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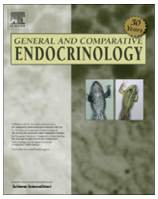

Minireview

Social behavior, chemical communication, and adult neurogenesis: Studies of scent mark function in *Podarcis* wall lizards

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ABSTRACT

Lacertid lizards have been hailed as a model system for the study of reptilian chemical communication. However, results obtained with the genus *Podarcis*, a diverse group of wall lizards with complex systematics, challenge emerging paradigms and caution against hasty generalizations. Here we review the available evidence on the role of chemical stimuli in male–female and male–male interactions in Iberian *Podarcis*. Males of several species can discriminate between chemicals left on substrates by females of their own or a different species, suggesting that differences in female chemical cues may underlie species recognition in this group. Females, on the other hand, do not respond differentially to conspecific and congeneric male scent marks. Males of *Podarcis liolepis* use scent marks to recognize rivals individually, evaluate their competitive ability (i.e., body size), and assess the threat posed by each individual rival neighbor. In contrast, females do not exhibit a preference for territories scent marked by larger (i.e., more competitive) males, which suggests a limited role for male scent marks in pre-copulatory mate choice. This behavioral sex difference is consistent with detailed neuro-ethological evidence showing that chemosensory brain areas in *P. liolepis* are sexually dimorphic. The accessory olfactory bulbs are larger (both in absolute and relative terms) in males than in females, probably as a result of sex-specific rates of adult neurogenesis. In both sexes, cell proliferation undergoes seasonal cycles that may have evolved to satisfy increased chemosensory demands at particular times of the year. Overall, and against recent generalizations, these results suggest that male scent marks have been shaped mainly by strong intrasexual selection.

1. Introduction: lacertids and the study of vertebrate chemoreception

Diurnal lizards provide an excellent material for studies of behavior and communication, as many of them show low vagility, have relatively small home ranges, occupy habitats that make them easy to observe in the field, and are amenable to laboratory studies [43]. During the last decade, lacertid lizards in particular have become an emerging model system for the study of vertebrate chemoreception (e.g., [27,34]). However, recent work with Iberian wall lizards has revealed that some generalizations regarding lacertid chemoreception may be premature, that a few claims are unjustified, and that lacertid chemoreception is more complex and interesting than previously suggested.

Wall lizards (genus *Podarcis*) have a circum-Mediterranean distribution, being found in northern Africa and in all the southern European peninsulas. They are a diverse group of small saxicolous or ground-dwelling lizards with considerable cryptic genetic diversity. As recently as the late 1970s, only three species were recognized in the Iberian Peninsula (*Podarcis bocagei*, *Podarcis muralis*, and *Podarcis hispanica*). Currently, however, experts suspect the presence of at least a dozen different evolutionary lineages which group into a monophyletic clade [9]. This review addresses the role of chemical stimuli in social signaling in *Podarcis* wall lizards. We consider the role of chemical stimuli in both intersexual (male–female) and intrasexual (male–male) interactions.

Mate choice has been a consistent focus in the study of sexual selection and intersexual interactions in lizards, and is a complex process that occurs at many levels, from recognizing a mate of the correct species to selecting a conspecific mate with certain characteristics (e.g., large, more colorful [45]). According to Johansson and Jones [29], studies of mate choice often conflate three different levels of mate choice: species recognition, mate recognition, and mate assessment. The latter corresponds to what most of us understand as mate choice in the narrow sense, i.e., the process whereby, once the set of potential mates has been narrowed down to individuals of the right species, sex and reproductive status, an animal chooses to mate with individuals with certain characteristics that maximize the reproductive success of the chooser and/or its offspring. Here we will ask to what extent chemical stimuli are involved in each of these three processes in *Podarcis* lizards.

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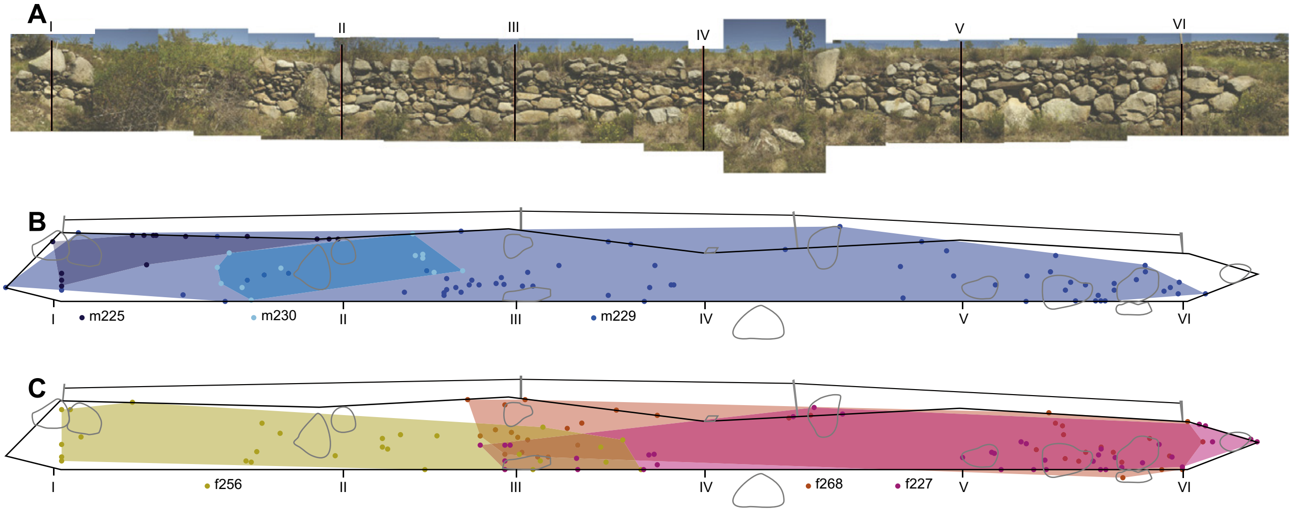

Fig. 1. Territoriality in *Podarcis muralis*. For the last five years we have been studying social and spatial behavior of a free-ranging population of *P. muralis* in the Pyrenees. The figure shows a photographic composition of a stone wall (A) in our field study site, and schematic representations of the home ranges of the male (B) and female (C) *P. muralis* observed in this wall during the 2009 breeding season. All the walls in our study site have been measured, mapped, and reference points painted in the field (using water-resistant paint) to allow us to locate lizards within an *x*–*y* coordinate system for each individual wall. *P. muralis* is a typical territorial species in which large adult males set out exclusive or nearly exclusive territories that encompass the home ranges of several females. Male m229, the dominant territorial male in this wall, was first spotted as a subadult in 2007 and remained the holding territorial male in this wall for two consecutive breeding seasons (2008 and 2009). Both m230 (a subadult male) and m225 (an adult but small – 2 year old – male) were chased and attacked by m229, and interactions between m229 and the three females within his home range (see Fig. 4) were frequently observed.

Studies of the functional significance of putative chemical signals in lizards are often complicated by the lack of relevant field data. In particular, systematic studies of lacertid social behavior with modern methods involving long-term observation of individually identified animals with known genetic relationships are almost nonexistent (but see [40,41]). As a result, important aspects of their social behavior such as territoriality, mate choice, mate guarding or the type of mating system are often assumed rather than tested. In *Podarcis* there is good evidence that, at least in some species, males set out territories that overlap the home ranges of several females and from which other adult males are aggressively excluded (Fig. 1). Therefore we will also review what we have learned about the role of male scent marks as territorial signals that mediate male–male interactions.

2. Sources of semiochemicals

Although there is some evidence that cloacal secretions/exudates and fecal pellets may contain socially relevant chemical stimuli, the main sources of semiochemicals in lacertids, as in other lizards, are believed to be the skin and the femoral glands [34]. Olfaction, vomerolfaction and possibly gustation [48] are involved in the perception of these stimuli, although research has focused almost exclusively on the tongue-vomeronasal system and has relied on counts of the number of tongue-flicks elicited by different stimuli as an index of vomeronasal chemoreception. In social interactions, tongue flicks are often directed at the body surface of conspecifics or at substrates previously occupied by conspecifics.

In reptiles, the outer layers of the integument are imbued with lipids which function as a permeability barrier, as protection against microorganisms, parasites and predators, and also as pheromonal compounds [54]. Compared to the amount of work devoted to the analysis of skin lipids in snakes, very little has been done in lizards [53]. In fact, there are no published studies of the chemical composition of skin lipids in any lacertid. Fig. 2 shows preliminary gas chromatograms of the acidic and neutral lipids in the skin of a female *P. hispanica* type 1.

Femoral glands are located on the ventral surface of the thigh of many lizards and produce a waxy secretion that is extruded through the pores as a solid plug. Femoral pores are sexually dimorphic and their secretory activity peaks during the reproductive season. Femoral pore secretions contain lipids and proteins, although only the former have been chemically analyzed (reviewed in [54]). This is surprising considering that in some species proteins make up 80% of the femoral gland secretions (unpublished results). The often repeated claim that only lipophilic compounds are important for lacertid chemoreception (e.g., [22]) has no empirical support and seems unjustified.

3. Chemically-mediated species recognition

Many of the *Podarcis* currently recognized in the Iberian Peninsula have parapatric distributions. However, in some cases the distribution ranges of two or more species abut or overlap. Although laboratory studies have shown that many species are reproductively compatible, hybridization in the wild is rare [9], and so it seems natural to ask to what extent are chemical stimuli involved in maintaining reproductive isolation.

For the study of chemically-mediated species recognition in *Podarcis* we use a repeated-measures design in which each experimental lizard is transferred from its home enclosure to a clean (unmarked) control terrarium or to a test terrarium previously occupied by a conspecific or heterospecific lizard of the opposite sex. Experimental lizards are observed for 10 min, during which time we record a number of behavioral variables including the number of tongue-flicks directed at the substrate. This procedure offers a more naturalistic approach than the alternative method based on presentation of chemical stimuli in cotton-tipped applicators. However, it has one potential drawback in that the researcher has no control over the source of semiochemicals deposited on the substrate, which is probably a mixture of cloacal exudates, fecal material, skin lipids and, particularly in the case of males, femoral gland secretions.

Fig. 3 shows results of an experiment conducted with *P. bocagei* and *P. hispanica* type 1, two closely related species with overlap-

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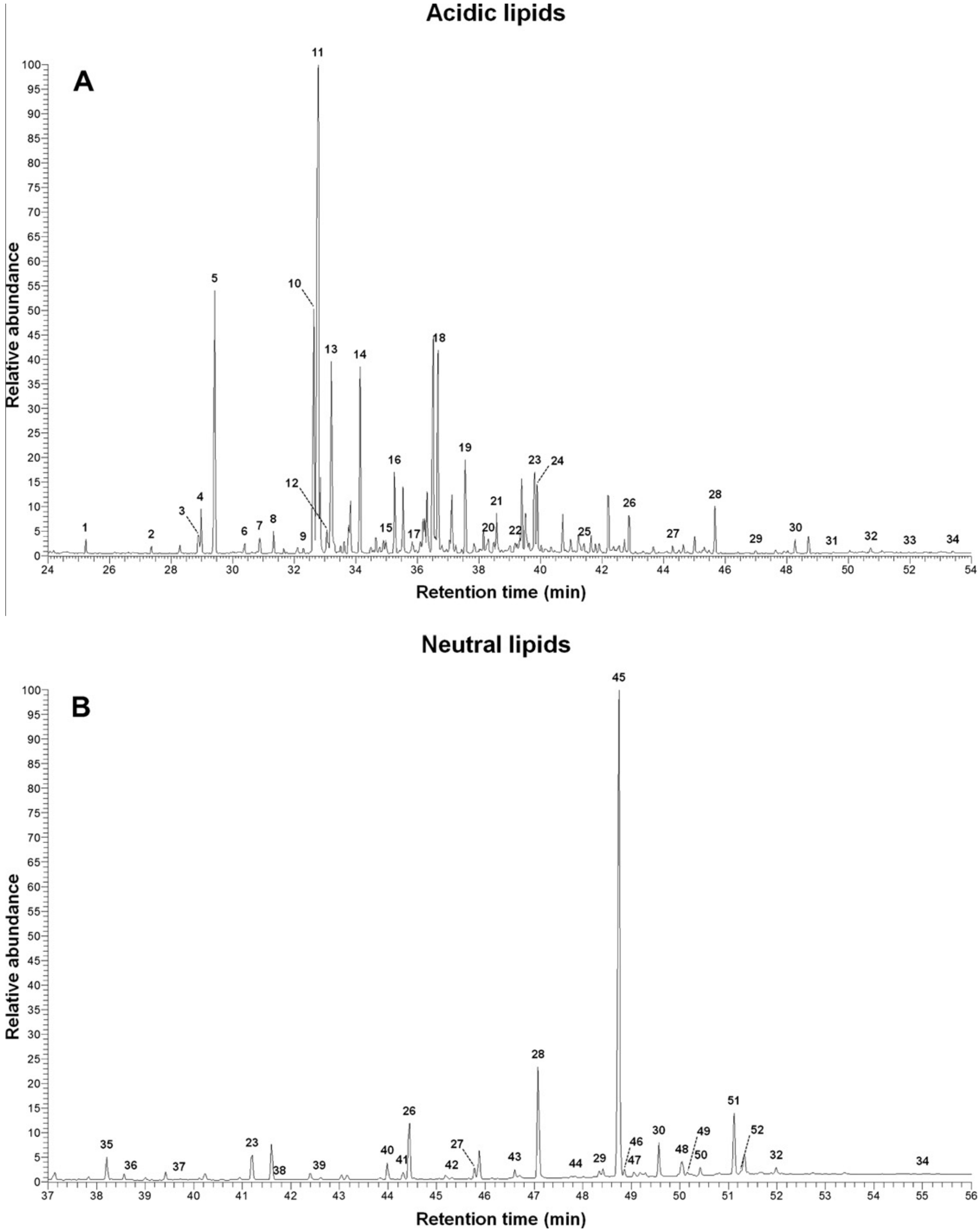

Fig. 2. Gas chromatograms from acidic (A) and neutral (B) skin extracts of female *Podarcis hispanica* type 1. Major lipophilic compounds identified are indicated by the number codes: 1-Tetradecanoic acid; 2-Pentadecanoic acid; 3–7-Hexadecenoic acid; 4–9-Hexadecenoic acid; 5-Hexadecanoic acid; 6–2-Hexadecenoic acid; 7-Heptadecenoic acid; 8-Heptadecanoic acid; 9–2-Heptadecenoic acid; 10–9,12-Octadecadienoic acid; 11–9-Octadecenoic acid; 12–3-Octadecenoic acid; 13-Octadecanoic acid; 14–2-Octadecenoic acid; 15-Nonadecanoic acid; 16–3-Methoxyoctadecanoic acid; 17–9-(3,4-Dimethyl-5-pentyl-2-furyl)-decanoic acid; 18-Eicosanoic acid; 19–2-Eicosenoic acid; 20-Henicosanoic acid; 21–3-Methoxyeicosanoic acid; 22–11-(3,4-Dimethyl-5-pentyl-2-furyl)-dodecanoic acid; 23-β-Hydroxyeicosanoic acid; 24-Docosanoic acid; 25-Tricosanoic acid; 26-Tetracosanoic acid; 27-Pentacosanoic acid; 28-Hexacosanoic acid; 29-Heptacosanoic acid; 30-Octacosanoic acid; 31-Nonacosanoic acid; 32-Triacontanoic acid; 33-Hentriacontanoic acid; 34-Dotriacontanoic acid; 35-β-Hydroxyoctadecanoic acid; 36-Henicosanol; 37-β-Hydroxynonadecanoic acid; 38-Tricosanol; 39-β-Hydroxyhenicosanoic acid; 40-β-Hydroxydocosanoic acid; 41-Squalene; 42-β-Hydroxytricosanoic acid; 43-β-Hydroxytetracosanoic acid; 44-β-Hydroxypentacosanoic acid; 45-Cholesterol; 46-Cholestanol; 47-β-Hydroxyhexacosanoic acid; 48-Campesterol; 49-Campestanol; 50-Stigmasterol; 51-β-Sitosterol; 52-Sitostanol.

ping distribution ranges in northern Portugal. Males perform more tongue-flicks in the presence of chemicals left by females of their own species than in the heterospecific or control treatments (Fig. 3A). Although a quantitatively different response to conspecific and heterospecific female chemicals does not demonstrate that males recognize the scent marks of either as belonging to a suitable mate [45], it is often assumed that a higher rate of tongue-flicking in this context indicates a mating preference (e.g., [30]). Similar results have been obtained with other *Podarcis* species (unpublished results, [1,14]). Taken together, these results clearly indicate that males are capable of discriminating between conspecific and congeneric females of a sympatric, closely related species using only substrate-borne chemical cues. Thus, differences in female chemical stimuli may underlie species recognition in this

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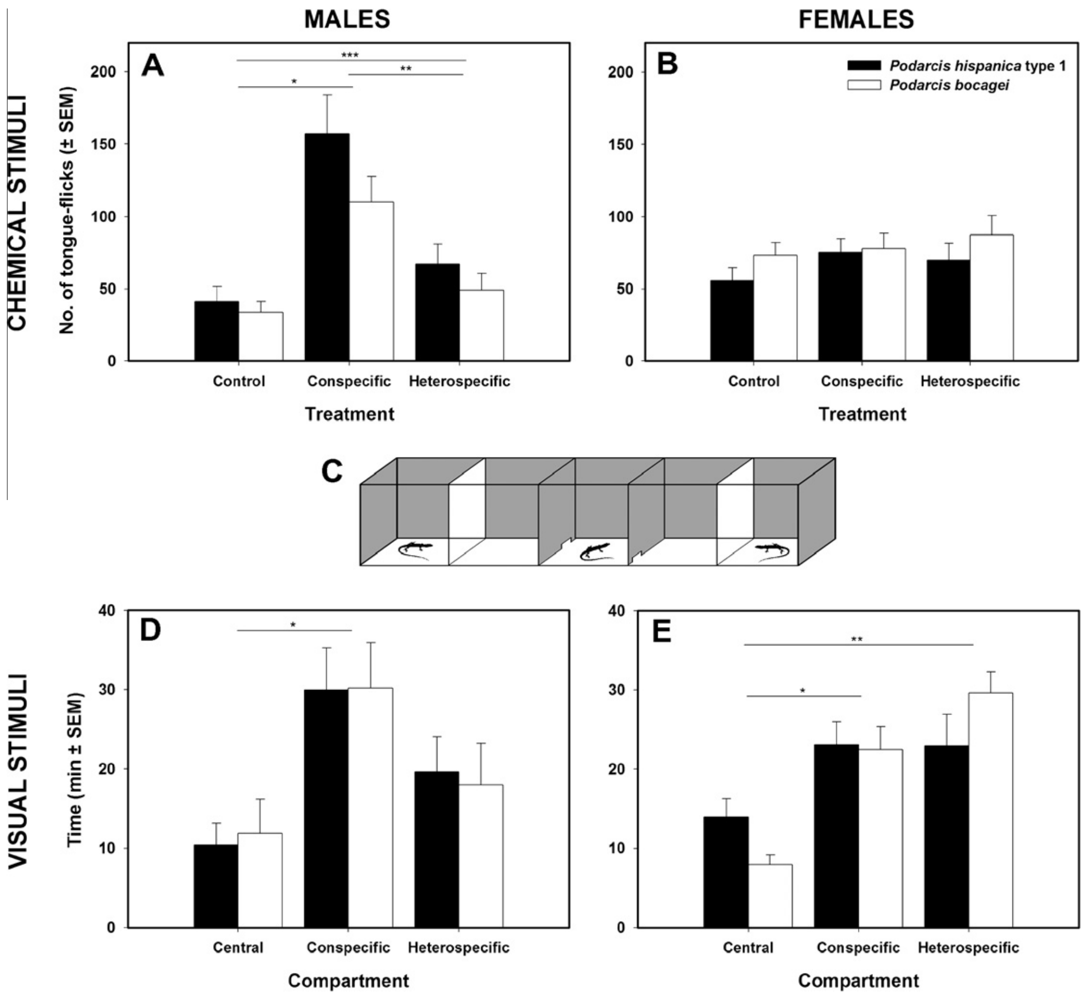

Fig. 3. Role of chemical and visual stimuli in species recognition in *Podarcis bocagei* and *P. hispanica* type 1. (A and B) Average number of tongue-flicks of *P. hispanica* type 1 and *P. bocagei* males and females directed at a clean substrate (control) or at a substrate scent marked by a conspecific or a heterospecific lizard of the opposite sex. (C) Experimental setup for the study of visually-mediated species recognition. A focal lizard was placed in the middle of the experimental terrarium and allowed to move freely between the three central compartments. The compartments on either end of the terrarium were occupied by a conspecific and a heterospecific lizard of the opposite sex as the focal lizard (the location of conspecific and heterospecific stimulus lizards was counterbalanced). The focal lizard had visual access to the lizards in the end compartments through a UV transparent filter. (D and E) Average time spent by male and female *P. hispanica* type 1 and *P. bocagei* in the central (control) compartment and in the compartments adjacent to those occupied by a conspecific or a heterospecific lizard of the opposite sex. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

group and may have evolved, at least in part, to promote chemosensory pre-mating reproductive isolation between sympatric congeners (see also [23,44]).

A surprising outcome of these experiments is a conspicuous and consistent sex difference in the response to chemical stimuli: in contrast to males, females do not perform more tongue-flicks or otherwise behave differently in the presence of substrates scent marked by males of their own or of a different species (Fig. 3B). The lack of differential tongue-flick rates of females confronted with scent marks of males belonging to different species is not due to the absence of species-specific male chemical cues, as shown by the fact that males are capable of discriminating between substrates scent marked by conspecific and heterospecific males (unpublished results, [33]). Negative results in experiments that rely on tongue-flick rate as the dependent variable are notoriously difficult to interpret [11]. For example, it is possible that females are perfectly capable of discriminating between scent marks of conspecific and heterospecific males but this is not reflected in the numbers of tongue-flicks they emit in response to either type of stimulus. Yet, the available evidence is consistent with the intriguing possibility that females are incapable of chemically discriminating conspecific from heterospecific males. This suggests that there has not been a selection pressure for the evolution of female chemical discrimination and that species recognition in this group is driven by male, not female, chemical discriminatory abilities [2].

The apparent lack of chemical discrimination does not necessarily imply that females are totally indiscriminate of species identity in their mating choices. Females could use stimuli in sensory modalities other than chemoreception (or a combination of stimuli in different sensory modalities) to choose a mate of the right species [2]. However, an experiment designed to test the lizards' ability to discriminate between conspecifics and heterospecifics of the opposite sex using visual rather than chemical stimuli yielded a pattern of results similar to the chemical discrimination experiments: males tend to associate with conspecific females, whereas females prefer to associate with males irrespective of their specific identity (Fig. 3C–E). Thus males are again more selective than females in their response to conspecific and heterospecifc individuals of the opposite sex.

It has been argued that the lack of discrimination by females may be due to female mate assessment overriding species recognition [58]. This could arise if the traits that females rely on to select high quality mates were present in heterospecific as well as in

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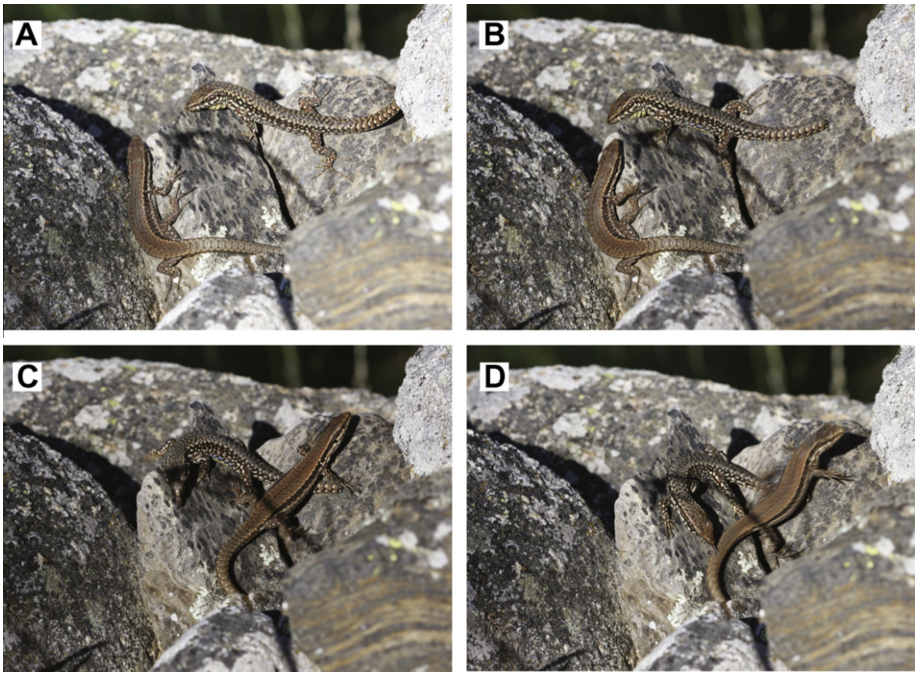

Fig. 4. Interaction between a male and a female *Podarcis muralis* in their natural habitat. During interactions between a territorial male and a female whose home range is overlapped by that of the male (see Fig. 1), both sexes typically perform visual displays while males do most of the tongue-flicking. In this photographic sequence the female is performing a foot shake display in (C) and (D). The male, located above the female in (A–C), is larger than the female and has a reticulated dorsal pattern. The male's tongue can be clearly seen in (C) and (D). Male tongue-flicks are directed at the substrate (in locations previously occupied by the female) and at the female's body, particularly around the base of the tail.

conspecific males. However, this is an unlikely explanation given the lack of evidence for female mate choice in lacertids (see below). In sum, it seems that, as far as *Podarcis* go, 'a lack of discrimination by females is the rule, with males playing the most active role' ([9] p. 257).

The latter statement agrees rather well with observations of the behavior of the animals in the field. In most species, males follow the scent trails of sedentary females rather than the other way around [39]. Also, when males and females interact at close range, it is the males that perform most of the tongue-flicking, directing tongue-flicks both at the substrates previously occupied by females and at the females' bodies, particularly around the base of the tail (Fig. 4). Therefore, the conclusion from both laboratory experiments and field observations is that females are less responsive than males to socially relevant chemical stimuli. Similar results have been reported in studies with other lizards: in many experiments comparing male and female chemosensory discrimination abilities, females make less tongue flicks than males and in general appear less responsive and discriminating than males (e.g., [12,13]).

4. Mate recognition and mate assessment

In addition to their role in species recognition, several studies have shown that chemical stimuli are also important for mate recognition in lacertids. For example, males in some species can discriminate between pregnant and non-pregnant females using chemical stimuli alone [14].

Much more controversial is the potential role of chemical stimuli in mate assessment. Recently, several studies have shown that female lacertids are capable of using chemicals in femoral gland secretions to discriminate among males that differ in a number of phenotypic traits, such as body size, age, immune response, symmetry, parasite load, social dominance, etc. This evidence has in turn been used to argue that females may be using the information contained in scent marks to settle in territories held by high quality males, and therefore that male scent marks may be important for female mate assessment in lacertids (reviewed in [34]). This is an uncanny claim considering that females in several species apparently do not discriminate between substrates scent marked by males of their own vs. a different species (see above). Indeed, the very notion that female lacertids exhibit chemically-mediated mate assessment runs counter to abundant evidence that indicates that pre-copulatory female mate choice is rare in lizards, particularly in territorial species [31,32,36,37,52,55].

To try to clarify this issue we conducted a spatial association experiment in which females of *Podarcis liolepis* (formerly *P. hispanica*) were offered a choice of substrates scent marked by males differing in body size [8]. Body size is the main determinant of male competitive ability and mating success in lizards [35,38]. The experiment was conducted in a large naturalized observation chamber that could be divided into three equal-size compartments by sliding partitions. Two males differing in size were allowed to scent mark two randomly determined compartments, whereas the third compartment was left as a clean, unmarked control. After removing the males and the partitions, a female was released in the observation chamber and its location recorded at 10 min intervals during the ensuing 9 h. Although females spent more time in areas previously occupied by males than in the control compartment, we found no evidence that they show a preference for areas scent marked by large males. Furthermore, in response to experimentally induced dusk at the end of choice trials, females preferentially took shelter in refuges scent marked by small males. These results indicate that, even though females are capable of discriminating between males of different size, they do not preferentially associate with areas scent marked by large (presumably higher quality) males [8].

The available evidence therefore shows that female lacertids are capable of extracting some information from male scent marks, but the role of scent marks in pre-copulatory female mate choice is still

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unclear. This does not negate the possibility that femoral gland secretions could function as mate assessment signals. Indeed, females could be using the information contained in male scent marks to bias fertilizations in favor of selected males by cryptic female choice [40].

What then are we to make of the claim that female lacertids use the information contained in male scent marks to select high quality mates? This claim is based on the assumption that increased chemical sampling and/or spatial association to a male's scent is a measure of the female's willingness to associate, and ultimately copulate, with that particular male. However, this is a *non sequitur*. Female lacertids may be capable of outstanding feats of chemical discrimination but this does not in itself constitute definitive evidence that there is mate choice in these species, nor that female choice (if it exists) is based on chemical assessment of male scent marks. Testing for female scent preferences is one thing, but actually providing evidence that these preferences translate into a given pattern of mate choice is something completely different. As noted by Johansson and Jones [29] 'ultimately, mate assessment pheromones must be shown to guide receivers to the mates that produce the most or/and best offspring' (p. 270). Even if it can be shown that possession of certain traits results in an increase in mate acquisition by males, the question still remains whether such an effect is achieved through rival deterrence (i.e., male–male competition) or female choice. Future studies should explore the link between female preferences in scent choice trials, their acceptance or rejection of copulas with associated males, and reproductive success [28,51].

5. The myth of lacertid pre-copulatory female mate choice

None of the studies that assert that female lacertids exhibit chemically-mediated mate assessment have really tested for female choice. In fact, conclusive evidence for the existence of pre-copulatory female mate choice in lacertids is almost entirely lacking (but see [17,18]). There are sound theoretical reasons to doubt that female mate choice is as prevalent in lizards as in other vertebrate groups [25,26,37,38,52,55,56]. For example, territoriality may limit or even preclude female mate choice because male territories are typically much larger than female home ranges, thus making it very costly in terms of time, energy, and risk of sexual harassment and predation for females to sample several potential mates. Many lacertids exhibit resource-based territorial systems which provide little opportunity for female mate choice due to the large costs of searching and sampling mates (e.g., [15]). In these species, females may be choosing high quality territories rather than high quality males [16]. However, it is also possible that females are choosing their mates based both on male and territory characteristics [5]. This is an area where the available information is clearly insufficient to draw any firm conclusions.

6. Territoriality, individual recognition and male–male competition

In lizards, particularly territorial species, male–male competition is a major force driving the evolution of traits used for social signaling. Much research has been devoted to the role of visual displays in intra-sexual competition, but chemical stimuli have received comparatively less attention. For decades, scent marks have been depicted as 'no trespass' signals, as mere chemical sign-posts for intruders. Recent studies, however, are unveiling a much more complex picture of scent mark function.

To investigate the functional significance of male scent marks in *P. liolepis* we set up an experimental procedure using scent marked terraria to simulate the situation faced by a male when intruding the territories of rival males. This experimental design allowed us to examine the role of scent marks in the context of territorial interactions from the perspective of both the receiver (the intruding male) and the sender (the territory owner). From the perspective of the intruding male, the results of these experiments indicate that scent marks do not function as keep out signals. In fact, early in the reproductive season intruding lizards spend more time in areas scent marked by other males of the same size or larger than themselves than in control, unmarked areas. This suggests that scent marks convey information about the competitive potential (i.e., size) of territory holders [6].

From the perspective of the territory owner, on the other hand, scent marks allow males to recognize potential rivals (i.e., intruding males) individually [7]. This is one of the first conclusive demonstrations of true individual recognition in any reptile, and suggests that at least some compounds in the scent marks of male *Podarcis* may be signature mixtures (*sensu* Wyatt [57]) rather than pheromones. Traditional interpretations of the function of territorial scent marks were framed in the context of the 'dear enemy' hypothesis. According to this hypothesis, the crucial variable affecting response to social signals is familiarity. However, our results with *P. liolepis* suggest that males are capable of much more interesting discriminations. They allocate their aggressive behavior to intruders not on the basis of familiarity but according to the degree of threat posed by the intruder. They use scent marks to identify the potential threat posed by each individual neighbor (i.e., degree of territorial overlap), allowing them to allocate their aggressive behavior accordingly and to adjust it to changes in rival males' territorial status. Therefore, scent marks can be broadly depicted as complex social signals that reduce the costs of territoriality, allowing males to strategically allocate their investment in territorial defense [7].

The picture of lacertid scent mark function that emerges from this review is more complex and interesting than previously suspected. Considering all the available evidence, we conclude that scent marks in *Podarcis*, and possibly in other lacertids, convey information regarding the sender's species, sex, individual identity, fighting ability, etc. Responses to scent marks are context-dependent and may involve learning [7]. Although females seem able to extract some information from them, the role of male scent marks in female choice is still unclear. Male scent marks seem particularly important as social signals mediating territorial interactions between males. This suggests that the evolution of scent marks in male *Podarcis* may have been driven largely by male–male competition, with female pre-copulatory mate choice playing a more limited role.

7. Adult neurogenesis in chemosensory brain areas: effects of sex and season

Given that males and females differ in their use of chemical stimuli, we wondered whether this would translate into a difference in the size of brain areas involved in chemoreception. The olfactory bulbs are the first processing stage of chemosensory information and their size has been used as an index of the extent to which an animal's behavior is dependent on chemoreception [3,4,10,24,49,50], so we looked for size dimorphisms in the main and accessory olfactory bulbs in a sample of *Podarcis liolepis*. As it turns out, males have larger (i.e., longer) main and accessory bulbs than females (Fig. 5). This is not completely unexpected because males are larger and have larger heads and brains than females [46]. However, the difference between males and females persists after correcting for body and brain size, although the results are slightly different depending on the variable used as covariate. Relative to body size, males have larger main and accessory bulbs than females. However, relative to brain size, males have larger accessory bulbs, but not larger main olfactory bulbs than fe-

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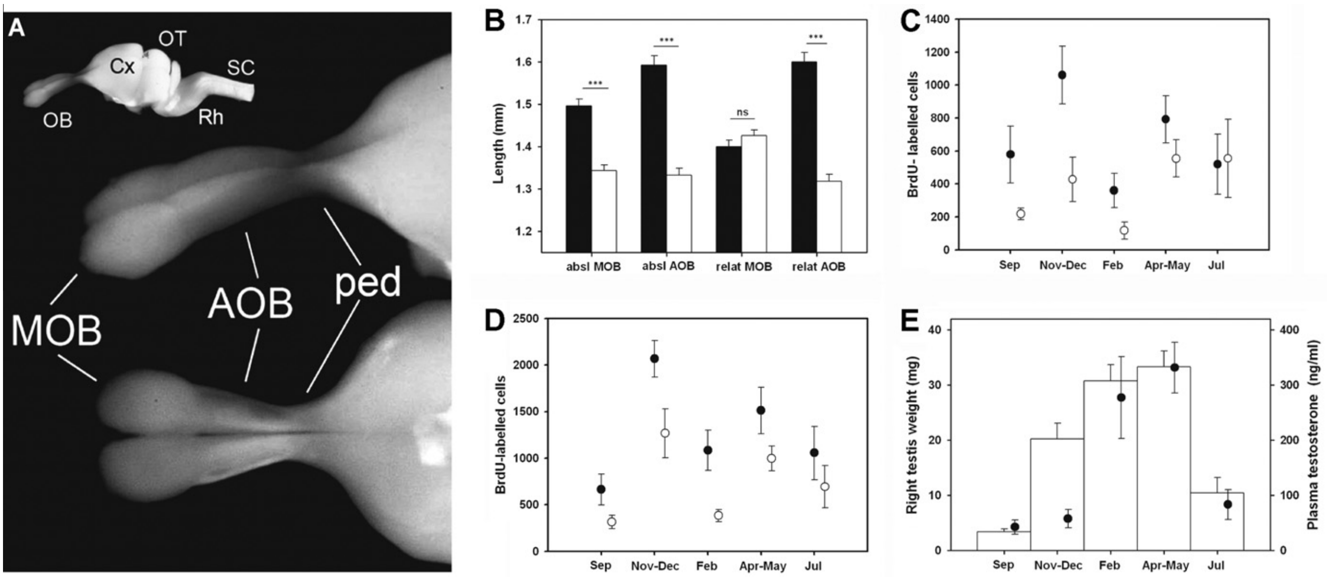

Fig. 5. Sexual dimorphism and seasonality in olfactory bulb size and neurogenesis in *Podarcis liolepis*. (A) Gross morphology of the olfactory bulbs. (B) Seasonal variation in olfactory bulb size. Relative values have been calculated using overall brain length as a covariate. (C and D) Seasonal cell proliferation (counts of BrdU labelled cells) in the main (C) and accessory (D) olfactory bulbs three weeks after systemic administration of the proliferation marker 5-bromo-2′-deoxyuridine (BrdU). Dark circles are mean (± SEM) values for males, white circles for females. (E) Seasonality in testis size and plasma levels of testosterone. Bar chart represents testis size and scatter plot represents plasma levels of testosterone. AOB: accessory olfactory bulb, Cx: cerebral cortex, MOB: main olfactory bulb, OB: olfactory bulbs, OT: optic tectum, ped: olfactory peduncle, Rh: rhombencephalon, SC: spinal cord, $^{***}p < 0.001$, ns: not significant.

males (Fig. 5B). Thus the olfactory bulbs of male *P. liolepis* are larger than those of females in absolute and, depending on the covariate, also in relative terms, confirming that differential use of chemical stimuli by the two sexes is associated to sexually dimorphism in chemosensory brain areas in this species [46].

How do males acquire their disproportionately large olfactory bulbs? Several brain areas of lizards continue to grow into adulthood due to the constant addition of new neurons in a process known as adult neurogenesis [19]. Interestingly, adult neurogenesis in lizards is particularly intense in chemosensory telencephalic areas (olfactory bulbs, lateral cortex, nucleus sphericus). We asked whether adult neurogenesis, like brain size, is sexually dimorphic in *P. liolepis*. Results reveal that male lizards produce more neurons in chemosensory brain areas than females (Fig. 5C and D), and at least in the olfactory bulbs, this sexually dimorphic neurogenesis cannot be explained solely by the differences in brain size [46]. Thus, the available evidence suggests that the sexual dimorphism in olfactory bulb size is due, at least in part, to sex-specific differences in the rate of adult neurogenesis (Fig. 5).

Adult neurogenesis in the olfactory bulbs and other chemosensory brain areas fluctuates seasonally in both sexes. Cell proliferation peaks twice throughout the year: first in November-early December (non-breeding season), and again in April–May (breeding season) (Fig. 5C and D). The latter peak coincides with a peak in testis size and testosterone levels in males (Fig. 5E [47]). These seasonal cycles of adult neurogenesis may have evolved to satisfy increased chemosensory demands at particular times of the year.

8. Suggestions for future research

There are several areas that have scarcely been investigated and where more research is needed before general principles of lacertid chemoreception can be derived. First, we need more studies of the chemical composition of skin lipids and of the proteic fraction of femoral gland secretions. Given the behavioral evidence, female skin lipids in particular are bound to play a crucial role in species recognition and reproductive isolation among syntopic congeners. Another area to which researchers should pay more attention is visual communication and the potential interaction between visual and chemical stimuli in species recognition, mate recognition, and mate assessment. Lacertids have a sophisticated visual system that allows them, among other things, to detect and capture fast flying insects. They have large eyes with all cone retinas that support tetrachromatic color vision, including the ability to perceive UV wavelengths [20,42]. Yet, their ability to produce and perceive signals in the visual modality has been seriously underappreciated. In addition to bright, conspicuous and often sexually dimorphic colorations, lacertids possess a repertoire of largely unexplored dynamic visual signals, including head bobs and foot shakes [21]. As stated above, the link between scent choice (i.e. in chemical preference and spatial association experiments) and mate choice still awaits rigorous study. Finally, there are conspicuous gaps in our knowledge of lacertid social behavior. This is an area in which additional research, particularly field studies of their mating behavior, is likely to yield important insights into the function and evolution of pheromonal communication in lacertid lizards, as social systems provide the context in which all the interactions analyzed in this review take place.

9. Conclusions

This review has focused on the evidence regarding the role of chemical stimuli in social interactions in Iberian wall lizards (genus *Podarcis*). As in other squamates, skin lipids (in both sexes) and femoral gland secretions (mainly in males) appear to be the main sources of semiochemicals. Substrate-borne chemical stimuli are important for species recognition and may play a major role in maintaining pre-mating reproductive isolation between sympatric congeners. Interestingly, only males appear to be capable of discriminating between substrates scent marked by conspecific vs. heterospecific individuals. Possible reasons for the apparent lack of female chemosensory species recognition are discussed. Chemical cues are also important for mate recognition, but their role in female mate assessment is controversial: females seem able to ex-

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tract some information from male scent marks but the evidence does not support the idea that they use the information contained in male scent marks to select high quality mates prior to copulation. In the context of territorial interactions, scent marks allow males to recognize rivals individually, evaluate their competitive ability (i.e., body size), and assess the threat posed by each individual rival neighbor. Thus, contrary to recent generalizations, the evidence so far suggests that the evolution of male scent marks has been driven mainly by male–male competition (intrasexual selection). Sex differences in chemoreception are consistent with sexual dimorphism in chemosensory brain areas. The olfactory bulbs are larger in males and grow continuously due to the steady addition of newly-generated neurons (adult neurogenesis).

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