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Review

Condition-dependent chemosignals in reproductive behavior of lizards

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ABSTRACT

Many lizards have diverse glands that produce chemosignals used in intraspecific communication and that can have reproductive consequences. For example, information in chemosignals of male lizards can be used in intrasexual competition to identify and assess the fighting potential or dominance status of rival males either indirectly through territorial scent-marks or during agonistic encounters. Moreover, females of several lizard species “prefer” to establish or spend more time on areas scent-marked by males with compounds signaling a better health or body condition or a higher genetic compatibility, which can have consequences for their mating success and inter-sexual selection processes. We review here recent studies that suggest that the information content of chemosignals of lizards may be reliable because several physiological and endocrine processes would regulate the proportions of chemical compounds available for gland secretions. Because chemosignals are produced by the organism or come from the diet, they should reflect physiological changes, such as different hormonal levels (e.g. testosterone or corticosterone) or different health states (e.g. parasitic infections, immune response), and reflect the quality of the diet of an individual. More importantly, some compounds that may function as chemosignals also have other important functions in the organism (e.g. as antioxidants or regulating the immune system), so there could be trade-offs between allocating these compounds to attending physiological needs or to produce costly sexual “chemical ornaments”. All these factors may contribute to maintain chemosignals as condition-dependent sexual signals, which can inform conspecifics on the characteristics and state of the sender and allow making behavioral decisions with reproductive consequences. To understand the evolution of chemical secretions of lizards as sexual signals and their relevance in reproduction, future studies should examine what information the signals are carrying, the physiological processes that can maintain the reliability of the message and how diverse behavioral responses to chemosignals may influence reproductive success.

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Introduction

Many animals, including many vertebrates, use chemosignals (also often referred as pheromones, semiochemicals or signature mixtures) in intraspecific communication (Müller-Schwarze, 2006; Wyatt, 2014). However, most traditional research on chemical signals has dealt with invertebrates, mainly insects, with studies of reptiles accounting for only 1% of all published papers on this topic (Symonds and Elgar, 2008). Moreover, much of the reptile work has been focused on snakes, and in particular garter snakes (e.g. Mason et al., 1989, 1990; Parker and Mason, 2012). This paucity of studies contrasts with the well recognized observation that the scent produced by the skin and/or diverse glands of many lizard and snake species seems to have an important role in social behavior and reproduction (Martín and López, 2011; Mason and Parker, 2010).

Several specific reviews have provided a more comprehensive treatment of chemosensory senses, odor detection and odor communication in different contexts in lizards and other groups of reptiles, particularly snakes (Alberts, 1993; Cooper, 1994; Halpern, 1992; Houck, 2009; Martín and López, 2011; Mason, 1992; Mason and Parker, 2010; Schwenk, 1993, 1995; Weldon et al., 2008). Here, we review the basis for which chemosignals of lizards could be used in intraspecific communication involved in different aspects of reproduction. Recent studies suggest that the information content of chemosignals may be reliable because it is based on physiological and endocrine-dependent relationships between the proportions of some chemical compounds in gland secretions and the characteristics (e.g. age, hormone levels, physiological health state, diet) of the producers (Alberts et al., 1992a; Kopena et al., 2011; López et al., 2006, 2009b; Martín et al., 2007a). This reliability would confer chemosignals a useful role when lizards have to take behavioral decisions with reproductive consequences. For example, male lizards often scent-mark their territories using gland secretions (Martins et al., 2006), and these scent-marks may inform on the characteristics and quality of the territory owner to other males and to females, which can have consequences in intra- and inter-sexual selection processes.

Sources and characteristics of lizards' chemosignals

Although the skin can be a first source of scent in lizards that, in many cases, is enough to allow species and sex recognition by conspecifics (Mason and Gutzke, 1990; Weldon and Bangall, 1987), lizards also have several specialized glands that produce abundant chemical secretions with a potential function as chemosignals (Mason, 1992). Among these glands, many lizards in different families have femoral, precloacal or preanal glands formed by an invagination of the stratum germinativum, which forms follicular units that produce copious amounts of holocrine "waxy" secretion (Gabe and Saint-Girons, 1965). Secretions, composed of lipids and proteins, are slowly secreted to the exterior from the glands through connected epidermal structures called femoral pores, if they are located on the ventral surface of the thigh, or precloacal or preanal pores, if they are located on the anterior edge of the cloacae (Alberts, 1993; Cole, 1966; Mason, 1992). Femoral (or the analogous precloacal or preanal) pores are present in both sexes, but in many species secretions are only observed in males and especially during the mating season while female pores often have little or no secretion. The number of pores was used as a taxonomic character in the literature historically, but their functional role was little considered until recent times.

Femoral (or precloacal or preanal) secretions of lizards are composed of proteins and many lipophilic compounds that may function as chemosignals (Martín and López, 2011; Weldon et al., 2008). However, the specific chemical compounds found in secretions are only known for a few species, including several species of lacertids (Gabirot et al., 2008, 2010a; Khannoon et al., 2011a, 2011b; Kopena et al., 2009; López and Martín, 2005b, 2005c, 2006, 2009a; Martín and López, 2006c, 2006d, 2010a; Martín et al., 2013c), an African cordylid

(Louw et al., 2007), an American teiid (Martín et al., 2011), several iguanians (Alberts, 1990; Alberts et al., 1992a, 1992b; Escobar et al., 2001, 2003; Martín et al., 2013b; Weldon et al., 1990), agamids (Chauhan, 1986; Martín et al., 2013a), gekkonids (Chauhan, 1986; Khannoon, 2012) and one amphisbaenian (López and Martín, 2005d, 2009b). Among the lipophilic compounds secreted, steroids, fatty acids, alcohols, waxy esters, squalene, tocopherol, ketones and aldehydes are commonly found in different proportions (reviewed in Weldon et al., 2008). Proteins are also found in secretions as a major component, but their role in communication has been little studied (Alberts, 1990, 1991).

There is a consistent interspecific variation in composition and patterns of femoral gland secretions (Alberts, 1991; Alberts et al., 1993; Martín and López, 2011; Weldon et al., 2008), which probably reflects a strong phylogenetic effect. However, signals used in intraspecific communication are expected to evolve to maximize efficacy of the signal under given climatic conditions (Alberts, 1992; Endler and Basolo, 1998; Martín and López, 2013b). Therefore, interspecific variations in composition might also reflect different climatic conditions and, furthermore, variation is also expected between populations within the same species if they live in different environmental conditions. These interpopulational differences in secretions have been found in several lizards, which is important because sexual chemosignals are often used in conspecific recognition, and, if differences between populations are large enough, they could lead to a lack of recognition, reproductive isolation and speciation (Gabirot et al., 2010a, 2010b, 2012a, 2012b, 2013; Khannoon et al., 2013; Labra, 2011; Martín and López, 2006c; Martín et al., 2013c). However, we have no yet precise knowledge of whether interpopulational variations in chemosignals are relevant for speciation processes in lizards.

In addition, many lizards have cloacal and urodecal glands that also produce secretions that are discharged into the cloacal ducts and may also function as chemosignals (Cooper and Trauth, 1992; Trauth et al., 1987). Cloacal secretions have lipids that may be especially important in communication of lizard species that do not have femoral glands (Cooper et al., 1986; Cooper and Garstka, 1987; Cooper and Trauth, 1992; Gonzalo et al., 2004). Moreover, cloacal secretions probably impregnate the surface of feces, which allows scent-marking and intraspecific communication using feces. Fecal pellets may function as composite visual and chemical signals, allowing conspecific and kin recognition in many species (Duvall et al., 1987; Carpenter and Duvall, 1995; López et al., 1998; Bull et al., 1999a, 1999b, 2000, 2001; Aragón et al., 2000).

Behavioral observations indicate that during social encounters, lizards often use their tongues to explore via chemoreception of the body areas of conspecifics that produce chemosignals. Also, these secretions are often deposited on substrates forming scent-marks, which conspecifics readily explore using their chemoreceptive systems (see reviews in Mason and Parker, 2010; Martín and López, 2011). In these chemosensory explorations, tongue-flicking, a characteristic lizard behavior associated with the use of the vomeronasal system, is often observed (Cooper, 1994; Halpern, 1992; Schwenk, 1995). Quantification of tongue-flick rates allows researchers to determine whether different scents are discriminated using the vomeronasal system alone and whether different scents elicit tongue-flick responses of different magnitude, indicating "preferences" or "more interest" for some specific chemical stimuli (Cooper, 1994, 1998; Cooper and Burghardt, 1990). This method has been extensively used in studies of chemical ecology of lizards.

Chemosignals in reproductive behavior

Intrasexual relationships between males

Chemosignals produced by male lizards have two potential different uses in intrasexual competition with other males, either indirectly

through the production of territorial scent-marks, without the need of actual physical contact between the two males, or directly during agonistic encounters. Moreover, information previously acquired from scent-marks may also later affect behavior when two males encounter each other.

Scent-marks

Male lizards often use chemosignals (e.g. femoral gland secretions or feces) for scent-marking territories (Martín et al., 2006), and information conveyed by scent-marks per se seems to affect behavioral decisions of other males. This is possible because many lizards are able to discriminate based on chemosensory cues alone the identity (familiar vs. unfamiliar recognition, or even true individual recognition) of the producer of the chemosignal (Alberts and Werner, 1993; Aragón et al., 2000, 2001a, 2001b; Bull et al., 1999a, 2000; Carazo et al., 2007, 2008; Cooper, 1996; Labra, 2006). The ability of territorial lizards to discriminate between neighbors and non-neighbors might help to stabilize social systems by reducing the frequency and intensity of costly aggressive encounters. This is explained because between neighboring familiar males, whose previous dominance relationships have already been established, additional fights are unnecessary to know who is dominant. Moreover, even if the two males are unfamiliar (i.e. previously unknown) and have not interacted before, many lizards are able to assess from chemosignals in scent-marks the relative fighting potential of other unfamiliar males (Aragón et al., 2001a; Carazo et al., 2007; Labra, 2006). Fighting potential in lizards is often directly related to the relative body size difference between the males (e.g. López and Martín, 2001b), and the proportion of some compounds in chemosignals may be directly related to the body size (or age) of the producer male (e.g. López et al., 2006). Also, within males of similar size, differences in chemosignals may be related to the dominance status of a male (Martín et al., 2007c; Moreira et al., 2006).

After rival-recognition or rival-assessment based on scent-marks has occurred, males may decide whether to avoid or fight the opponent. A relatively subordinate individual may retreat well in advance, avoiding entering the scent-marked area of a dominant individual, thus, avoiding further costly agonistic interactions (Aragón et al., 2001c, 2003). This reinforces the idea of these lizard chemosignals functioning as honest signals in intrasexual relationships. However, assessment of rival competitive ability may also function as an indirect assessment mechanism of territory resource quality, which may attract relatively dominant males to the scent-marked territory of other males because of the benefits of exploiting that area after displacing the current owner (Carazo et al., 2007). So, it is likely, that scent-marking decisions of territorial males also vary depending on their relative fighting potential.

Agonistic interactions

Scent may be also used during direct physical interactions between males, and the information signaled by the scent seems to modulate their fighting decisions. One first step is the correct species or sex determination of a given individual found. For example, in visually similar species of North American skinks of the genus *Plestiodon* (previously included in *Eumeces*), chemosensory recognition allows males to avoid fighting with heterospecifics, directing aggression only to conspecifics, or to heterospecifics whose body odor was experimentally manipulated to resemble the other species (Cooper and Vitt, 1987). Also, many lizards are able to discriminate sex based on chemosignals, as shown by the differential tongue-flick rates to scents of males and females (e.g. Cooper and Pérez-Mellado, 2002; Cooper and Vitt, 1984). Moreover, sex identification based on chemosignals may take precedence over visual cues in some species; manipulations of the scent and color of male and female Iberian wall lizards, *Podarcis hispanica*, showed that sex discrimination at close range is based mainly on chemical cues

rather than on known sexually dimorphic visual traits (López and Martín, 2001a; López et al., 2002a). Male wall lizards direct aggression to other males even if they are painted as females or towards females impregnated with scent of males independently of their coloration. Nevertheless, coloration appears to be more important in long-distance sex recognition in these species.

The different ranges at which visual and chemical cues are perceived allow, in some species, that young or competitively inferior males adopt an alternative satellite-sneaking mating tactic by concealing their sexual identity with a female mimicry coloration. This may preclude identification and help avoid aggression by dominant territorial males, at least at long range. At close range, however, dominant males are able to use chemosignals to identify and evict satellite males, as shown by experimental manipulations of color and scent in *Psammotromus algirus* (López et al., 2003b) and Augrabies flat lizards, *Platysaurus broadley* (Whiting et al., 2009). Because the chemosignals produced by males and females very likely depend on sex-specific reproductive hormones, the scent may be a reliable signal of the sex of an individual, which might be impossible or very costly to mimic in vertebrates without negative reproductive consequences, even if other conflicting visual traits may be more easily mimicked.

Individual or familiar recognition, as explained above, is important to determine behavioral decisions to enter or stay in a territory but also during fighting itself. In wall lizards, *P. hispanica*, the second encounter and fight of the same pair of males is less aggressive, suggesting that males can recognize individual opponents and that they use this information to reach a contest outcome more quickly, thus reducing unnecessary aggression levels in subsequent interactions (López and Martín, 2001b). This recognition may be often based on chemosignals as indicated by an experimental manipulation of the scent of familiar and unfamiliar males (López and Martín, 2002). This study showed that familiarity, as indicated by the scent that has an opponent male (either natural or manipulated), determines the number of aggressive interactions in agonistic contests (i.e. less interactions occur when a male is truly familiar, or when he is unfamiliar but has been impregnated with scent of a familiar male) (López and Martín, 2002). This suggests that when two males have already interacted, their scents become familiar to both males, and that the detection in successive encounters of the familiar scent suffices to reduce their aggressive responses.

When two unfamiliar males engage in an agonistic interaction, chemosignals may also provide other types of information, such as fighting potential or dominance status, that may affect the intensity and/or outcome of the fight. In staged encounters in neutral cages between two unfamiliar and size-matched male rock lizards, *Iberolacerta cyreni*, when cholesterol in the scent of one of these males was experimentally increased, the opponent male lost more agonistic interactions against the manipulated male than in control tests (Martín and López, 2007). The proportion of cholesterol secreted by femoral glands increases with body size (López et al., 2006) and depends on sex steroid levels (Alberts et al., 1992a; Sheridan, 1994). Thus, there may be a relationship between cholesterol in scent and fighting potential (body size), motivation or aggressiveness (induced by higher T levels). This would make cholesterol in scent a potentially reliable signal of fighting potential or dominance (see below). In fact, male rock lizards, but not females, respond aggressively by biting swabs bearing cholesterol alone when these are presented close to the snout (Martín and López, 2008a). During an agonistic encounter, visual estimation of size or fight motivation should occur first at long range, but in an encounter between similarly sized males, it may be quicker and more reliable to assess a rival's fighting ability from the perceived scent such that potentially inferior males may retreat before a costly, escalated fight occurs.

In other related species of rock lizard, *Iberolacerta monticola*, the dominance status of a male is clearly related to the proportions of an alcohol (hexadecanol) in his femoral secretions (Martín et al., 2007c).

Males respond with stronger chemosensory responses and more aggression towards swabs bearing hexadecanol (and to a lesser extent to cholesterol) but not to other chemicals, according to their own dominance status; less-dominant males respond more strongly, probably because even an approaching swab “signaling” dominance is a major threat requiring a defensive response for a subordinate individual than for a dominant male. Similarly, male, but not female, spiny-footed lizards, *Acanthodactylus boskianus*, show avoidance or aggressive behavior in response to substrate scent-marks artificially made with cholesterol or blends of long-chain alcohols (e.g. hexacosanol and tetracosanol), which are components of the femoral secretions of this lizard (Khannoon et al., 2011a, 2011b).

Holders of a territory are generally more likely than intruders to escalate aggression to defend the territory given that a specific area has greater value to residents than to intruders because of familiarity with the physical and social environment (e.g. Aragón et al., 2006; Grafen, 1987; López and Martín, 2001b). Thus, to reduce costly agonistic encounters with resource holders, males should be able to identify territory owners by directly comparing the scent of substrate marks with the scent of any male they later encounter nearby, assessing whether these two scents match or not, a mechanism known as ‘scent matching’ (Gosling and McKay, 1990). This mechanism also occurs in rock lizards, *I. cyreni* (López and Martín, 2011). In an experiment where scent of males and of scent-marks were manipulated, intruding males in a territory reduced their aggressive behavior and won less interactions with males which scent matched that of scent-marks than with other non-matching individuals. This difference in behavior may be explained because a male who scent matches the scent-marks would be considered as the territory owner (López and Martín, 2011).

Female mate choice

Although the existence of female mate choice in lizards has been a controversial topic in the literature (e.g. Olsson and Madsen, 1995), it does not seem reasonable to expect that female lizards, in contrast to most animals (Johansson and Jones, 2007), would not exert any type of mate choice and passively accept any male that approached them. Some studies suggest that females select some particular territories based on habitat features, thermal or food quality rather than individual males per se (e.g. Hews, 1993), and that males would fight one another for access to the better territories, which should also allow them access to more females. However, experiments of mating behavior and genetic analyses of paternity have shown that female lizards very often accept matings and have offspring not only from the owner of the territory where the females reside but also from other extra-territory males, and that accepted males and those that sire offspring have non-random characteristics that may have been selected by females (Calsbeek and Sinervo, 2002; Fitze et al., 2010; Huyghe et al., 2014; Laloi et al., 2011; Salvador et al., 2008; While et al., 2014). One potential problem when assessing female mate choice is that most experiments do not consider whether selection of male traits that may be important for females, such as health state, occurs. In contrast, the lack of selection for some other traits (e.g. body size) was interpreted as an entire lack of female mate choice (e.g. Carazo et al., 2011). Studies where interindividual variation in chemosignals and their relationships with several male traits are considered could, however, help clarify this issue by examining female preference for the actual male traits that might be under selection.

Females of several lizard species “prefer” to occupy, or at least to spend more time on areas scent-marked by males with a better health (e.g. heightened immune response, lower parasite load) or higher “quality” (Kopena et al., 2009; López and Martín, 2005a; López et al., 2002b, 2003a; Martín and López, 2000, 2006a, 2006b), a better body condition (Huyghe et al., 2012; Martín and López, 2010b) or of a higher genetic compatibility (i.e. inbreeding avoidance) (Olsson et al., 2003). In

contrast, in many cases females do not select, nor often avoid, areas scent-marked by large dominant males or those with higher bite force capacities (Carazo et al., 2011; Huyghe et al., 2012, 2014; López et al., 2002b). These latter traits confer advantages in intrasexual selection to males when fighting with other males, but per se (e.g. if they are not related to good health) may not give any advantage to females in terms of direct benefits or inherited genetic quality. This suggests that females might instead be “interested” in male quality or condition, which can be reflected in their chemosignals as described in the sections below. By preferring to use a particular territory, females would increase their opportunities to mate with the individual male that has scent-marked that territory (Martín and López, 2012). Also, even if a female could not avoid copulating with any male found that approached her, females might discriminate some characteristics of chemosignals of males during the copulation to later bias fertilizations in favor of preferred males by cryptic female choice (e.g. Olsson et al., 1996). These strategies would have reproductive consequences for females irrespective of whether females actively select or not males, or just good territories, or irrespective of the origin of such a choice (e.g. even if females are attracted to a scent just because it resembles food; sensory bias hypothesis, see below). Therefore, selecting an area scent-marked with chemosignals reflecting male or, indirectly, territory quality may have direct and indirect benefits for females and their offspring (see Johansson and Jones, 2007) and be evolutionarily favored.

Information from male scent-marks may not only reflect male quality. Males do not hold exclusive territories, but in some cases males of different ages, social status or even with different reproductive strategies extensively overlap in their home ranges such that scent-marks of different individual males are often found close together (Aragón et al., 2004). This may provide complex information from multiple sources on the social structure of the population that may also affect female spatial decisions. For example, in an experiment controlling for signal intensity, female rock lizards preferred areas scent-marked by two males of similar age to areas of similar size marked by a single male (Martín and López, 2013a). This may increase the probability of obtaining multiple copulations with different males, which may favor sperm competition and cryptic female choice or may be a way to avoid infertile males. However, the extent of home range overlap between a territorial male and a competing younger satellite male, which can be inferred by the degree of over-marking or counter-marking of scent-marks, does not affect female preference for a given area (Martín and López, 2013a).

With respect to the chemical characteristics of male lizards' chemosignals selected by females, in the few examined species females prefer individual males with high proportions of some compounds in chemosignals that, rather than arbitrary compounds, have other important metabolic functions within the organism, such as provitamin D (López and Martín, 2005a, 2012; Martín and López, 2006a, 2006e, 2012), vitamin E (Kopena et al., 2011), or oleic acid (López and Martín, 2012; Martín and López, 2010b). This has been tested not only by correlational studies examining characteristics of chemosignals of preferred males, but also by experimentally manipulating the natural content of scent-marks, or even by testing these specific compounds alone. For example, when ergosterol (= provitamin D₂) is experimentally increased in field territories of male rock lizards, female density in those areas increases in comparison to control territories (Martín and López, 2012). When vitamin E is increased in femoral secretions of male green lizards through diet supplementation, the scent-marks of supplemented males are more attractive to females (Kopena et al., 2011). These results suggest that the potential physiological- and endocrine-dependent trade-offs that males would have when producing these chemosignals (see below) would lead to reliable sexual signals useful for female assessment of the condition of a male.

Why may chemosignals be reliable? Physiological regulation of chemosignals

Because chemosignals, such as those secreted by the femoral glands, are produced by the organism or come from the diet, they should reflect physiological changes, such as those induced by different hormone levels or different health states, and reflect the quality of the diet or the different environmental stressors (parasites, inclement weather, etc.) experienced by an individual. In addition, some compounds that may function as chemosignals also have other important functions in the organism, so there could be trade-offs between allocating these compounds to secretions or to attending physiological needs (Fig. 1). All of these factors may contribute to maintain the reliability of the chemical secretions as condition-dependent sexual signals (see Hill, 2011 for a review of potential mechanisms that can link expression of ornamental sexual traits with condition), which can inform conspecifics on the characteristics and state of the sender.

Effects of hormones on production and composition of chemosignals

Reproductive hormones

Chemosignals of many lizards are clearly implied in reproductive behavior and, thus, it is expected that their production is regulated by reproductive hormones. For example, it is well known that femoral gland secretions of male lizards depend on testosterone (T). Indirectly, it is commonly observed in most lizards that the amount of secretion is maximal during the mating season, while it decreases or disappears following the reproductive season (e.g. Alberts et al., 1992a; Martins et al., 2006). Therefore, there is a clear seasonal production of secretions by the femoral glands, which has been directly related to testicular

activity (e.g. Chiu and Maderson, 1975; Cole, 1966; Regamey, 1935; Van Wyk, 1990). Manipulative experiments showed that castration of males or supplementation of estrogen caused atrophy of femoral glands (Fergusson et al., 1985; Forbes, 1941). This atrophy can be later reversed with T supplementation. Moreover, female lizards, which usually do not have femoral glands or that have femoral pores but without secretory activity, can develop femoral glands and start to form femoral secretions after supplementation of androgens (Chiu et al., 1970; Fergusson et al., 1985). Both male and female juvenile striped plateau lizards, *Sceloporus virgatus*, increased their femoral pore secretions when they were given testosterone-filled implants (Abell, 1998).

Also, with respect to other glands that produce chemosignals, male lizards *Sceloporus spinosus* supplemented with T and estrogen seem to increase the secretory activity of cloacal glands (Forbes, 1941), and female skinks *Plestiodon laticeps* treated with estradiol seem to maximize production of the secretions of the urodaeal glands, which induces male courtship (Cooper and Garstka, 1987; Cooper et al., 1986). Female and male leopard geckos, *Eublepharis macularius*, treated with androgens evoked more attacks from conspecific males than control geckos or geckos treated with estradiol, probably due to an increase of production of chemosignals in the skin (Rhen and Crews, 2000). Similar effects of hormones on chemosignal production have been observed in snakes. For example, implanted estrogen activates the production of female skin pheromones in adult red-sided garter snakes (Parker and Mason, 2012) and, in the field, as the breeding season progresses, estradiol concentration decreases, resulting in changes in the female pheromones and subsequent loss of sexual attractivity (Uhrig et al., 2012).

The relationships between chemical compounds found in femoral gland secretions and reproductive hormones have been less studied, although there is some indirect evidence. Natural seasonal increases in circulating T levels increase the productivity of femoral secretions and the proportion of unsaturated lipids in femoral gland secretions of adult male *Iguana iguana*, which is thought to enhance volatility and detectability of secretions (Alberts et al., 1992a, 1992b). Also, there is an age-related variability in the relative proportions of lipophilic compounds in secretions of some male lizards. This variation may be directly related to age-related differences in hormonal levels in species with age-related reproductive strategies, with older-dominant-territorial males having larger testes and higher T levels than younger-subordinate-floater males (Díaz et al., 1994). Thus, femoral gland productivity, pore size, and the percentage of lipids in femoral secretions are correlated with plasma T levels in dominant, although not in subordinate, male *I. iguana*, and dominants produce more secretions than the subordinates (Alberts et al., 1992a). In the lacertid lizard, *P. algirus*, age differences in composition of femoral secretions are mainly based on an increase in older/larger lizards of some steroids of vegetal or microbial origin, such as campesterol or ergosterol and a decrease of some fatty acids (e.g. linoleic, oleic and arachidonic) (Martín and López, 2006d). In another lacertid, the spiny-footed lizard, *Acanthodactylus erythrus*, adult and subadult males also differ in the relative composition of secretions (López and Martín, 2005c). These differences are related to an increase in older males of the proportion of low volatility carboxylic acids (C₁₆–C₂₀) and dehydrocholesterol and a decrease of cholesterol, while in younger males C₉ to C₁₅ carboxylic acids are more abundant. Because the persistence of scent-marks would be more important for reproductive-territorial (= older) males than for younger-floater males, older males should increase the proportion of less volatile chemicals (e.g. higher molecular weight compounds) in their femoral secretions. In contrast, fatty acids and steroids found in femoral secretions of *I. iguana* do not differ between adult and juvenile males (Weldon et al., 1990). In lizard species that show color polymorphism, morph-specific hormone profiles (Huyghe et al., 2009; Sinervo et al., 2000) might account for the observed matched polymorphism in proportions of lipids allocated to femoral secretions in the lizards *I. monticola* (López et al., 2009a) and *Podarcis muralis* (Pellitteri-Rosa et al., 2014).

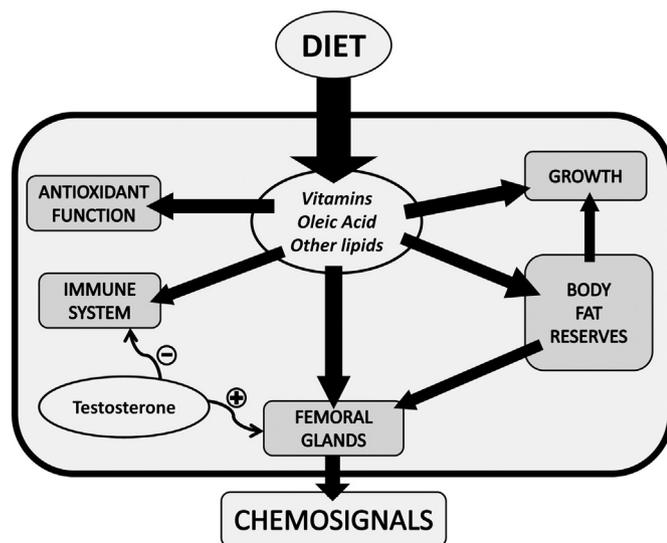


Fig. 1. A schematic representation of the physiological pathways occurring inside a lizard's body that underly regulation of the lipophilic compounds that are also used as chemosignals. Compounds acquired from the diet have to be assigned to diverse metabolic functions (antioxidant function, maintenance of the immune system, growth), stored in the body fat reserves, or secreted by diverse secretory glands to the exterior of the body as chemosignals for intraspecific communication. This may create several trade-offs in the way how compounds are differentially allocated to different functions, which are reflected in the final composition of chemosignals. On the other hand, reproductive hormones, such as testosterone, are needed to stimulate the secretory activity of glands that produce chemosignals, but testosterone has immunosuppressive effects. Stressful situations, such as inclement weather or predation risk, increase levels of corticosterone with some negative effects on metabolism. Also, parasites and other pathogens have negative effects, which result in re-allocation of compounds to the immune system. Therefore, the diet, and the metabolic, endocrine and health states of an individual will be directly reflected by characteristics of chemosignals. This will confer reliability to the messages carried by these sexual signals. Only individuals of genuine "high quality" will be able to maintain all body metabolic functions while producing enough chemical sexual ornaments of high quality.

More direct evidence of the effects of T on male chemosignals comes from experimental manipulation of T levels. Supplementation of T to male Iberian wall lizards, *P. hispanica*, increases detectability of males' scent by females (i.e. females show higher tongue-flick rates to femoral gland secretions of males with T implants in comparison with control males with empty implants) (Martín et al., 2007a). This might suggest that T increases the concentration of chemosignals in secretions. However, supplemented T also induces changes in chemical composition of the femoral gland secretions, with T-males decreasing the relative proportions of cholesta-5,7-dien-3-ol (= provitamin D₃) allocated to secretions (Martín et al., 2007a). This change was explained because variations in T levels are implicated in lizards and other taxa in modulating immunity and lipid and steroid biochemistry (e.g. Lacy et al., 2002; Sheldon and Verhulst, 1996). On the one hand, increased T levels have immunosuppressive effects, as it has been shown in related lacertid lizard species (Belluire et al., 2004; Oppliger et al., 2004). Also, there is a negative relationship between T levels and total amount of liver or plasma lipids and fat body mass in lizards and tortoises (Lacy et al., 2002; Lance et al., 2002). It is possible that T-males with decreased immunocompetence (Belluire et al., 2004), decreased body lipids (Lacy et al., 2002), increased metabolic rate (Oppliger et al., 2004) and possibly decreased feeding rates (Marler and Moore, 1991) might not be able to allocate enough cholesta-5,7-dien-3-ol to femoral secretions without detrimental effects for metabolic functions. This is explained because cholesta-5,7-dien-3-ol is a precursor of vitamin D₃, which is essential in calcium metabolism and a potent immune system modulator that may enhance innate immunity and inhibit the development of autoimmunity (Fraser, 1995; Griffin et al., 2003; Hayes et al., 2003). Otherwise, the allocation of cholesta-5,7-dien-3-ol to secretions would decrease the production of vitamin D that may be needed in metabolic functions to compensate the detrimental effects of increased T levels.

An additional experiment showed that, in mate choice trials, female *P. hispanica* do not respond differently to scent-marks of T-implanted males compared to control males, suggesting that T may increase production and detectability but not necessarily the attractiveness of chemosignals of males. Moreover, females prefer scent-marks of males that maintain higher levels of cholesta-5,7-dien-3-ol in secretions independently of the experimental manipulation (López and Martín, 2005a; Martín et al., 2007a). These results suggest that there might be a trade-off among increasing T levels to increase the amounts of chemical secretions produced, maintaining metabolism functions and producing chemosignals attractive for females (Folstad and Karter, 1992) (Fig. 1). Only males of high quality would be able to allocate in femoral secretions high proportions of chemical compounds "attractive" for females despite the immunosuppressive effects of high circulating T levels required to produce enough secretions.

Stress hormones

Stressful situations such as starvation, inclement weather, increased predation pressure or agonistic interactions can modulate some physiological aspects of animals, including lizards (Romero and Wikelski, 2001). These stress-induced physiological responses include increased circulating levels of hormones such as corticosterone, which might affect the production or composition of chemosignals. However, this possibility has rarely been studied.

Juvenile male *I. iguana* exposed to visual and chemical signals from adult dominant males show signs of chronic stress with high corticosterone levels. This leads to reduced growth rates and lower T levels in juveniles, which may explain their reduced frequencies of headbob displays (Alberts et al., 1994) and should also decrease production of chemosignals. However, social stress does not affect diameter of femoral pores in juvenile males, in spite of another study showing that pore size is positively correlated with plasma T levels in juveniles (Alberts et al., 1992a).

When predation risk level was increased experimentally by simulating multiple predator chasings (5 times per day, 7 days), relative

proportions of compounds in femoral gland secretions of male rock lizards, *I. cyreni* were affected. Thus, in disturbed, presumably more stressed lizards, proportions of two carboxylic acids (hexadecanoic and octadecanoic acid) decreased, whereas proportions of at least three steroids (campesterol, sitosterol and ergosta-5,8-dien-3-ol) increased (Aragón et al., 2008). At least two nonexclusive potential mechanisms may explain the underlying physiological mechanism mediating the observed changes. Stressful situations may lead to an increase in circulating corticosterone in vertebrates (Moore et al., 1991; Romero and Wikelski, 2001; Sapolsky et al., 2000). Glucocorticoids regulate lipid and steroid metabolism in a variety of vertebrates, including lizards (Sheridan, 1994). More specifically, corticosterone levels produced by stressful situations are associated with the rapid change of free fatty acid concentrations in blood (Harris et al., 1994; Palokangas and Vihko, 1971), which may later be reflected in femoral gland secretions composition. Alternatively, or in addition, the observed changes might be a product of increased physical activity per se during the repeated escape responses (Hancock et al., 2001), which can lead to decreased growth rates in juvenile lizards (Civantos et al., 2010). Whatever the mechanism involved, it is likely that increased corticosterone levels due to the stress of higher predation risk produce metabolic changes that may also be reflected in chemical composition of chemosignals (Fig. 1). Further studies are needed to determine the trigger and relevance for communication of these stress-induced changes in chemosignals.

Physiological health state and chemosignals

In many animals, the variations in the responses of females to scents of different males suggest that parasitic infections and health might affect the information conveyed by chemosignals (e.g. Penn and Potts, 1998; Zala et al., 2004). This may also occur in lizards. For example, there is a relationship between parasites, health state and chemicals in femoral secretions of male *P. algirus* lizards; males with higher blood parasite loads and lower immune responses (estimated from the phytohemagglutinin, PHA, injection test) have femoral gland secretions with lower proportions of two alcohols (octadecanol and eicosanol) and higher proportions of their correspondent fatty acids (octadecanoic and eicosanoic acids). Moreover, females respond with higher chemosensory tongue-flick rates to scents of healthier males, suggesting that the scents of these males are more attractive (Martín et al., 2007b). Alterations in scent due to parasite infection have been suggested to be a pathological by-product of infection, a consequence of parasite manipulation of the host, or an adaptive response to cope with infection (Penn and Potts, 1998; Zala et al., 2004). In lizards, blood parasites, such as hemogregarines, destroy erythrocytes, which results in depressed hematocrit levels, reduced hemoglobin concentrations and reduced capacity for oxygen transportation (Oppliger et al., 1996). These physiologically detrimental effects, together with the activation of the immune system to fight the infection, may constrain the allocation of certain compounds to femoral secretions (Fig. 1).

Similarly, in the wall lizard, *P. muralis*, more parasitized males and those with a lower immune response have secretions with lower proportions of some waxy esters of oleic acid and higher proportions of hexadecanoic and octadecanoic acids (Martín et al., 2008). Waxy esters in secretions might confer more stability to scent-marks under conditions where high levels of humidity increase evaporation (Alberts, 1992; Martín and López, 2006c). However, allocation of oleic acid to secretions might be costly because this is the main unsaturated fatty acid in energetic fat reserves of lizards (e.g. Simandle et al., 2001), and it helps to maintain cell membranes in a fluid state necessary for biological functioning (Funari et al., 2003). Thus, it is likely that only healthier males could divert enough oleic acid from lipid reserves or metabolism to produce more efficient scent-marks.

Also, total time spent at optimal body temperatures may affect average metabolic rates and general health of lizards and modify

chemical composition of gland secretions. The amount of time that male wall lizards, *P. muralis*, spend thermoregulating affects the chemical composition of femoral gland secretions (i.e. higher proportions of campesterol, oleic acid and hexadecanal are found in secretions of males maintained experimentally in a high quality basking treatment), and these changes can be detected by females by chemosensing (Heathcote et al., 2014). Basking time would depend on the thermal quality of the territory or the ability of a male to thermoregulate adequately, so these changes in chemosignals may inform the receiver about the quality of a male and/or his territory.

Even within healthy males, the amount of oleic acid available for secretions might be directly related to the current amount of body fat reserves (i.e. body condition) (Fig. 1). Thus, the proportions of oleic acid in femoral secretions may be a condition-dependent honest signal of body condition, a variable that has been shown to determine mating and reproductive success in lizards (Fitze et al., 2010; Hofmann and Henle, 2006; Salvador et al., 2008). This might be partly explained by the role of chemosignals as scent-marks; male rock lizards, *I. cyreni*, that produce territorial scent-marks with more oleic acid have a better body condition and might increase their mating success because females can discriminate the amounts of oleic acid with their chemosensory systems, are more attracted and spend more time in these territories (López et al., 2002b; Martín and López, 2010b).

Relationships between the strength of the immune response, as a general indicator of health, and compounds in chemosignals have been found in several lacertid lizards. For example, individual male ocellated lizards, *Lacerta lepida*, that have higher proportions of α -tocopherol (=vitamin E) in their femoral secretions have a heightened immune response (Martín and López, 2010a). Male rock lizards, *I. cyreni*, with higher immune responses allocate more cholesta-5,7-dien-3-ol (=provitamin D₃) and ergosterol (=provitamin D₂) to femoral secretions (Martín and López, 2006a). Also, male Iberian wall lizards, *P. hispanica*, with more cholesta-5,7-dien-3-ol in secretions have heightened immune responses (López and Martín, 2005a). Interestingly, these changes in chemical composition of secretions affect the attractiveness of the scent of an individual male for females (see “female mate choice” section above). As has been suggested for visual sexual signals in many animals, the energetic costs of producing and maintaining the immune response to fight against parasites may create a trade-off between the immune system and elaboration of sexual ornaments (Wedekind, 1992; Wedekind and Folstad, 1994). Therefore, only individuals in good health can mount strong defenses and produce expensive sexual ornaments attractive for females (Folstad and Karter, 1992; Hill, 2011; Sheldon and Verhulst, 1996; Westneat and Birkhead, 1998) (Fig. 1).

If chemosignals honestly reflect current health and if a trade-off between immune function and elaboration of chemical ornaments exists, activation of the immune system should reduce the “intensity” of chemical displays. This was experimentally tested by a challenge of the immune system of male lizards *P. hispanica* with a bacterial antigen (lipopolysaccharide; LPS). LPS is identified by the immune system as a pathogen that elicits an immune response without being pathogenic, and its injection to experimental male lizards results in decreased proportions of cholesta-5,7-dien-3-ol in femoral secretions in comparison with controls (López et al., 2009b), which render their scent less attractive to females (López and Martín, 2005a). This result may explain why proportions of this steroid in secretions are related to health state in this and other lacertid lizards. Similarly, visual colorful signals are negatively affected by the activation of the immune system in many birds (e.g. Faivre et al., 2003) and lizards (López et al., 2009c), which suggest a similar mechanism maintaining reliability of both visual and chemical sexual signals.

Diet and chemosignals

Some lipophilic compounds found in gland secretions of lizards are synthesized by plants or microorganisms and cannot be produced by the organism in animals (Weldon et al., 2008); thus, some of the compounds in chemosignals must have a direct dietary origin. In that case, it is very likely that changes in the diet may be reflected in the compounds found in secretions (Fig. 1). Also, it is possible that interpopulational or interspecific differences in secretions might be related to different diets or differently available food sources, as may occur in some insects (Symonds and Elgar, 2008). However, these possibilities have been scarcely tested.

Diet supplementation of α -tocopherol (= vitamin E) results in increased proportions of vitamin E in femoral gland secretions of male green lizards, *Lacerta viridis* and *L. shreiberi* (Kopena et al., 2011, 2014). This relationship between diet and secretions is important because vitamin E is the main compound in secretions of green lizards (Kopena et al., 2009; López and Martín, 2006), and females seem to prefer areas scent-marked by males with large proportions of vitamin E in secretions (Kopena et al., 2011), suggesting that this compound may function as a chemosignal probably indicating the quality of the male (i.e. the ability to obtain or select food of high quality) or his territory (i.e. the availability of high quality food within it). Within the organism, vitamin E is the main lipophilic antioxidant and radical scavenger involved in membrane defense and immuno stimulatory activity (Brigelius-Flohe and Traber, 1999). Thus, only males of high quality could allocate large amounts of vitamin E to the femoral secretions without causing a concomitant reduction in their antioxidant capacity.

In rock lizards, *I. cyreni*, diet supplementation of vitamin D, which does not appear in femoral secretions of males, allows lizards to increase proportions in secretions of a precursor of vitamin D (i.e. cholesta-5,7-dien-3-ol), which increases attractiveness of male scents to females (Martín and López, 2006b). The additional intake of dietary vitamin D may allow males to divert a greater amount of provitamin D from general metabolism (i.e. from production of vitamin D in the skin using solar UV radiation) and allocate it to secretions. Thus, a male that is able to obtain a better diet (i.e. richer in vitamin D) because of the quality of either the male or his territory might also allocate more provitamin D to secretions.

Many other compounds that are frequently found in secretions of lizards such as many steroids and fatty acids should also be dependent on the quality of the diet, and future studies should examine this potential relationship, especially when some of these compounds are known to have a communicative function in secretions.

The relationship between diet and chemosignals also may apply to the receivers of the signal. A pre-existing sensory bias for detecting and selecting chemical compounds found in food (Cooper and Pérez-Mellado, 2001; Cooper et al., 2002) might be involved in the origin of the chemosensory preferences of females for the same compounds found in male scents (López and Martín, 2012; Martín and López, 2006e, 2008a). Males could exploit this pre-existing sensory bias in females to make their scent-marks more attractive for females. In an experiment, food-deprived female lizards *I. cyreni* had increased chemosensory responses (i.e. higher tongue-flick rates) to chemical stimuli from both food and femoral secretions of males, whereas their basal chemosensory responses to water were not affected by hunger level. Therefore, hungry females seem more sensitive and react with a stronger response to chemical stimuli from both food and males than do the same females when they are well-fed (Martín and López, 2008b). Moreover, increasing experimentally the amount of a chemical attractive to females (i.e. provitamin D) in scent-marks of males has a strong effect on preferences of females when they are hungry, but less so when females are well-fed. Similarly, female swordtail fishes prefer chemical cues of well-fed males to cues of food-deprived males, but this preference is stronger in experimentally food-deprived females (Fisher and Rosenthal, 2006). Also, female red-sided garter snakes

with a higher body condition, and skin lipids from these females, stimulate more intense courtship by males (Shine et al., 2003).

This sensory bias hypothesis (Fuller et al., 2005) requires that a pre-existing tendency to respond to chemicals in food later led to the incorporation of these chemicals into males' chemosignals. Male lizards might have exploited the sensory bias of females by allocating lipids that are also found in and obtained from food items to their chemosignals. There are similar examples of attraction of females to food chemicals that are also found in male sexual traits in other animals. For example, some female moths are attracted by chemicals from fruit juices sequestered by males in their pheromones (Löfstedt et al., 1989; Nishida et al., 1982, 1985). Nuptial food gifts given by male crickets to females at mating may be a sensory trap that exploits the gustatory responses of females, favoring the selective retention of sperm of gift-giving males (Sakaluk, 2000). However, because these strategies may be differentially costly for different individual males due to the physiological trade-offs exposed above, only genuinely high quality males could allocate these compounds to chemosignals. This might allow the further evolution of the initially deceptive sensory trap into an honest signal (Kokko et al., 2003).

Conclusions and future prospects

The studies reviewed above suggest that the relationship between the production of chemosignals of lizards and vital physiological processes has favored the evolution of reliable condition-dependent sexual chemical signals. These chemosignals may have a more important role in reproduction of lizards than previously thought. We suggest that many new experiments with a wide range of species and situations are required to test this hypothesis. However, these studies should be designed with a previous understanding of the characteristics of the chemosignals involved, the exact potential messages inside them and the physiological and endocrine processes that can maintain the reliability of these messages. For this, we also need to know the proximate mechanisms of chemosignal synthesis or acquisition and secretion, including the targets of hormone action, the development of signal production and its associated behaviors and the neural substrates for processing chemosignals of both male and female receivers. Moreover, we should understand how diverse behavioral responses to chemosignals may influence reproductive success and sexual selection processes even if these behaviors are apparently unrelated to reproductive behavior and not as obvious as, for example, a direct mate choice.

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