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REVIEW

Social behavior and pheromonal communication in reptiles

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Abstract The role of pheromones in orchestrating social behaviors in reptiles is reviewed. Although all reptile orders are examined, the vast majority of the literature has dealt only with squamates, primarily snakes and lizards. The literature is surprisingly large, but most studies have explored relatively few behaviors. The evolution of chemical signaling in reptiles is discussed along with behaviors governed by pheromones including conspecific trailing, male-male agonistic interactions, sex recognition and sex pheromones, and reptilian predator recognition. Nonreptilian prey recognition by chemical cues was not reviewed. The recent literature has focused on two model systems where extensive chemical ecology studies have been conducted: the reproductive ecology of garter snakes and the behavioral ecology of Iberian lacertid lizards. In these two systems, enough is known about the chemical constituents that mediate behaviors to explore the evolution of chemical signaling mechanisms that affect life history patterns. In addition, these models illuminate natural and sexual selection processes which have lead to complex chemical signals whose different components and concentrations provide essential information about individuals to conspecifics. Reptiles provide excellent candidates for further studies in this regard not only in squamates, but also in the orders where little experimental work has been conducted to date.

Keywords Pheromone · Reptile · Snake · Lizard · Tongue-flick · Vomeronasal organ · Trailing · Reproduction

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Introduction

The study of chemical communication, semiochemicals and pheromones in reptiles has benefited from a great deal of attention in recent years. Chemical communication is a major facet of reptilian life. For example, it is used in prey detection or foraging, predator detection, and pheromonally mediated behaviors such as species and individual recognition, mate choice, alarm signaling, and territoriality. Studies have evolved from astute observations of natural history to elegantly designed experiments that elucidate the causal mechanisms responsible for mediating behavioral responses to chemical cues and pheromones. The literature pertaining to this area of research is surprisingly large but weighted to investigations of relatively few behaviors. Sources of semiochemicals in these diverse taxa vary widely as well. Because of limitations of space, the goal of this review will not be an exhaustive examination of all aspects of chemical signaling in reptiles. Rather, it will focus on the methodologies employed by investigators in documenting and elucidating the behavioral and chemical mechanisms that subserve pheromonal communication in reptiles. In this review, representative studies are grouped according to the type of behavior and not in a phylogenetic hierarchy. In addition, we have tried to cite reviews from the literature that are significant in their completeness and timeliness.

History and evolution of chemical communication in reptiles

The study of chemical communication in reptiles began in earnest in the 1920s and 1930s with the pioneering work of Baumann and Noble. Baumann studied life history patterns in the European adder (*Vipera aspis*) (Baumann 1927,

1929). At approximately the same time, G.K. Noble was conducting complementary studies in the North American colubrids *Thamnophis* and *Storeria* (Noble and Clausen 1936; Noble 1937). The discipline has grown rapidly since, and now references number in the thousands. Many substantive and informative reviews have been written in the interim (Evans 1961; Carpenter and Ferguson 1977; Madison 1977; Burghardt 1970, 1980; Simon 1983; Gillingham 1987; Mason 1992; Halpern 1992; Cooper 1994; Mason et al. 1998; Weldon et al. 2008; Houck 2009). As a result, the field of chemical communication in reptiles has been well and thoroughly covered in the recent past.

The evolution of chemical signaling in reptiles is open to debate. Certainly, chemical cues are very efficient energetically in that they may be cheap to produce, they relay information after the producer is gone, and they work in the dark and potentially over very great distances. On the other hand, more recent studies have shown that some semiochemicals are metabolically important molecules that have been diverted from internal physiological homeostasis and when secreted to the outside serve as honest signals that advertise the quality of the signaler to potential mates (Martín and López 2006e). Duvall (1986) proposed a mechanism for the evolution of chemical communication by pheromones in reptiles, hypothesizing that chemical exudates such as feces or urine, skin lipids, or other metabolic byproducts are inexpensive in the sense that they are continually available for use as chemical signals. Evolution would then favor the coopting or exaptation of these chemical cues to serve as semiochemicals or chemicals with signal function (Graves et al. 1986; Maderson 1986). In this line of reasoning, an individual may passively mark or deposit secretions as it moves through the habitat leaving cloacal cues or integumental cues as it rests or drags its ventral surface and cloacal area across the ground. This could easily evolve into the femoral gland marking seen in present day lizards. Conversely, individuals might also be actively marking the environment by performing a specific behavior in order to leave a chemical cue on the substrate by chin wiping, cloacal rubbing, or expulsion of cloacal gland constituents. Finally, specialized exocrine glands are known to produce behaviorally active semiochemicals such as chin glands in tortoises and cloacal scent glands in snakes.

Olfaction and vomerolfaction

As Cooper (1994) stated, tongue-flicking is the quintessential squamate behavior. The tongue serves as an environmental sampler and delivery device to the vomeronasal (Jacobson's) organ found in the roof of the mouth or in the nasal passages. The vomeronasal organ is common to most vertebrate taxa but is most highly developed in squamates (Halpern 1992; Halpern and Martinez-Marcos 2003). The olfactory sense, although well-developed in reptiles, has not been extensively studied. Gustation has not been studied systematically to date, although taste buds do exist in squamates (Schwenk 1985). Tongue-extrusion, or tongue-flicking in reptiles is associated with vomeronasal chemoreception. Because of the ease of observing and quantifying tongue-flicks in social contexts, this behavior is commonly reported in investigations of chemical communication in reptiles, especially lizards.

The reception and perception of chemical cues from the environment by the vomeronasal system has been termed vomerolfaction (Cooper and Burghardt 1990). Thus, vomodors are those chemical cues detected by the vomeronasal system. Definitive evidence of the vomeronasal organ's role in mediating socially important chemical cues has been obtained by means of complicated physiological experiments in which the vomeronasal nerves are either anesthetized, ablated, or severed. Sectioning the olfactory nerves and vomeronasal nerves of male garter snakes leads to deficits in courtship behavior (Kubie et al. 1978; Halpern and Kubie 1980) and aggregation behavior (Heller and Halpern 1982). Males with olfactory nerve lesions alone continue to court attractive females, while those with sectioned vomeronasal nerves fail to recognize and court attractive females. Identical results were found in the European adder (*Vipera berus*) (Andrén 1982). The vomeronasal organ is also essential for detecting prey, at least in squamates. Impairment of the vomeronasal system, but not the olfactory system, renders garter snakes (*Thamnophis*) unable to recognize earthworms as a food source (Halpern and Frumin 1979). This is also the case in lizards (Graves and Halpern 1989, 1990; Cooper and Alberts 1991).

Turtles have received far less attention in this regard, but the vomeronasal organ of turtles does respond to general odorants (Hatanaka et al. 1988; Shoji and Kurihara 1991; Franceschini et al. 1996). Fadool et al. (2001) studied activation of vomeronasal neurons in musk turtles, *Sternotherus odoratus*, in response to male and female urine and musk and concluded that vomeronasal neurons are sexually dimorphic in their response profiles. Further studies demonstrated that the musk turtle's vomeronasal sensory neurons respond via the phospholipase C system (Brann and Fadool 2006). Crocodilians do not possess a functional vomeronasal organ.

Attractants and repellents

All snakes possess at least a pair of cloacal scent glands that are under voluntary control. Upon being disturbed or handled, snakes often express foul-smelling fluids from

these glands into the cloaca and into the environment. Handling often causes snakes to writhe and smear this malodorous secretion onto the handler. It has been suggested that these secretions serve either a defensive or alarm function or perhaps both. Cloacal gland secretions removed from Texas blind snakes (*Leptotyphlops dulcis*) repelled ants of the species *Labidus coecus, Neivamyrmex nigrescens,* and *Solenopsis geminata* (Gehlbach et al. 1968). In two-choice tests where animals were scored on how many times a snake entered either half of an aquarium and how much time was spent on each side, conspecific blind snakes were attracted to the cloacal gland secretions. Individuals of other snake species that compete for ant and termite larvae with Texas blind snakes were significantly repelled by these secretions.

Cloacal gland secretions in snakes may also serve an alarm function in addition to their defensive role. Prairie rattlesnakes (*Crotalus viridis*) experience a significant rise in their heart rate after exposure to a threatening stimulus in the presence of cloacal gland materials from conspecifics (Graves and Duvall 1988). Those animals not exposed to conspecific cloacal gland material and subsequently threatened responded with significantly lower heart rates. Presumably, animals not being threatened would have lower heart rates.

Lizards also have glands in their lower gastrointestinal tract and cloaca. Lipid components from the urodaeal gland of male broad-headed skinks (*Eumeces laticeps*) and black-lined plated lizards (*Gerrhosaurus nigrolineatus*) elicit significantly more tongue-flicks than do water controls (Cooper et al. 1986; Cooper and Trauth 1992). When the gland was removed and macerated then presented to courting males, tongue-flick rates to the homogenate were significantly higher than those directed towards cloacal lavages, suggesting that the courtship pheromone in these skinks is contained primarily in this gland. Solvent extracts of these glands indicate that the sex pheromone is probably a lipid (Cooper and Garstka 1987). Male broad-headed skinks (*E. laticeps*) tongue-flick female-derived cloacal cues significantly more than those of males or controls (Cooper and Vitt 1984). Males of this species can also recognize the cloacal cues of females of their own species when compared to female cloacal cues from two closely related species (Cooper and Vitt 1986a). Exogenous estrogen injections to female broad-headed skinks render their cloacal chemical cues more attractive to breeding male skinks than do cloacal cues from sham-injected females (Cooper 1995). Furthermore, males with brighter orange head coloration, which may indicate higher circulating androgen concentrations, respond with more tongue-flicks to the cloacal cues of estrogen-treated females than to sham-injected females.

Turtles have several specialized glands that secrete aromatic odoriferous semiochemicals into the environment. Inguinal, axillary, and Rathke's glands along the angle formed by the plastron and carapace and possess pores that empty into the environment. Almost all turtle families possess these glands. In the stinkpot turtle (*Sternotherus odoratus*), the contents of their musk glands are ejected when the turtles are handled or molested. Voluntary control of these malodorous glands implies a defensive role for the semiochemicals (Eisner et al. 1977). The secretions deter feeding by small fish, but tests with larger predators are needed (Eisner et al. 1977). The long-necked turtle (*Chelodina longicollis*) also possesses inguinal musk glands, but the secretions although malodorous, do not deter feeding by potential predators including mammals, birds, and reptiles (Kool 1981). Polo-Cavia et al. (2009) showed that native Spanish terrapins (*Mauremys leprosa*) avoid waters containing chemical cues from an introduced invasive, the red-eared slider (*Trachemys scripta*) and hypothesize that this behavior may be causal to the displacement of the native species by the invasive.

Crocodilians possess two sets of actively secreting semiochemical glands. Paired mandibular glands in the throat region and cloacal scent glands become active and secretory during the breeding season, especially in males. Males can be observed rubbing their mandibular glands across the snouts of females during courtship, perhaps introducing a courtship pheromone (McIlhenny 1935; Evans 1961; Burrage 1965; Garrick 1978).

The cloacal glands in alligators are thought to play a role in territorial behavior among breeding bulls. Secretions from these glands are quite odoriferous. During the breeding season, bull alligators are thought to use these glands to mark territories and ward off competing males (Evans 1961). Alligators (*Alligator mississippiensis*) were scored for the amount of gular pumping observed in response to several synthetic chemical stimuli as well as secretions from the cloacal glands, mandibular glands, and blanks responding most strongly to the cloacal gland secretions of male alligator donors (Johnsen and Wellington 1982). Experiments conducted under controlled conditions are needed before conclusions regarding the role of these glands in chemical communication can be reached.

Trailing

The trailing ability of reptiles, especially squamate snakes and lizards is well known. Snakes and many lizards rely on chemical cues to detect and, at times, trail prey items, and this vast literature has been extensively reviewed (Burghardt 1970, 1980; Ford 1986; Mason 1992; Cooper 1994, 2007; Mason et al. 1998). Reptiles will also trail

conspecifics to aggregation sites, overwintering hibernacula, and for access to mates. The methodology of choice in examining trailing behavior now seems to have settled on the use of mazes, especially the Y-maze. In these experiments, chemical cues are laid down on the floor of the maze on removable paper including one arm of the maze. The other arm is usually left blank or contains solvent controls (Fig. 1).

Trailing to overwintering hibernacula was examined in neonatal timber rattlesnakes (*Crotalus horridus*) (Brown and MacLean 1983). Neonates successfully trailed adult conspecifics in the maze. Integumental cues and cloacal chemical cues almost certainly play a role. Shed skins and skin lipids may serve as chemical "sign posts" guiding juvenile prairie rattlesnakes back to their dens (Graves et al. 1986). Burger (1989) followed up on these leads and also examined the ability of juvenile snakes to trail adults. In this case, juvenile pine snakes (*Pituophis m. melanoleucus*) were able to distinguish and trail chemical cues from adult conspecifics. This ability would confer a selective advantage to those individuals using this behavior to successfully locate overwintering hibernacula. Chemical cues undoubtedly play a role in den location by snakes. However, other cues, such as celestial, solar, and visual cues, as well as topographic landmarks have been implicated (Gregory et al. 1987).

More often trailing studies focus on the role of trailing in mate location and recognition. In one of the earliest studies, conducted in the breeding season, chemical cues from the integument and cloacae of female Eastern garter snakes (*Thamnophis sirtalis*) and brown snakes (*Storeria dekayi*) were examined for their ability to elicit trailing

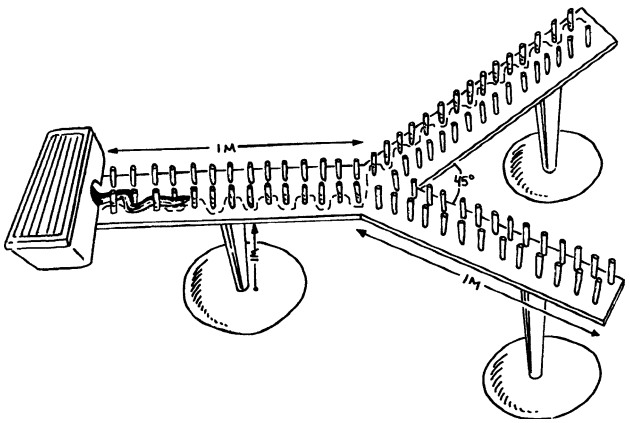

Fig. 1 Schematic of a typical Y-maze for assaying trailing behavior in snakes. A chemical trail (*dashed lines*) is laid on a paper substrate covering the maze and brushed against straw-covered pegs (*hatch marks*). The snake is then allowed to exit a holding box and peruse the maze. When two trails are laid in the maze, the trails are crossed at the junction to force the snake to relocate the trail and continue down one arm. Redrawn from LeMaster and Mason (2001a, b)

from males (Noble and Clausen 1936). Males significantly preferred conspecific trails from integumental cues over those from the cloaca. Females did not prefer the trails of either sex. Similar results have been obtained with the European viper (*Vipera berus*) (Andrén 1982, 1986).

Trailing of chemical cues has also been tested both within and between species. The eastern garter snake (*Thamnophis s. sirtalis*), the red-sided garter snake (*T. s. parietalis*), the western aquatic garter snake (*T. couchi*) and the western terrestrial garter snake (*T. elegans*) were tested for their ability to trail either conspecific or congeneric individuals in a Y-maze experiment (Heller and Halpern 1981). Interestingly, snakes in these experiments tended to follow the trail of the animal immediately preceding it in the maze. Both conspecific and heterospecific individuals were followed with similar frequencies. These results suggest a mechanism by which animals of different species can locate and utilize group hibernacula.

The trailing abilities of garter snakes of the genus *Thamnophis* have been extensively studied by Ford and his colleagues. In initial experiments, a five-armed maze was used to demonstrate that male garter snakes are quite successful at following trails of conspecific females, and not those trails of heterospecifics (Ford 1978, 1981). In studies with a Y-maze, male garter snakes still tended to follow the trails of their own females, but in addition, they also followed trails of heterospecifics rather than a blank arm (Ford 1982; Ford and Schofield 1984; Ford and O'Bleness 1986). The results of these experiments may indicate that closely related species use either similar chemical constituents or even identical constituents but in different ratios or blends. More research is necessary to elucidate the actual mechanisms of discrimination.

Directionality of a trail is a critical piece of information that the follower needs to determine. Experiments in a test arena with removable pegs elucidated a probable mechanism by which snakes determine the direction of a trail (Ford and Low 1983). When a stimulus snake deposited a trail in the test box, snakes were able to trail in the correct direction. Then, by removing and reversing the direction of the pegs, the trailing snake would also reverse direction. Under natural conditions, snakes deposit chemical cues in a similar fashion on objects in the environment that they have crawled over and past.

The trailing abilities of red-sided garter snakes (*Thamnophis sirtalis parietalis*) have provided a useful model for the study of chemical communication and allow for careful experiments examining the role of pheromones in mediating reproduction in snakes. In addition to its role in eliciting male courtship behavior, it has been hypothesized that the sexual attractiveness pheromone of female garter snakes (see section below), when laid down with skin lipids on the substrate when the female passes, is the chemical

cue utilized by courting males to follow the trails of sexually attractive, unmated females. In Y-maze tests conducted in the field during the breeding season, LeMaster and Mason (2001a) demonstrated that skin lipids from females, but not males, elicited trail following behavior from males and that this trailing pheromone was the same as the female sexual attractiveness pheromone. Only one study has specifically tested pheromone trailing behavior in the field under natural conditions with bioassays using known chemical cues (LeMaster et al. 2001). In that study, courting male garter snakes were able to locate unmated females by following skin lipid pheromone trails on the substrate. Females did not follow female or male trails. In the fall, when garter snakes return to their hibernacula from the summer feeding grounds, neither male nor female snakes followed pheromone trails of either sex thus indicating that homing back to communal hibernacula relies on different sensory cues (LeMaster et al. 2001).

Trailing male garter snakes can also discriminate the trails of unmated females from mated females (O'Donnell et al. 2004). This is clearly adaptive as this would reduce the amount of time a searching male garter snake would spend on locating a recently mated female that still possesses a mating plug and thus would be unable to mate. Using a Y-maze, O'Donnell et al. (2004) demonstrated that courting male garter snakes avoid the trails of recently mated females and continue to do so until after the copulatory plug has dissolved in approximately 2 days. They also concluded that the sex attractiveness pheromone of females is unaltered by mating and that the addition of the copulatory pheromone (see section below) is responsible for the change in the mated female's attractivity.

Few studies of European snakes have been conducted with relation to trailing with the exception of the *Vipera* studies. Fornasiero et al. (2007) examined the ability of male European whip snakes, *Hierophis viridiflavus*, to follow trails of both male and female conspecifics during the breeding season. Reproductively active males discriminate pentane-extracted skin lipids from males and females on a Y-maze and greatly prefer to trail females. Males also trail other male trails in a similar fashion to results found with brown tree snakes, *Boiga irregularis* (Greene et al. 2001), but not with garter snakes, *Thamnophis sirtalis parietalis*, tested either in the laboratory (LeMaster and Mason 2001a) or in the natural environment (LeMaster et al. 2001). Greene et al. (2001) hypothesized that breeding males may trail other males if male–male combat is known to occur in that species. In this way, males may gain access to breeding females by finding and displacing a rival male and thus gain access to females nearby. Fornasiero et al. (2007) report that European whip snakes display male–male combat and thus their findings in these Y-maze experiments support this hypothesis.

Lizard trailing behavior has also been observed in Y-mazes. Male broad-headed skinks (*Eumeces laticeps*) can distinguish and follow the trails of females by detecting chemical cues through tongue-flicking and tongue-touching the substrate (Cooper and Vitt 1986b, c). Breeding male anguid slow-worms, *Anguis fragilis*, can discriminate male and female scents applied to a T-maze and choose scents of females (Gonzalo et al. 2004). They did not avoid the scents of other males, but they did explore other male scents more than their own scents, suggesting that this species is not territorial.

Sexual behavior

Snakes

In most species of snakes, sexual behavior is characterized by the male investigating the female with rapid tongue-flicking to her dorsal surface. The male then presses his chin onto the female's dorsal surface, rubbing forward towards her head while continuing to rapidly tongue-flick. The occurrence of these two behaviors simultaneously is characteristic of courtship and sex behavior. Noble (1937) first hypothesized that males detected an odor or pheromone in the skin of female garter snakes that elicited male courtship. A considerable body of work has since been conducted on the chemical ecology of red-sided garter snake, *Thamnophis sirtalis parietalis*. Field and laboratory studies have unequivocally identified, characterized and synthesized the sex attractiveness pheromone of the red-sided garter snake (*Thamnophis sirtalis parietalis*) (Mason et al. 1989, 1990; Mason 1993). Hexane extracts of skin lipids from sexually attractive females were isolated and tested in a bioassay. Liquid aliquots of fractions from these skin lipids were applied to paper towels or filter paper. Positive responses in the bioassay were scored when courting male garter snakes exhibited significantly increased tongue-flicks to the sample in conjunction with the chin-rubbing and caudocephalic wave behavior that is exclusive to courtship behavior. In additional tests, the latency to court, number of tongue-flicks elicited, and tongue-flick rate were examined (Mason et al. 1990). The nonvolatile long-chain saturated and monounsaturated methyl ketones identified are the sex pheromone of the red-sided garter snake (Fig. 2), and these compounds elicit membrane responses from vomeronsasal sensory neurons (Huang et al. 2006). This is the first identified pheromone in Class Reptilia.

Armed with the knowledge of the structure of the pheromone, studies on garter snakes went onto explore the behavioral, ecological and evolutionary consequences of pheromonal communication in shaping the life-history

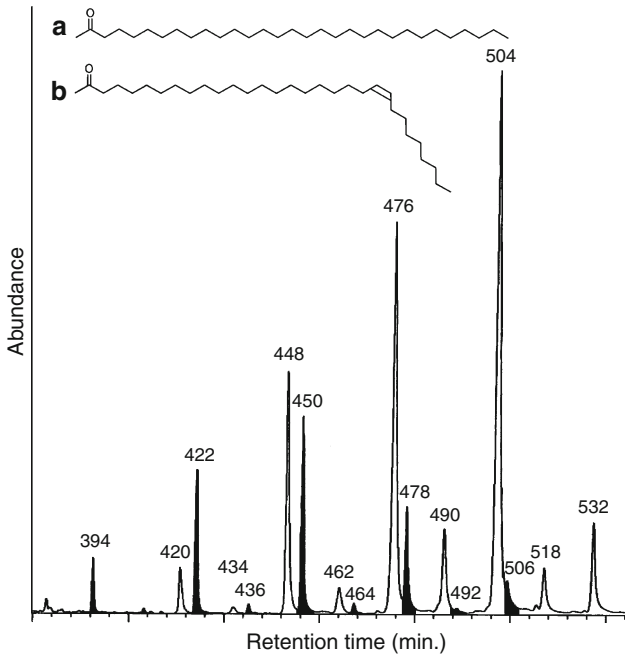

Fig. 2 Gas chromatogram (GC) of the sexual attractiveness pheromone blend from a female red-sided garter snake. The blend is composed of 17 unique methyl ketones (394–532 Da in molecular weight; unsaturated methyl ketones are unshaded peaks, saturated are shaded). Most peaks in the chromatogram occur in couplets, with the first peak in each representing the unsaturated methyl ketone (**b**), and the second is the saturated methyl ketone (**a**) of the same chain length

strategies of these model reptiles. LeMaster and Mason (2001b) showed that variation in the methyl ketone components and their relative concentrations from females collected in the same dens over multiple years were remarkably consistent. However, differences in the relative concentrations of methyl ketones between the breeding season and the nonbreeding season among these same females showed significant variation. Hibernation plays a critical role in the annual cycle of the red-sided garter snake, and Parker and Mason (2009) demonstrated that the female sex pheromone of this species changes in quantity and quality throughout laboratory-simulated hibernation, being dominated by unsaturated methyl ketones upon spring emergence. Thus, these methyl ketone pheromones are able to transmit information to males about the reproductive status of the females producing them, which is intimately associated with season (LeMaster and Mason 2001b; Parker and Mason 2009). In further studies, Shine et al. (2003) demonstrated that male garter snakes can assess the body size and body condition of females based solely on female pheromone cues alone. This is important because in red-sided garter snakes larger males prefer to mate with larger females (Shine et al. 2000d), and larger females in better body condition produce more offspring per litter in this species (Gregory 1977). Thus, the chemoreceptive system of these garter snakes provides rapid and sophisticated information about attributes of potential partners likely to predict reproductive output (Shine et al. 2003). LeMaster and Mason (2002) demonstrated the mechanism by which males are able to make this discrimination among variable female body lengths and body conditions based on the finding that the methyl ketone pheromone blend in female garter snakes becomes dominated by the longest chain, unsaturated methyl ketones with increasing body length and body condition. Finally, both male and female garter snakes choose to court and mate with individuals from their own dens versus those from different dens and males can make this choice based on detection of female pheromones alone (LeMaster and Mason 2003). Variation in the presence and relative abundance of the methyl ketone components of the garter snake pheromone blend provides information on species-specificity (Fig. 3) and even population-level differences within this genus and species.

Similar studies to those conducted in garter snakes using similar experimental methods have identified saturated, mono-, and diunsaturated methyl ketones in another colubrid, the brown tree snake of Guam (*Boiga irregularis*) (Murata et al. 1991). Greene and Mason (1998) demonstrated that male brown tree snakes respond with courtship behavior to hexane extracts of female skin lipids. Although methyl ketones have been identified in these snakes similar to those serving as sex pheromones in garter snakes, in brown tree snakes they do not serve as pheromones. Males also respond to skin lipid pheromones from males that induce combat behavior (Greene and Mason 2000). This study concluded that skin lipid pheromones from both males and females induce behavioral responses from males. Female skin lipid pheromones induce courtship behavior while male skin lipid pheromones induced combat behaviors.

Skin lipid pheromones have now been implicated or demonstrated in viperids (Weldon et al. 1992) and boids (Chiaraviglio and Briguera 2001) as well as colubrids. However, perhaps the most striking example of the role sex attractiveness pheromones play in snakes is an illuminating investigation of mating behavior in sea snakes. Said to be the least adapted of the sea snakes to a marine existence, the banded sea kraits (genus *Laticauda*) exhibit stereotypical courtship behavior only on land, involving chin-rubbing, rapid tongue-flicks, and body alignment as males attempt to court and copulate with females (Shine et al. 2002). This courtship behavior was shown to be mediated by skin lipid pheromones produced by females. Shine et al. (2002) studied the role of sex pheromones as reproductive isolating mechanisms in two species of sea kraits. The banded sea krait, *Laticauda colubrina*, and its sister species, *Laticauda frontalis*, have long been considered so

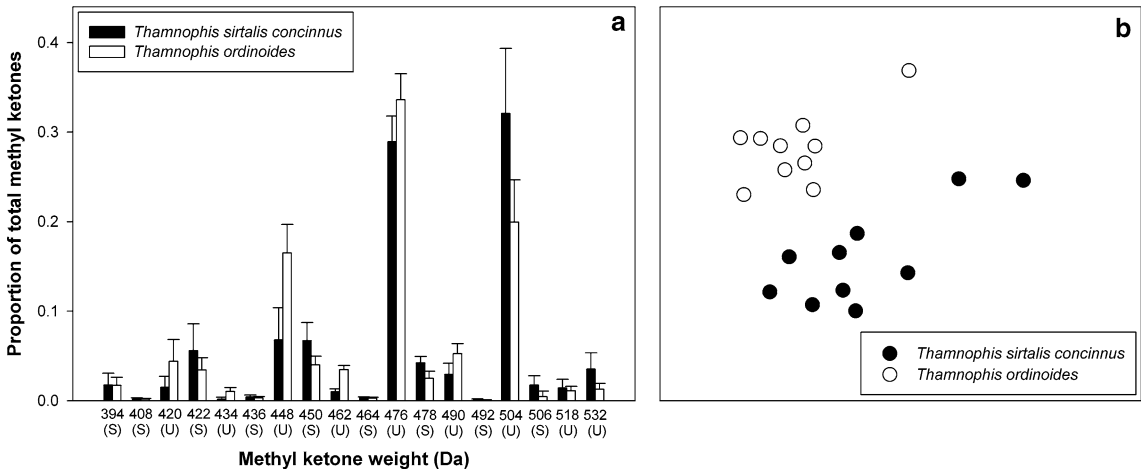

Fig. 3 **a** Relative contributions of individual methyl ketones to the overall pheromone profiles of the sympatric red-spotted garter snake (*Thamnophis sirtalis concinnus*) and northwestern garter snake (*Thamnophis ordinoides*). The relative contributions of individual methyl ketones to the overall pheromone profiles were significantly different between the two sympatric species (mrpp, $P < 0.001$). **b** Nonmetric multi-dimensional scaling (NMS) plot of individual pheromone profiles for the sympatric red-spotted garter snake and northwestern garter snake. The NMS plot graphically illustrates the similarity between individual pheromone profiles by plotting each profile as an *X*–*Y* coordinate, though the entire procedure utilizes relative proportion data for all 18 methyl ketones of the pheromone profile to generate the plot; points that are close together represent individual snakes with more similar pheromone profiles than those farther away. Of particular interest are the distinct clusters formed by the pheromone profiles of these sympatric species, demonstrating unique, species-specific composition in their pheromone profiles

similar morphologically that until recently they were considered conspecific (McCarthy 1986). The limited distribution of *L. frontalis* entirely within the broader distribution of *L. colubrina* raises the intriguing possibility that speciation in this lineage may have occurred through sympatric or peripatric processes (Shine et al. 2002). This study suggests that the current separation between the taxa is maintained by species-specificity in the pheromones that elicit male courtship behavior in both species.

Even in species of sea snakes that are entirely aquatic, skin lipid pheromone cues play an important, though slightly different role than in their more terrestrial relatives. Thus, in the turtle-headed sea snake, *Emydocephalus annulatus*, visual cues are utilized by males to locate potential mates (Shine 2005). Upon locating females, reception of female skin lipid pheromones by tongue-flicking males are necessary for males to continue courtship and mating. Aldridge et al. (2005) propose that even semi-aquatic snakes are unable to rely on nonvolatile skin lipid pheromones and propose that volatile pheromones are responsible for eliciting male courtship in the northern watersnake, *Nerodia sipedon*. They hypothesize that since males cannot trail female pheromone cues in the water, volatile pheromones may be acting in this and other semi-aquatic snakes. However, Shine and Mason (2001) and Shine et al. (2005b) demonstrated that in garter snakes, mate-searching males are likely to use any cues that provide information on the sex and reproductive status of another snake including visual cues, thermal cues, and behavioral cues. In the Aldridge et al. (2005) study, skin lipid extracts from females were not studied, so there was never a critical test of the current paradigm of sex pheromones that act in a wide variety of snake taxa. Subsequent research on this species would further the field by directly addressing the question of volatile and nonvolatile pheromones in the same study as well as the role of other sensory cues.

Inhibitory pheromones

Male garter snakes (and other snakes) deposit a gelatinous plug in the cloaca of the female immediately following mating. Sexually active males refuse to court mated females immediately after the female has mated and up to 48 h later (Ross and Crews 1977). In addition, a pheromone associated with the copulatory plug in the plains garter snake (*Thamnophis radix*) renders captive males sexually refractory for periods of 24–72 h after exposure (Ross and Crews 1978). Thus, there appear to be pheromones either in the copulatory plug or the fluids associated with its deposition that not only render mated females temporarily unattractive and unreceptive but also cause sexually active males to become sexually quiescent, ceasing courtship behavior after exposure to this pheromone (Ross and Crews 1977, 1978; Whittier et al. 1985; Mendonça and Crews 2001; O'Donnell et al. 2004). Similar studies in the Swedish viper (*Vipera berus*) did not yield any behaviors similar to those exhibited by garter

snakes (Nilson and Andrén 1982). It is still a matter of controversy whether the inhibitory pheromone is expressed in the copulatory plug, in the male's ejaculate, the female's cloaca, or some combination of the aforementioned. In field experiments where unmated attractive females were initially courted by males then subsequently treated with copulatory plugs, the copulatory fluids associated with mating, or controls (Shine et al. 2000b), the results indicate that the copulatory fluids from mating males contained the inhibitory pheromone and not the plug. The plug, therefore, seems to serve as a physical barrier to subsequent matings by rival males and/or as a simple plug to prevent the leakage of sperm from the female's cloaca.

Chemical isolation of the inhibitory pheromone in the copulatory plugs of garter snakes has not been completed. However, Mason et al. (1989, 1990) identified squalene as a major component of the male sex recognition system in garter snakes. In field tests, Shine et al. (2005a) demonstrated that squalene was able to render sexually attractive females transiently unattractive to male courtship in a similar manner to what is observed in newly mated females. In a similar fashion, in brown tree snakes which either have no copulatory plugs or very small ones, female cloacal secretions are used to repulse unwanted courtship from courting males by decreasing the intensity and duration of courtship (Greene and Mason 2000, 2003). The compounds involved in these secretions remain unknown.

Female mimicry in garter snakes

An interesting facet to the sex pheromone system of the red-sided garter snake is pheromone mimicry. During the spring breeding season and upon first emergence, male garter snakes produce the female sex pheromone and are courted as if they were females. These sexually attractive males were termed "she-males" (Mason and Crews 1985, 1986). In simultaneous choice tests, female and she-male garter snake trails were indistinguishable to courting males, suggesting that the chemical composition of the pheromone produced by she-males and females is similar or identical (LeMaster and Mason 2001a). Male garter snakes have been shown to exhibit male-oriented courtship in the laboratory (Noble 1937; Vagvolgyi and Halpern 1983), but the Manitoba red-sided garter snakes are the only ones where female mimicry is consistently observed in the field under natural conditions. Mason and Crews (1985) initially reported that she-males appear to gain a selective advantage in the highly competitive scramble mating system by confusing other males. However, the most recent work on this phenomenon has clarified findings from the earlier work. Shine et al. (2000a, c) concluded that most, if not all, newly emerged male garter snakes in the Manitoba populations are briefly courted as if they are females. Further, the evolution of this trait may not have been driven by sexual selection, but rather natural selection. Shine et al. (2001) report that male garter snakes that mimic females may benefit simply because large mating balls of warmer, courting males form around them, transferring heat to the she-males and protecting them by reducing their exposure to predators.

Results from courtship trials demonstrated that newly emerged males are attractive to other males, although not to the same degree as females (LeMaster et al. 2008). Subsequent chemical analyses of skin lipids from females and newly emerged males showed no quantitative or qualitative difference in the components constituting the sexual attractiveness pheromone. Thus, it appears that the majority of males in this species emerge with a female-like pheromone profile and subsequent, unidentified physiological changes, over the course of just 24–48 h, are responsible for the short- versus long-term nature of this phenomenon.

In seeking to understand the hormonal control of pheromone production in garter snakes, earlier investigators had identified estrogen as critical to the production and expression of the sex attractiveness pheromone in garter snakes (Crews 1976; Kubie et al. 1978). In studies of she-males, it was demonstrated that the skin of she-males expressed significantly higher levels of aromatase activity than that of normal males, suggesting that localized formation of estrogens in the skin contributes to the feminization of the skin and the production and expression of the female sexual attractiveness pheromone (Mason 1993). Current research in the Mason laboratory is clarifying the role of gonadal steroid hormones in the regulation of pheromone production both in females and males. The current working hypothesis is that the organization of the skin as a specific pheromone-producing organ occurs during development, most likely directed by steroid hormones experienced during gestation (Parker and Mason, unpublished). The results of long-term (2 years) experimental treatments (castration, hormone implantation) on pheromone production can be seen in Fig. 4.

Turtles

In turtles, the mental glands of desert tortoises (*Gopherus* spp.) have been extensively studied with regard to pheromone production. Both males and females possess a large mental gland on the head that hypertrophies during the breeding season and secretes odorous fluids (Auffenberg 1966). Both male and female gopher tortoises (*G. polyphemus*) rub their forearms against their chin glands and wave their forearms only at males during courtship (Auffenberg 1969; Weaver 1970). Presumably, males are challenging other males while females may be soliciting

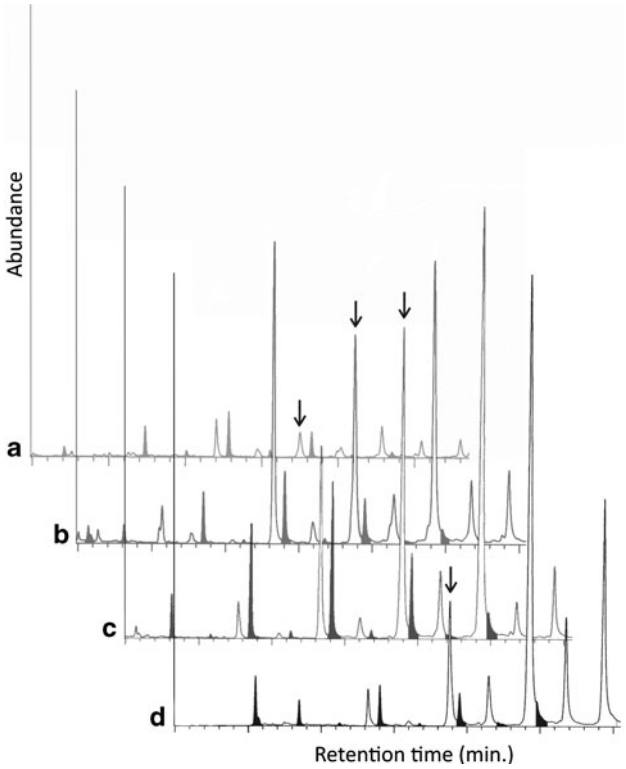

Fig. 4 GC traces from red-sided garter snakes (**a** control male, **b** castrated male, **c** control female, **d** estrogen implanted male). The relative proportions between the abundances of unsaturated methyl ketones (*unshaded peaks*) and saturated methyl ketones shifts as a result of sex or hormone treatment. The *arrow* in each chromatogram indicates the same methyl ketone (476 Da) for reference

matings from conspecific males. Gopher tortoises challenge one another by confronting an approaching individual with a head challenge (Auffenberg 1964). If the challenge is not returned (female response), the male proceeds to the posterior of the animal and sniffs its cloacal area. If the second individual is a sexually attractive female, he mounts. Thus, terrestrial tortoises probably have at least two significant sources of pheromones: the mental glands which may be most important in male-male combat, and the cloaca which provides sex pheromones that are important in mating behavior. Texas tortoises (*Gopherus berlandieri*) respond to the mental gland secretions of conspecific males with combat behavior (Rose 1970). Plaster models of tortoises painted with mental gland secretions from conspecific male tortoises elicited head bobbing and ramming of the model by males and females. Females responded primarily with head bobbing, a courtship behavior.

In aquatic turtles, courtship behavior seems to rely on pheromones produced and expressed from the cloaca. There are no experimental studies specifically investigating the existence of these chemical cues; however, anecdotal reports do suggest their presence. In Florida redbelly turtles (*Pseudemys nelsoni*) (Kramer and Fritz 1989), painted turtles (*Chrysemys picta*) (Ernst 1971), Suwanee river cooters (*P. concinna suwanniensis*) (Jackson and Davis 1972), map turtles (*Graptemys* spp.) (Ernst 1974), Florida east coast terrapin (*Malaclemys terrapin tequesta*) (Seigel 1980), mud turtles (*Kinosternon* spp.) and stinkpot turtles (*Sternotherus* spp.) (Mahmoud 1967), courting males chase females and sniff their cloacal areas, implying that chemical cues important in coordinating mating behavior are expressed by females. In European pond turtles, *Emys orbicularis*, male and female responses to pheromones were tested in simultaneous binary choice tests of tanks containing water from conspecific males or females (Poschadel et al. 2006). Females did not show a preference for either sex, but males preferred the water with female cues and, in addition, preferred chemical cues from the largest females which would be selectively advantageous since larger females produce more eggs. Males tended to avoid larger males but oriented toward chemical cues from smaller males. This may reflect social interactions in this species where males form dominance hierarchies. Similar studies in the stripe-necked terrapin, *Mauremys leprosa*, compared male and female responses to chemical cues in water both in and out of the mating season (Muñoz 2004). Outside of the mating season both sexes avoided waters with chemical cues from the opposite sex. During the breeding season, males greatly prefer water with female cues and avoid water with male cues. Females avoid water from males, but prefer water with female chemical cues. Similar results are found in simultaneous choice tests with common musk turtles, *Sternotherus odoratus* (Lewis et al. 2007).

Lizards: males

Licking behaviors and integumental chemical cues

Behavioral responses to integumental cues and cloacal cues, such as substrate rubbing and licking, are widespread in lizards (see Mason 1992 for review). Licking behaviors may be analogous to tongue-flicking in snakes when observed in a reproductive context. In an early study, male western banded geckos (*Coleonyx variegatus*) licked females repeatedly before taking a neck grip and initiating copulation attempts (Greenberg 1943). Male leopard geckos (*Eublepharis macularius*) are aggressive and territorial. Males routinely lick all individuals that they contact. If the animal contacted is a female in breeding condition, she is courted. If the animal contacted is a male, a fight quickly ensues. Sex recognition cues seem to be related to skin lipids as shedding causes territorial males to misinterpret the sex of the stimulus animals. Shedding caused territorial males to bite females as if they were males

(Mason and Gutzke 1990). Further, male *Eublepharis* responded to the chemical cues of female *Eublepharis* with significantly more tongue-flicks as well as tail vibrations which are only observed in a reproductive context. Males did not respond to females that were out of sight or when airborne chemical cues were presented, and substrate-borne female cues were more effective at eliciting courtship behavior from males than visual cues alone (Brillet 1990). In isolated chemical cues from leopard geckos, Cooper and Steele (1997) showed that males act aggressively to male scents but direct courtship to female scents. Licking behaviors in lizards are also frequently directed toward the cloacal region, especially during the breeding season. These behaviors have been noted in side-blotched lizards, *Uta stansburiana* (Ferguson 1966; Tinkle 1967), Mallee dragons, *Amphibolurus fordi* (Cogger 1978), horned lizards, *Phrynosoma platyrhinos* and *P. coronatum* (Tollestrup 1981), desert iguanas, *Dipsosaurus dorsalis* (Glinski and Krekorian 1985), *Tropidurus delanonis* (Werner 1978), and amphisbaenians, *Blanus cinereus* (Cooper et al. 1994).

Male Iberian wall lizards, *Podarcis hispanica*, can use tongue-flicks to discriminate chemical cues on cotton swabs isolated from femoral, cloacal, lateral, and upper body surfaces and to discriminate females from males, nongravid from gravid females, and conspecific males and females from heterospecific *P. bocagei carbonelli* males and females (Cooper and Perez-Mellado 2002). In behavioral trials where male *P. hispanica* were exposed to stimulus males painted with aqueous-extracted chemical cues from either familiar or unfamiliar males, resident males were less aggressive to familiar males and to unfamiliar males painted with familiar male chemical cues (López and Martín 2002). Males were more aggressive to familiar males painted with unfamiliar male chemical cues. Thus, chemical cues again seem to be used in individual recognition. Since chromatic signals are also important social cues in this species, a set of studies were conducted to examine the role of color patterns and chemoreception in sex recognition by male and female *P. hispanica* (López and Martín 2001a; López et al. 2002a). In staged encounters in the home-cage of the responding male, the results were clear. Resident males acted aggressively to unmanipulated males, males painted to look like females, males with other male chemical cues, and females with other male chemical cues. Unmanipulated females, females with other female chemical cues, and males with female cues all elicited courtship behaviors from the resident male. Similar results were found in a study of *Psammodromus algirus* (López et al. 2003b). Thus, chemosensory cues appear to be more important in sex recognition than visual cues at least at close range. An interesting aside is that some males of one species of flat lizard, *Platysaurus broadleyi* (Whiting et al. 2009) and the previously mentioned *Psammodromus algirus* (López et al. 2003b) both display behavioral female mimicry. The mimicry is only effective until the deceived male can chemically investigate the mimic, suggesting that chemical cues override behavioral cues for sex recognition in these species.

Dear enemy hypothesis: male dominance

A closely related group of Iberian lacertid lizard species has provided a robust model for understanding how chemoreception of pheromones relates to the evolution of mechanisms affecting the behavioral ecology and life history strategies of reptiles. In male Iberian rock lizards, *Lacerta monticola*, resident males directed more tongue-flicks to fecal pellet chemical cues on swabs from other males as compared to their own fecal pellets' odor cues (López et al. 1998). Males spent less time on the half of a terrarium containing fecal pellets of strange males versus a blank pellet. In addition, tongue-flick rates to fecal pellet cues of familiar males decreased as compared to unfamiliar males. Body size of the donor lizard compared to the responder is important. If the source of the fecal pellet is a larger unknown male, more tongue-flicking is needed to ascertain information. If the source of the fecal pellet is a smaller unknown male, less information is needed as that male is less of a threat (Aragon et al. 2000). Chemical cues from fecal pellets also help juvenile lizards to assess their social environment and avoid aggressive and possibly cannibalistic interactions with adult males (Moreira et al. 2008). In this study, fecal pellets from donors were extracted in dichloromethane and applied to filter papers placed on one side of a two-choice arena. Fecal chemical cues were compared between the juvenile's own cues, another juvenile's, or adult female or male cues. Juveniles could discriminate between fecal chemical cues from juveniles and adults, and they avoided remaining in substrates labeled by adult male fecal chemical cues.

In further studies, resident males were able to recognize familiar (neighbor) males versus unfamiliar males based on tongue-flicking chemical cues (feces, femoral gland secretions, skin lipids) left on the substrate in stimulus source cages for 1 week (Aragon et al. 2001a, b, c). Tongue-flick response rate was again influenced by the differences in body sizes between the donor male and the responder. When the responding male acted as a simulated intruder male into another male's previously marked territory (in the absence of the source male), the responding male displayed significantly more escape behaviors in response to unfamiliar male chemical cues than to chemical cues from familiar neighbor males (Aragon et al. 2003). The authors invoke the "Dear Enemy Hypothesis" (Fisher 1954) in their discussion of these findings. To investigate this hypothesis, Moreira et al. (2006) classified male

Iberian rock lizards as to their dominance status by staging aggressive encounters. Subsequently, individual males were then presented with femoral gland secretions on cotton swabs of their own odors or those of another male. They were also presented with chemical cues from their own copulatory plugs or those of another male. Males were able to discriminate the dominance status of other males from information in both the femoral gland secretion and the copulatory plugs. Thus, femoral gland secretions may be important in scent-marking territories, but these cues along with copulatory plug chemical cues may be important in marking the female's body and may be a different form of expression of mate-guarding. Males with higher dominance status have higher concentrations of hexadecanol and octadecanol in their femoral gland secretions and males exhibited significantly more tongue-flicks in response to these isolated synthetic compounds (Martín et al. 2007a). Males also displayed aggressive behaviors only toward hexadecanol by biting the test swabs. Because dominant males had greater T-cell-mediated immune responses, this suggests that a male's dominance status and his relative state of health (immune function) are honestly signaled to other males in femoral gland secretions.

Although cholesterol did not serve as a signal of dominance in *L. m. monticola* (=*Iberolacerta monticola*), it does appear to have this role in the closely related *L. monticola cyreni* (=*Iberolacerta cyreni*) which does not secrete hexadecanol in its femoral gland secretions (Martín and López 2007). Cholesterol in femoral glands was highly correlated with male body size, and males discriminated with increased tongue-flick rates cholesterol from other chemical compounds and responded aggressively by biting the test swabs. In staged interactions between size-matched males, males augmented with cholesterol on their bodies won the encounters as compared to controls. Whether this effect is due to higher levels of testosterone in dominant males is suggested.

Femoral glands

Many lacertilian reptiles possess epidermal structures on the ventral surface of the thigh or the precloacal abdominal area. These femoral glands exude a waxy secretion, are usually larger in males, and respond to rising androgen concentrations in the blood, especially during the breeding season (Chiu and Maderson 1975). In the earliest study, desert iguanas, *Dipsosaurus dorsalis*, tongue-touched tiles coated with femoral gland secretions significantly more than paraffin-coated tiles or controls. Since there were no consistent differences in behavioral responses to male and female secretions, the femoral pore secretions were thought to be more important in individual recognition than sex recognition (Alberts 1989).

Although technically not femoral glands, the precloacal pores of the amphisbaenian, *Blanus cinereus*, were investigated for their possible role as a pheromone source (Cooper et al. 1994). Cotton swabs rubbed over the precloacal pores of male and female *B. cinereus* and presented to males elicited significantly more tongue-flicks to female precloacal pore chemical cues than to those of males or water blanks. López and Martín (2009b) repeated these studies and found similar results, while also finding that males differed most in concentrations of squalene, and males, but not females, respond to this compound aggressively. Thus, squalene appears to serve as a male sex recognition pheromone to males but not females.

The femoral gland secretions of lizards are composed of both proteins (Alberts et al. 1992) and lipids, but the lipids are thought to be the main components with pheromonal function (Mason 1992). The chemical composition of the lipids in the femoral gland secretions have been described for relatively few lizard species (Chauhan 1986; Alberts 1990; Weldon et al. 1990; Alberts et al. 1992; Escobar et al. 2001; López and Martín 2005a,b, c, 2006; Louw et al. 2007; Gabirot et al. 2008; Kopena et al. 2009; López and Martín 2009a, b; reviewed by Weldon et al. 2008). Population and interspecific variation in these lipids has been attributed to environmental constraint selecting for different lipid components best suited to persist under varying microclimatic conditions (Escobar et al. 2003; Martín and López 2006a; López and Martín 2009a), age of the males (López and Martín 2005b; Martín and López 2006b), and as a response to simulated predation (Aragon et al. 2008).

Lizards: females

Female assessment: fluctuating asymmetries

Females gather information about potential mates through chemical cues. Female Iberian rock lizards, *L. monticola*, were exposed to male chemical cues expressed onto filter paper strips and placed in a male's home cage for 10 days (López et al. 2003a). These papers presumably contained cloacal, fecal and femoral gland secretions. Females chose to associate with the scents of older males, and their response suggested size assortative mating since larger females preferred older males while smaller females were not as selective. When offered the choice of femoral pore secretions from two different males, females chose to associate with the scents of males that display lower levels of fluctuating asymmetry in their femoral pores, the source of the pheromone (Martín and López 2000). The authors propose that males with lower fluctuating asymmetry are higher quality mates, and females can recognize this quality by chemical cues alone. In further studies, dominance statuses of male *L. monticola* were classified by

staging aggressive encounters (López et al. 2002b). Males with larger heads were the most dominant, but females did not use this cue in mate choice, rather choosing heavier males and those with more symmetrical femoral pores. Thus, factors that may benefit males in intrasexual competition may have little bearing on their mating success.

Female assessment: honest signaling of male immune status

Female Iberian wall lizards, *P. hispanica*, appear to assign more value to specific chemical components of male femoral gland secretions. Cholesterol and cholesta-5, 7-dien-3-ol are the most prevalent steroids found along with hexadecanoic and octadecenoic acid as the most prevalent fatty acids (López and Martín 2005d). Individual variation in relative proportions of these components is high in males in the population. Martín and López (2006c) showed that females tongue-flick more to synthetic cholesta-5,7-dien-3-ol and can respond positively to higher concentrations of this compound. Females also responded to cholesterol, but their response did not differ from that to the femoral gland secretion as a whole, perhaps because cholesterol accounts for more than 50% of the entire composition of the lipids in the gland material. In addition, females did not prefer male femoral gland scent marks with higher concentrations of cholesterol (López and Martín 2005d), but they did prefer substrates marked with male femoral gland secretions possessing the highest concentrations of cholesta-5,7-dien-3-ol. Why females may be so discriminating of cholesta-5,7-dien-3-ol could be due to the fact that males with greater T-cell-mediated immune responses show correspondingly higher concentrations of this steroid in their femoral gland secretions (López and Martín 2005d; López et al. 2006). Why this relationship exists is not clear. Cholesta-5,7-dien-3-ol (provitamin D_3) is a precursor of Vitamin D_3, so diverting this compound from metabolism to femoral gland secretions may be a costly way for males to honestly signal their health status to choosy females. Lizards can obtain vitamin D through their diet, so perhaps fitter males are better at acquiring vitamin D through their diet and advertise this to potential mates in their femoral gland secretions. Martín and López (2006d) tested this hypothesis by supplementing the diet of male *L. monticola*, with vitamin D and then observing that females were able to discriminate by tongue-flicking increases in the levels of provitamin D_3 in male femoral gland secretions and preferred to associate with areas scent marked by these supplemented males. If provitamin D_3 is being used by males as an honest signal of health, then activation of the immune system in males should have consequences to their femoral gland chemical signaling because males should allocate most of their provitamin D_3 to maintenance of the immune system and not secrete it as a chemical signal. López et al. (2009) challenged male *P. hispanica* immune systems with a nonpathological bacterial antigen and found that levels of cholesta-5,7-dien-3-ol (provitamin D_3) in femoral gland secretions decreased suggesting the existence of a trade-off between maintenance of a healthy immune system and expression of sexually selected chemical ornaments in these lizards.

In studies of the related, *Psammodromus algirus,* Martín et al. (2007b) correlated levels of blood-borne hemagregarine parasites and T-cell-mediated immune response in males to the attractiveness of their femoral gland secretions to females. Males with lower parasite infections and greater immune responses had femoral gland secretions with higher proportions of octadecanol and eicosanol and lower proportions of their corresponding fatty acids, octadecanoic and eicosanoic acids. Females responded with higher tongue-flick rates to secretions from healthier males and to the two long-chain alcohol compounds when tested alone. If these alcohols are being diverted from metabolism to scent gland secretions, this may be energetically costly and thus may serve as "chemical ornaments" that signal a male's potential fitness. In a similar study in the close relative *Podarcis muralis*, behavioral results were similar except that this species expressed higher concentrations of octadecenoic acid methyl ester (Martín et al. 2008).

Female assessment: preexisting sensory bias

How the chemical signaling system in these lizards evolved may be due to preexisting sensory bias in females. Martín and López (2008a) showed that food-deprived females expressed higher tongue-flick rates to both mealworm prey items and to male femoral gland secretions. Hungry females expressed stronger chemosensory responses and increased their exploratory and searching rates in response to cholesta-5,7-dien-3-ol (provitamin D_3), an essential nutrient found in insect prey items and in male femoral gland secretions. Thus, there is a correlation between prey stimulus feeding cues and male sex pheromones suggesting that a preexisting sensory bias to essential nutrients in food may have led to the evolution of this compound as a sexual signal in males as proposed by Martín and López (2010). This same reasoning was explored in the Carpetane rock lizard, *Iberolacerta cyreni* (formerly *Lacerta monticola cyreni*) (Martín and López 2010). Females show stronger chemosensory responses and prefer the scent of males with higher concentrations of cholesta-5,7-dien-3-ol (provitamin D_3) and ergosterol in their femoral gland secretions (Martín and López 2006e, 2008b). Oleic acid (*cis*-9-octadecenoic acid) is found in high concentration in femoral gland secretions of many lizards and is a major constituent of

their energetic fat reserves. Males in better body condition may advertise this to females by allocating oleic acid to their femoral gland secretions. Females were able to discriminate and preferred to associate with male scent gland secretions that had been augmented with oleic acid. Because oleic acid is also common in their insect prey, the possibility that this sexual signal evolved from a preexisting sensory bias to prey odor cues is suggested. Females also responded to cholesterol, but their response was low. Cholesterol and oleic acid concentrations were negatively related, and this may reflect the facts that cholesterol is correlated to body size in males and other males selectively respond to this steroid in femoral gland secretions. Thus, chemical signals in males may have evolved under different selection pressures: cholesterol serving as a signal of male dominance or fighting ability to other males and oleic acid serving as a sexual attractant reflecting a male's body condition.

Since male femoral gland secretions are known to affect female mate choice and the glands are under direct androgenic control and vary seasonally, Martín et al. (2007c) tested whether testosterone (T) implants affect both the concentration and chemical composition of femoral gland secretions and their attractiveness to females. By tongue-flicking, females were able to discriminate cotton swabs containing femoral gland secretions of T-implanted and controls males, but T-treatment did not affect the time spent by females on papers scented with femoral gland secretions from both T-implanted and control males. Rather, females selected to associate with papers scented by those males maintaining the highest concentrations of cholesta-5,7-dien-3-ol (pro-vitamin D_3) irrespective of treatment. T-treatment led to decreased levels of cholesta-5,7-dien-3-ol in femoral gland secretions suggesting that males face a trade-off in allocating cholesta-5,7-dien-3-ol for general metabolism or for chemical signaling to potential mates. In this lizard, levels of cholesta-5,7-dien-3-ol are positively correlated to immune function, thus perhaps only males in good condition can mount a strong immune response and produce an extravagant sexual "chemical ornament" (Martín et al. 2007c). Further study is necessary to work out these complex mechanisms.

Reptile predator/reptile prey recognition

Many reptiles exhibit stereotyped behaviors in response to predators. A common defensive behavior exhibited by over 30 taxa of pit vipers and some colubrids to snake-eating (ophiophagous) snakes is a posture known as body bridging (Weldon 1982). In this posture, a body loop can be used to strike at the attacking snake, thus disabling or driving it off. In tests examining the source of the chemical compounds eliciting this behavior, cloacal cues and lipids removed from the dorsal surface of kingsnakes, *Lampropeltis getulus*, prompted body bridging from rattlesnakes even if they were blindfolded (Bogert 1941). Methanol was used to extract chemical cues from kingsnakes, and these cues elicited body bridging from several species of pit vipers and colubrids (Weldon and Burghardt 1979). Juvenile garter snakes can distinguish between the skin lipids of the ophiophagous common kingsnake, *L. getulus*, and two nonophiophagous snakes, the western hognose snake, *Heterodon nasicus,* and plains garter snake, *Thamnophis radix*, by exhibiting increased tongue-flicks to the ophiophage skin extracts (Weldon 1982). However, this was not always the case as the prairie rattlesnake, *Crotalus viridis*, and cottonmouth, *Agkistrodon piscivorus*, gave the opposite response and increased tongue-flick rates when exposed to chemical cues from a kingsnake (*Lampropeltis* spp.) and a nonophiophagous hognose snake (*Heterodon* spp.) (Chiszar et al. 1978). These conflicting results demonstrate the need for studies in which additional behaviors are needed to supplement the tongue-flick data. Such additional behaviors should more directly address the motivational state of the animal. Tongue-flick data are often only a sign of increased activity of the animal. In any case, they are strengthened by including additional response variables.

One unusual example used tongue-flick attack scores with repeated measures and ingestive behaviors to examine the predatory response of brown tree snakes, *Boiga irregularis*, to human skin lipids (Greene et al. 2002). Brown tree snakes on the island of Guam attack and bite humans with an unusually high frequency. Most of the victims were below the age of five and most of the bites were directed to the fingers and hands of the victims suggesting that the snakes were trying to ingest the victims in the same manner they would a prey item (Fritts et al. 1990). Greene et al. (2002) presented human skin lipids, mouse skin lipids (a natural prey item) and lipid and solvent controls to brown tree snakes both in the laboratory and in the field in Australia, the species' native range. The brown tree snakes responded with significantly increased tongue-flick rates and also with ingestive bites, not defensive bites. In addition, the rates of attack to human skin lipids did not differ from the rates of attack directed toward mouse skin lipids which are a natural prey item for the snakes. The authors concluded that there may be skin lipids cues expressed in common across mammals and that brown tree snakes, being generalist predators, have evolved feeding responses to these generalized feeding cues.

Y-mazes have also been utilized to study the response of snakes to chemical cues from potential predators. Juvenile pine snakes, *Pituophis m. melanoleucus,* significantly avoid the arm of a maze treated with skin lipids from an

ophiophagous predator, the common kingsnake, *L. getulus* (Burger 1989). In further studies, soiled bedding from the cages of nonophiophagous rat snakes, *Elaphe obsoleta*, corn snakes, *E. guttata*, and ophiophagous milk snakes, *L. triangulum,* and common kingsnakes, *L. getulus*, were deposited on one arm of a Y-maze (Burger 1990; Burger et al. 1991). Juvenile pine snakes, *P. melanoleucus*, were able to discern and avoid the odors of the ophiophagous snakes and either ignored the nonophiophagous snakes or were attracted to them while preferring to follow the trails of conspecifics. These responses would be adaptive to young pine snakes that need to avoid syntopic snake-eating snakes. However, it benefits them to be able to distinguish chemical cues of predators from those of conspecifics and nonophiophagous snakes, such as corn snakes that occasionally hibernate with pine snakes. Shortly after hatching, pine snakes need to migrate to overwintering hibernacula. The ability to follow chemical cues from conspecifics and corn snakes would thus be beneficial. Corn snakes, *E. guttata* can distinguish between ophiophagous versus nonophiophagous snakes by responding with more tongue-flicks to the ophiophagous snake's skin lipids (Weldon et al. 1990).

Cloacal scent gland secretions are commonly thought to act as predator deterrents. Several mammalian predators avoid food treated with the cloacal scent gland secretions of the desert kingsnake, *L. g. splendida* (Price and LaPointe 1981). Cloacal scent gland secretions from western diamondback rattlesnakes, *Crotalus atrox,* cause coyotes and dogs to roll and rub the substrate around these secretions, although the reasons for this behavioral response are not discussed by the authors. The secretions may distract the predators long enough for the snake to escape predation (Weldon and Fagre 1989).

Lizards will also respond to chemical cues from snake predators with increased tongue-flick rates (Thoen et al. 1986). When the common lizard, *Lacerta vivipara*, was housed in the cage of lizard-eating snakes (adders, *Vipera berus*, and smooth snakes, *Coronella austriaca*), the lizards responded with higher tongue-flick rates to chemical cues from those predators than to the chemical cues of a non-lizard eater, the grass snake (*Natrix* spp.). The lizards also altered their movement patterns by moving more slowly, vibrating their tails and shaking their feet. The preceding experiments were duplicated in order to determine whether common lizards (*L. vivipara*) show innate responses to chemical cues from predatory snakes from birth, or learn them through experience (Van Damme et al. 1995). Seventeen juvenile common lizards (*L. vivipara*) were exposed to a clean cage or to a cage that had previously housed the lizard-eating adder (*V. berus*) or smooth snake (*C. austriaca*). Juveniles that had never been exposed to predator chemical cues before behaved like the animals used in the previous study by Thoen et al. (1986). One difference in the behavior of juvenile and adult lizards is that juveniles exposed to predator chemical cues almost completely refrain from basking behavior while adults do not alter their time spent in this behavior after exposure to the snake predator chemical cues (Van Damme et al. 1995). Two subspecies of Iberian wall lizard, *Podarcis hispanica,* are able to identify the snake predator Lataste's viper (*Vipera latastei*) solely through detection of chemical cues left in a previously occupied cage (Van Damme and Castilla 1996). One of the subspecies has been isolated from predation by the viper for over 100 years while the second subspecies still occurs sympatrically with the snake. The isolated subspecies still responded to chemical cues of snakes in the same fashion as did the sympatric subspecies even after 100 years of isolation.

White-throated monitor lizards, *Varanus albigularis*, eat nonvenomous snakes while venomous snakes prey on the monitor lizards. When presented with the nonvenomous sand snake, *Psammophis leightoni*, monitor lizards attack and consume the snakes (Phillips and Alberts 1992). However, when the same lizards were presented with two venomous snakes, the spitting cobra, *Naja nigricollis*, and the horned adder, *Bitis caudalis* (all are known to eat monitor lizards), the lizards never attacked these snakes. Finally, when insect prey was covered with the skins of the venomous snakes, the lizards did not attack them after investigating with tongue-flicking. However, if the insect prey were covered with the sand snake skin, or they were not investigated with tongue-flicking, then the lizards attacked and devoured the insect. Thus, integument-based chemical cues from predatory snakes are recognized by these lizards and discriminated from those of nonpredatory snakes, even if the lizards were naïve to snake predation.

The ambush smooth snake, *C. austriaca*, is able to recognize its main prey species, the wall lizard, *P. muralis*, by increasing its tongue-flick rate to lizard cloacal and femoral gland secretions applied to cotton swabs (Amo et al. 2004a). Wall lizards were also able to recognize the scent of the ambush smooth snake and avoided shelters containing its chemical cues; however, this behavior decreased after repeated exposure to the snake chemical cues (Amo et al. 2005). Wall lizards were also able to discriminate, via tongue-flicking, chemical cues from saurophagus (lizard-eating) and nonsaurophagus snakes, but they responded similarly to all three species of saurophagus snakes (Amo et al. 2004b). Wall lizards are exposed to multiple predators and respond to avian and mammalian predators by fleeing into rock crevices. However, ambush snakes use a sit-and-wait strategy while hiding within these same rock crevices. Wall lizards can detect chemical cues from ambush snakes and rapidly flee the area (Amo et al. 2004c). Lizards were then tested with

two predators, one that searches for prey in the open (simulated by the investigators) and the ambush snake that waits for prey in refuges. Upon attack, lizards in the refuge were not influenced by the presence of visual cues of an ambush snake, chemical cues from the snake or a combination. Lizards quickly hid in the shelters seeking to avoid the predator in the open regardless of any cues in the refuge. Lizards left the refuge sooner when both snake visual and chemical cues were present. In a followup experiment, Amo et al. (2004d) sought to determine whether information gained about a refuge in a first attack altered the refuge choice in a second attack. After first attacks, lizards spent more time in a refuge with snake odors suggesting that lizards may be gaining information on the age of the signal or reduce their movements to avoid visual detection if the snake were indeed present. After second attacks, lizards chose to enter refuges they previously occupied and had thus investigated. A similar experiment was conducted to determine whether wall lizards can discriminate between visual, chemical or a combination of cues from both saurophagus snakes and nonsaurophagus snakes (Amo et al. 2006). On subsequent simulated attacks, lizards spent less time in refuges with visual and chemical cues from snakes or just chemical cues alone, but they did not discriminate between the two types of snakes.

That chemosensory discrimination of chemical cues from predatory snakes is thermally dependent was examined in wall lizards, *P. muralis*, by Amo et al. (2004e). Wall lizards often hide in cold refuges where they also encounter ambush smooth snakes, *C. austriaca*. Lizards with optimal body temperatures were able to discriminate and avoid refuges marked with snake scents, while lizards with suboptimal body temperatures could not. Wall lizards also avoided snake-scented refuges regardless of whether the refuge was warm or cold (Amo et al. 2004f). Because the optimal body temperature of the snake predator is close to the suboptimal temperatures of the lizards in this study, it suggests that wall lizards may be susceptible to increased snake predation because of this thermal relationship to chemoreception.

Amphisbaenids, *Blanus cinereus*, recognize and show defensive behaviors in response to chemical cues on cotton swabs from the southern smooth snake, *Coronella girondica,* and a predatory scolopendromorph centipede, but not to a nonpredatory Bedriaga's skink, *Chalcides bedriagai* (López and Martín 2001b). Similar results were found in the slow-worm, *Anguis fragilis*, which was able to detect and discriminate chemical cues applied to cotton swabs from the predatory smooth snake *Coronella austriaca*, the nonpredatory grass snake, *Natrix natrix*, or a nonpredatory three-toed skink, *Chalcides striatus* (Cabido et al. 2004). The lizards responded with more tongue-flicks and avoidance behaviors to the scents of the predatory smooth snake but not to the other two species. Thus, chemosensory detection of predators seems to be highly developed in fossorial species of reptiles where visual cues may be limited.

Conclusions

Clearly, the study of pheromonal communication in reptiles holds great promise for elucidating the evolution of complex life histories in these important early terrestrial tetrapods. In this review, we have concentrated on those studies and methodologies that seem to be generally applicable to the investigation of specific behaviors elicited by chemical cues. We have not attempted to extensively cover all the literature, but rather have tried to cover fewer topics in greater detail. In so doing, we have, by necessity, ignored some important areas such as the role of chemoreception in the detection of insect prey in lizards or aggregation in snakes. Further, some very promising areas of research dealing with chemical signaling and pheromones have scarcely been investigated.

Chemical isolation of putative pheromones has benefitted from technological advances in analytical chemistry techniques. Gas chromatography–mass spectrometry is now approachable enough that biologists are increasingly taking advantage of these powerful analytical tools. Studies of the chemical ecology of reptiles are beginning to become as sophisticated as similar studies in insects. In the past, investigators were only able to study behaviors in response to whole secretions or crude extracts at best. However, the methodologies developed for quantifying behavioral responses to chemical cues are critically important for continuing studies of the chemical ecology of these interesting animals. To elucidate the chemical cues responsible for eliciting social behaviors, investigators must have rigorous, unequivocal bioassays. Reptiles exhibit behaviors in response to chemical cues that are relatively simple, discriminating, and tractable. They can also be extremely sensitive to chemical cues, perhaps more so than any other vertebrates.

It is also clear that there is much work to be done in exploring the chemical ecology of reptiles. The most comprehensive studies in reptiles have been conducted primarily in only two models, garter snakes and Iberian lacertid lizards. Both of these systems have capitalized on the ability to analyze chemical constituents of pheromone mixtures and conduct discriminating bioassays. As a result, these models systems have provided robust experimental paradigms to now examine the selective pressures leading to the evolution of chemical signaling and related behaviors. The complexity and concentration of chemical signal constituents have provided the components for both natural

and sexual selection mechanisms that are only now being discovered. Clearly, there are many other squamate species that should be studied, and even whole orders of reptiles have received little study in this regard. Turtles and crocodilians seem to offer exciting opportunities to study the role of pheromones in orchestrating social behaviors.

Reptiles continue to provide robust models for the study of chemical communication. Because reptiles occupy a number of widespread habitats, they bridge our understanding of the aquatic and terrestrial environments and provide a unique level of ecological and evolutionary inference. Comparisons of both the similarities and differences between chemically mediated behaviors in these groups may lead to general principles that are applicable to studies of similar behaviors in other vertebrates, such as mammals, where behaviors often result from multicomponent sensory input.

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