in the unfamiliar odour treatments (Odour effect: $F=16.99$, $df=1.15$, $P<0.001$), but did not vary significantly in relation to the familiarity with the intruder male (Male effect: $F=0.25$, $df=1.15$, $P=0.62$), and the interaction was not significant ($F=0.01$, $df=1.15$, $P=0.91$) (Fig. 1).

When comparing the first encounter with the experimental treatments, the total number of interactions did not vary significantly between treatments ($F=0.32$, $df=4.60$, $P=0.86$). However, the number of neutral ($F=31.72$, $df=4.60$, $P<0.0001$) and aggressive interactions ($F=9.11$, $df=4.60$, $P<0.0001$) differed significantly between treatments (Fig. 1). The number of neutral and aggressive interactions did not differ significantly between the first encounter and the second encounter with the familiar male impregnated with unfamiliar odour (Fm/Uo), or between the first encounter and the second encounter with an unfamiliar male impregnated with unfamiliar odour (Um/Uo) (Tukey's HSD test, $P>0.90$ in all cases). These two treatments were not significantly different in the number of neutral ($P=0.99$) and aggressive interactions ($P=0.99$).

In contrast, in the encounter with the familiar male impregnated with familiar odour (Fm/Fo) and in the encounter with the unfamiliar male impregnated with the familiar odour (Um/Fo), the number of neutral interactions significantly increased (Tukey's HSD test, $P=0.01$ and $P=0.02$, respectively), and the number of aggressive interactions significantly decreased ($P=0.004$ and $P=0.02$, respectively) with respect to the first encounter. These two treatments were not significantly different in the number of neutral ($P=0.99$) and aggressive interactions ($P=0.97$). In addition, when comparing the Fm/Uo and the Um/Fo conditions, the number of neutral interactions was significantly higher ($P=0.004$), and the number of aggressive interactions was significantly lower ($P=0.025$) in the Um/Fo treatment.

Discussion

The results from our experiment show that male *Podarcis hispanica* discriminate between classes of individuals based on chemical cues, and the results are compatible with the possibility of individual discrimination. Males recognized as familiar ones by a resident male were expected to receive a lower aggression level in their second encounter (López and Martín 2001a). In contrast, when familiar males were impregnated with scents from unfamiliar males, they elicited an aggressive response similar to that expected for a new unfamiliar male. This suggests that resident males were unable to recognize familiar males whose scents had been replaced with a scent from an unknown individual. Interestingly, a similar situation occurs in crayfish, where urine cues play a role in individual recognition, and fights are longer and more intense when urine cues are absent than when they are present (Zulandt Schneider et al. 2001). Also, lobsters lacking the ability to sense chemicals are unable to recognize familiar opponents, and the intensity of the second fight is similar to that of first fights (Karavanich and Atema 1998).

Our results also showed that responding males were less aggressive towards males bearing scents of familiar males, suggesting that when two males have already interacted, their scents become familiar for both males, and that the detection in successive encounters of the same familiar scent is enough to reduce the aggressive response of territorial males. Therefore, chemical cues seem to be used to recognize individuals during agonistic interactions in the lizard *P. hispanica*, whereas other possible cues such as morphological traits and colour patterns seem to be less important in individual recognition.

These findings agree with those from studies of tongue-flicking behaviour that showed the ability to discriminate between scents of familiar and unfamiliar conspecifics in several other species of lizards, such as iguanas (Alberts and Werner 1993), skinks (Cooper 1996), geckos (Steele and Cooper 1997) and lacertids (Aragón et al. 2001). Discriminations among individuals based on pheromonal components may be more reliable than other cues due to chemical properties of pheromones. Femoral

gland secretions are composed of both lipids and proteins (Alberts 1990). Lipids have a high degree of molecular diversity, which increase the potential information content of a pheromone, and individual differences in chemistry of secreted proteins are consistent over time (Glinsky and Krekorian 1985; Alberts 1992). Therefore, at least in some lizards, discriminations based on pheromonal components may provide more detailed information about the conspecific than might be obtained from colour patterns or other visual cues.

During agonistic encounters we observed that males performed tongue flicks to the body of the opponents when close, but also to the substrate behind them. Another study of male territorial contests in the lacertid lizard, *Gallotia galloti*, showed that this tongue-flicking behaviour was more frequent in winners than in losers in staged territorial contests (Molina-Borja et al. 1998). Such tongue-flicking may be a means of acquiring information about the other individual, which could be important in successive encounters, but also might give information on the fighting ability of the other male.

Our results are consistent with several interpretations, including individual recognition, discrimination between familiar and unfamiliar individuals, and habituation to pheromones of frequently found individuals. Habituation, which is characterized by an observable decrement in response to a repeated stimulus, and the recovery of response in the presence of a novel stimulus, has been proposed as a mechanism responsible for the dear enemy recognition effect (Peeke 1984; Owen and Perrill 1998). The response to a novel stimulus demonstrates that the decrease is not due to fatigue or sensory adaptation (Peeke 1984). Habituation to a scent found twice in two consecutive days might be the mechanism that allowed resident male lizards to discriminate between the scent of a familiar neighbour and that of an unfamiliar male. Nevertheless, habituation is only one of several potential mechanisms, and lizards might be capable of individual recognition without previous habituation. This raises the need for further studies to determine how long a male will be able to discriminate a familiar scent, and whether there are different levels of habituation or capacity of remembering different scents as a function of the frequency with which they are found. This is important because, in the field, it would allow resident males to respond differentially to different individuals that pose different threats for his territory ownership, thus avoiding unnecessary fights. In agreement with this, a previous study with the lizard, *Lacerta monticola*, showed that the tongue-flick rate to other males' scent decreased with the degree of overlap (i.e. degree of familiarity) between the home ranges of familiar individuals, which might reflect the need for more information or a lesser ability to discriminate the scent of infrequently encountered individuals than those often encountered (Aragón et al. 2001).

We conclude that the ability to recognize individual conspecifics may help to decide the outcome of conflicts quickly and energetically cheaply. When two males have already determined their relative statuses, additional fights

may be both unnecessary and potentially costly. Therefore, recognition mechanisms based on chemical cues during agonistic encounters contribute to reducing the intensity and the costs of fighting in *P. hispanica* and may play an important role in the organization of their social system.

References

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, Werner DI (1993) Chemical recognition of unfamiliar conspecifics by green iguanas: functional significance of different signal components. Anim Behav 46:197–199

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

Archer J (1988) The behavioural biology of aggression. Cambridge University Press, Cambridge

Barnard CJ, Burk T (1979) Dominance hierarchies and the evolution of "individual recognition". J Theor Biol 81:65–73

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 (1990) Prey odor detection by teiid and lacertid lizards and the relationship of prey odor detection to foraging mode in lizard families. Copeia 1990:237–242

Cooper WE Jr (1996) Chemosensory recognition of familiar and unfamiliar conspecifics by the scincid lizard *Eumeces laticeps*. Ethology 102:454–464

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

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

Gil MJ, Pérez-Mellado V, Guerrero F (1988) Estructura del hábitat y dominios vitales en *Podarcis hispanica* (Steindachner, 1870). Misc Zool 12:273–281

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

Gómez A, Font E, Desfilis E (1993) Chemoreception in the Lacertidae: exploration and conspecific discrimination in the Spanish wall lizard, *Podarcis hispanica*. In: Valakos ED, Böhme W, Pérez-Mellado V, Maragoú P (eds) Lacertids of the Mediterranean region. Helenic Zoological Society, Athens, pp 213–230

Gosling LM (1982) A reassessment of the function of scent marking in territories. Z Tierpsychol 60:89–118

Halpin ZT (1986) Individual odors among mammals: origins and functions. Adv Stud Behav 16:39–70

Höjesjö J, Johnsson JI, Peterson E, Järvi J (1998) The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*). Behav Ecol 9:445–451

Huntingford F, Turner A (1987) Animal conflict. Chapman & Hall, London

Jaeger RG (1981) Dear enemy recognition and the costs of aggression between salamanders. Am Nat 117:962–974

Johnsson JI (1997) Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. Ethology 103:267–282

Karavanich C, Atema J (1998) Olfactory recognition of urine signals in dominance fights between male lobster, *Homarus americanus*. Behaviour 135:719–730

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

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

López P, Martín J, Cuadrado M (2001) Pheromone mediated intrasexual aggression in male lizards, *Podarcis hispanica*. Aggr Behav 27

Marler CA, Moore MC (1988) Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behav Ecol Sociobiol 23:21–26

Marler CA, Moore MC (1989) Time and energy costs of aggression in testosterone-implanted free-living male mountain spiny lizards (*Sceloporus jarrovi*). Physiol Zool 62:1334–1350

Martín-Vallejo J, García-Fernández J, Pérez-Mellado V, Vicente-Villardon JL (1995) Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of central Spain. Herpetol J 5:181–188

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

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Maynard Smith J, Price GR (1973) The logic of animal conflict. Nature 246:15–18

Molina-Borja M, Padrón-Fumero M, Alfonso-Martín T (1998) Morphological and behavioural traits affecting the intensity and outcome of male contests in *Gallotia galloti galloti* (Family Lacertidae). Ethology 104:314–322

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 (1994) Rival recognition affects male contest behavior in sand lizards (*Lacerta agilis*). Behav Ecol Sociobiol 35:249–252

Owen PC, Perrill SA (1998) Habituation in the green frog, *Rana clamitans*. Behav Ecol Sociobiol 44:209–213

Peeke HVS (1984) Habituation and the maintenance of territorial boundaries. In: Peeke HVS, Petrinovich L (eds) Habituation, sensitization, and behavior. Academic Press, Orlando, Fla, pp 1–14

Pérez-Mellado V (1998) *Podarcis hispanica* (Steindachner, 1870). In: Ramos MA (ed) Fauna Ibérica, vol 10. Museo Nacional de Ciencias Naturales, CSIC, Madrid, pp 258–272

Qualls CP, Jaeger RG (1991) Dear enemy recognition in *Anolis carolinensis*. J Herpetol 25:361–363

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

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

Steele LJ, Cooper WE Jr (1997) Investigations of pheromonal discrimination between conspecific individuals by male and female leopard geckos (*Eublepharis macularius*). Herpetologica 53:475–484

Whitfield DP (1987) Plumage variability, status signalling and individual recognition in avian flocks. Trends Ecol Evol 2:13–18

Whiting MJ (1999) When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. Behav Ecol Sociobiol 46:210–214

Zulandt Schneider RA, Huber R, Moore PA (2001) Individual and status recognition in the crayfish *Orconectes rusticus*: the effects of urine release on fight dynamics. Behaviour 138:137–153