



Review

D'scent of man: A comparative survey of primate chemosignaling in relation to sex



Christine M. Drea*

Department of Evolutionary Anthropology, Duke University, Durham, NC 27708-0383, USA
 Department of Biology, Duke University, Durham, NC 27708-0383, USA

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ABSTRACT

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

As highly visual animals, primates, in general, and Old World species (including humans), in particular, are not immediately recognized for reliance in their daily interactions on olfactory communication. Nevertheless, views on primate olfactory acuity and the pervasiveness of their scent signaling are changing, with increased appreciation for the important role of body odors in primate social and sexual behavior. All major taxonomic groups, from lemurs to humans, are endowed with scent-producing organs, and either deposit or exude a wealth of volatile compounds, many of which are known semiochemicals. This review takes a comparative perspective to illustrate the reproductive context of primate signaling, the relevant information content of their signals, the sexually differentiated investigative responses generated, and the behavioral or physiological consequences of message transmission to both signaler and receiver. Throughout, humans are placed alongside their relatives to illustrate the evolutionary continuum in the sexual selection of primate chemosignals. This ever-growing body of evidence points to a critical role of scent in guiding the social behavior and reproductive function throughout the primate order.

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* Department of Evolutionary Anthropology, Duke University, 08 Biological Sciences Bldg., Box 90383, Durham, NC 27708-0383, USA. Fax: +1 919 660 7348.
 E-mail address: cdrea@duke.edu.

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Introduction

A historical legacy

“The sense of smell is of the highest importance to the greater number of mammals ... But the sense of smell is of extremely slight service, if any [to man] ... No doubt he inherits the power in an enfeebled and so far rudimentary condition, from some early progenitor, to whom it was highly serviceable and by whom it was continually used.”

[Charles Darwin, *The Descent of Man and Selection in Relation to Sex* (1871, pp. 23–24).]

Darwin's (1871) view about the minimal importance of the sense of smell to humans, and indeed many other anthropoid primates, has been an enduring one that is reflected in the relative emphasis we, as researchers, have placed on examining our different senses. Reviews of primate chemical communication, whether dated by 30 or 40 years (e.g. Albone, 1984; Epple, 1974b; Michael et al., 1976a) or commenting on the more current state of the field (e.g. Heymann, 2006), invariably mention how little is known about the primate olfactory sense. Today's more nuanced summation may be that, although we know far more about our visual and auditory senses, we at least increasingly recognize the importance of our olfactory sense. Considering representation of a single taxonomic group – the order Primates – the body of evidence about our reliance on olfaction is not inconsequential and is ever growing. The first aim of this review is to survey part of this literature from a comparative perspective, spanning lemurs to humans. Whenever possible, concepts and illustrative examples are drawn specifically from the primate literature. In the case of multiple examples, the ordering of genera follows Fleagle (2013, p. 5), providing inclusive (albeit not exhaustive) data to further cement the importance of the olfactory sense across the order.

Sexual selection in chemical communication

“In most cases, when during the breeding-season the male alone emits a strong odour, this probably serves to excite or allure the female ... The odour emitted must be of considerable importance to the male, inasmuch as large and complex glands ... have in some cases been developed. The development of these organs is intelligible through sexual selection, if the more odoriferous males are the most successful in winning the females, and in leaving offspring to inherit their gradually-perfected glands and odours.”

[Charles Darwin, *The Descent of Man and Selection in Relation to Sex* (1871, p. 281).]

Given the complexity of mammalian chemical signals, including those produced by primates, it is likely that animal scent conveys multiple messages and serves various functions (Albone, 1984); however, as predicated by the second of Darwin's (1871) quotes above, one of these functions is in the service of reproduction. Notably, Darwin's

theory of sexual selection posits that traits used to attract or compete for the opposite sex – intersexual and intrasexual selection, respectively – should differ between the sexes, particularly when one sex competes more intensely than the other for access to reproductive partners (reviewed in Setchell and Kappeler, 2003). Insofar as olfactory characteristics (such as glands, the chemical content of their secretions, or the behavioral patterns of scent dispersal) may function as sexually selected traits (Heymann, 2003; Kappeler, 1998), they should, at a minimum, differ quantitatively or qualitatively between the sexes (Blaustein, 1981). Beyond gross sex differences, a reproductive function of scent signaling also predicts within-sex variation according to major reproductive events, such as sexual maturation, the onset of breeding seasons, or reproductive senescence, and in females, by more subtle changes accompanying the fertile phase of ovarian cycles and even pregnancy or lactation. Moreover, for olfactory traits to function as badges or ornaments, they should reliably signal one's fixed or variable quality (e.g. genotypic diversity or dominance status, respectively) in a manner detectable by conspecifics and with measurable, usually beneficial, consequences for both signaler and receiver. The second aim of this review is to examine the evidence specifically relevant to uncovering relationships between chemical communication and these various aspects of reproductive function.

Changing emphases in the study of olfactory communication

Unlike vocal or visual signals that are ephemeral and serve to communicate an immediate message often to a specific individual, olfactory signals can be longer lasting and broadcast information into the environment, typically for later detection by any animal that encounters the signal and is sensitive to its message. Early research in the field of primate olfactory communication thus grew out of a tradition focused on the unique benefit of chemical signals, namely as a means of information transfer in the absence of social interaction or contact. In this tradition, primatologists or anthropologists often focus their investigations on the territorial function of scent marking (e.g. Charles-Dominique, 1977; Mertl, 1977), for which the frequency and placement of the signal, as well as the receiver's ability to differentiate between species (e.g. Epple et al., 1987; Harrington, 1979), signaler familiarity (e.g. Smith et al., 1997) or individuals (e.g. Harrington, 1976; Mertl, 1975; Wallace, 1977), hold particular significance. Concurrently, early psychobiologists or neuroscientists were specifically interested in understanding the reproductive function of body odors and focused on identifying primate pheromones or isolating chemical attractants (e.g. Curtis et al., 1971; Epple, 1974b). More recently, researchers in this tradition have been joined by evolutionary psychologists who apply modified techniques to test for human pheromones (reviewed in: Alvergne and Lummaa, 2010; Grammer et al., 2005).

Importantly, researchers in both traditions increasingly recognized the prominent role of chemical communication in the social and sexual lives of primates (Epple, 1974b; Heymann, 2003; Schilling, 1979). Beyond a broadcast function, primate olfactory signals often serve more immediate, intra-group communicatory functions (Kappeler, 1998; Oda, 1999; Palagi et al., 2003; Scordato and Drea, 2007). For humans

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