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Review

Chemosignals, hormones, and amphibian reproduction

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ABSTRACT

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

Amphibians are often thought of as relatively simple animals especially when compared to mammals. Yet the chemosignaling systems used by amphibians are varied and complex. Amphibian chemosignals are particularly important in reproduction, in both aquatic and terrestrial environments. Chemosignaling is most evident in salamanders and newts, but increasing evidence indicates that chemical communication facilitates reproduction in frogs and toads as well. Reproductive hormones shape the production, dissemination, detection, and responsiveness to chemosignals. A large variety of chemosignals have been identified, ranging from simple, invariant chemosignals to complex, variable blends of chemosignals. Although some chemosignals elicit straightforward responses, others have relatively subtle effects. Review of amphibian chemosignaling reveals a number of issues to be resolved, including: 1) the significance of the complex, individually variable blends of courtship chemosignals found in some salamanders, 2) the behavioral and/or physiological functions of chemosignals found in anuran "breeding glands", 3) the ligands for amphibian V2Rs, especially V2Rs expressed in the main olfactory epithelium, and 4) the mechanism whereby transdermal delivery of chemosignals influences behavior. To date, only a handful of the more than 7000 species of amphibians has been examined. Further study of amphibians should provide additional insight to the role of chemosignals in reproduction.

Contents

Introduction . . . 4
Reproductive strategies . . . 4
Chemosignals in urodele reproduction . . . 4
  Finding females . . . 4
  Finding males . . . 5
  Courtship and mating . . . 5
    Female-derived chemosignals . . . 5
    Male-derived chemosignals . . . 5
    Courtship chemosignals and aquatic mating . . . 5
    Courtship chemosignals and terrestrial mating . . . 6
  Male–male competition for mates . . . 7
Chemosignals in anuran reproduction . . . 7
  Finding and choosing a mate . . . 7
  Courtship and mating . . . 8
  Male–male competition for mates . . . 8
Chemosensory systems . . . 8
  Anatomy and chemoreceptors . . . 8
  Evolution of the VNO and VRs . . . 9
  Neurobiological responses to chemosignals . . . 9

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Hormonal modulation of chemical communication . . . 9
Hormonal modulation of chemosignal production . . . 9
Hormonal modulation of chemosignal delivery during courtship . . . 10
Hormonal modulation of chemo-investigation . . . 10
Sexual dimorphism and hormonal modulation of the VNO . . . 10
Conclusions . . . 11
Acknowledgments . . . 11
References . . . 11

Introduction

Amphibians are excellent models to understand vertebrate chemosignaling. Amphibian chemical communication is amenable to study at molecular, developmental, physiological, behavioral, ecological, and evolutionary levels. Urodele (salamanders, including newts) reproductive behavior is orchestrated by a rich array of chemosignals. Anurans (frogs and toads) are best known for their remarkable calling behavior during breeding, but many anuran species possess specialized glands that emit chemosignal-like substances. Amphibians are sometimes viewed as transitional between fish and reptiles, or as stand-ins for basal tetrapods, but these are not correct views. Instead, the major families of amphibians diversified very early in their evolutionary history, and modern representatives, especially anurans, have many derived characters (Duellman and Trueb, 1994; San Mauro et al., 2005). Amphibians are well known for their complex life cycles, where aquatic larvae metamorphose into terrestrial or semi-aquatic adults. However in some species, individuals are aquatic or terrestrial their entire lives while in other species, adults transition between terrestrial and aquatic life styles for breeding every year. Thus, chemical signaling can be compared and contrasted in aquatic versus terrestrial environments from a developmental perspective (within a species) and from an evolutionary perspective (across species). Another advantageous feature is that many amphibian chemosignals are peptides or proteins so there is a relatively direct link between the chemosignal and the genome. In this way, the evolution of chemosignal sequence, structure, and function can be studied.

Amphibian chemosignals function in reproductive contexts, and chemical communication is modulated by reproductive hormones. Studies of hormones and chemical communication, although not numerous, indicate that there are bi-directional interactions between hormones and chemical communication. With this review, I describe the diversity of amphibian chemical communication in an effort to identify themes and insights relevant to vertebrate chemosignaling in general. I focus on urodeles and anurans, because much less is known about chemical communication in caecilians (Gymnophiona), a secretive, little studied amphibian order (but see Reiss and Eisthen, 2008). This review is not comprehensive, and readers are referred to prior reviews for more details (Dawley, 1998; Eisthen and Polese, 2006; Houck, 2009; Kikuyama et al., 2005; Woodley, 2010, 2014). Finally, although many amphibian chemosignals have been described as pheromones, I avoid using the term pheromone because its definition and usefulness is debated (Doty, 2010; Wyatt, 2010, 2014).

Reproductive strategies

Amphibians as a group display a variety of reproductive strategies, and chemical communication typically facilitates breeding. Many amphibians are explosive breeders, where adults aggregate briefly in ponds in high densities with intense male–male competition. Other species have more prolonged breeding systems, where the availability of mates is extended and asynchronous, allowing for female choice and multiple mating (Sullivan et al., 1995). In most species of anurans, the male clasps the female in a tight embrace called amplexus that constrains her so that the male can fertilize her eggs when she spawns. In most species of anurans, fertilization is external, with males and females releasing gametes into the environment at the same time. In most species of salamanders, fertilization is internal, occurring after a male externally transfers sperm to a female via a spermatophore. Both modes of fertilization require coordination between males and females, and chemosignals coordinate with other sensory modalities like visual, tactile, vibrational, and acoustic signals to enable reproductive success.

Chemical cues contribute to mating success because they enable species, sex, and mate recognition (Johansson and Jones, 2007). Chemical cues can be transmitted over short to long ranges and can be transitory (volatile or waterborne chemosignals) or more lasting (non-volatile, substrate-bound). When compared to the energetic costs of acoustical signaling practiced by many anuran species (Taigen and Wells, 1985), chemosignals are relatively cheap to produce, although some amphibians engage in energetically costly behaviors to disperse chemosignals (Green, 1991). Among vertebrates, amphibian skin is unique, containing a rich glandular dermis with a host of functions, including chemosignal production (Toledo and Jared, 1995). Many types of molecules serve as amphibian chemosignals, including peptides, proteins, prostaglandins, terpenes, alcohols, and macrolides (Table 1).

Chemosignals in urodele reproduction

Finding females

Salamanders often gather in large numbers at breeding sites like ponds or streams, and long-range chemical cues provide information about the location, sex, and reproductive condition of conspecifics. In an early field study, male California newts swam many meters upstream toward sponges saturated with water that had previously housed breeding females (Twitty, 1955). Similar attractive properties of

Table 1
Amphibian chemosignals that have been molecularly and behaviorally characterized. See text for details.

	Type	Taxon	Sex	Detected by	Properties
Sodefrin	Peptide	Red-bellied newt	Male	VNO	Water- soluble
Silefrin	Peptide	Sword-tailed newt	Male	VNO	Water-soluble
Splendipherin	Peptide	Magnificent tree frog	Male	?	Water-soluble
15(epi)-PGF2α	F-series prostaglandins	Korean salamander	Female	MOE	Water-soluble
phoracantholide J, 8-methyl-2-nonanol	Macrolides, secondary alcohols	Mantelline frogs	Male	?	Volatile
PRF	Protein	*Plethodon* salamanders	Male	VNO	Non-volatile
PMF	Protein	Plethodontid salamanders	Male	VNO	Non-volatile
SPF	Protein	Plethodontid salamanders	Male	Non-olfactory	Non-volatile