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Review

Condition-dependent chemosignals in reproductive behavior of lizards

José Martín *, Pilar López

Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, 28006 Madrid, Spain

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ABSTRACT

This article is part of a Special Issue "Chemosignals and Reproduction".

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.

Contents

* Corresponding author. Fax: +34 91 564 5078.
E-mail address: Jose.Martin@mncn.csic.es (J. Martín).

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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 teid (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 urodeal 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