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Photoperiod and aggression induce changes in ventral gland compounds exclusively in male Siberian hamsters

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ABSTRACT

Chemical communication is a critical component of social behavior as it facilitates social encounters, allows for evaluation of the social partner, defines territories and resources, and advertises information such as sex and physiological state of an animal. Odors provide a key source of information about the social environment to rodents; however, studies identifying chemical compounds have thus far focused primarily on few species, particularly the house mouse. Moreover, considerably less attention has been focused on how environmental factors, reproductive phenotype, and behavioral context alter these compounds outside of reproduction. We examined the effects of photoperiod, sex, and social context on chemical communication in the seasonally breeding Siberian hamster. We sampled ventral gland secretions in both male and female hamsters before and after an aggressive encounter and identified changes in a range of volatile compounds. Next, we investigated how photoperiod, reproductive phenotype, and aggression altered ventral gland volatile compound composition across the sexes. Males exhibited a more diverse chemical composition, more sex-specific volatiles, and showed higher levels of excretion compared to females. Individual volatiles were also differentially excreted across photoperiod and reproductive phenotype, as well as differentially altered in response to an aggressive encounter. Female volatile compound composition, in contrast, did not differ across photoperiods or in response to aggression. Collectively, these data contribute to a greater understanding of context-dependent changes in chemical communication in a seasonally breeding rodent.

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Introduction

Chemical communication plays an important role in the social behavior of virtually all animals. Communicative signals are used to facilitate social encounters, evaluate social partners, establish territories, and advertise information such as identity, sex, and physiological state of an animal (Bradbury and Vehrencamp, 2011). Various types of communication can occur through the transmission of visual, auditory, tactile, or chemical signals between sender and receiver. Whereas communication has been studied across many vertebrate taxa, rodents offer an excellent opportunity as a comparative model for mammalian chemical communication (Liberles, 2014; Tirindelli et al., 2009). For most species of rodents, the sense of smell is the most dominant sensory modality; therefore, olfaction provides a critical source of information about the environment for rodents (Johnston, 2003). In fact, rodents with disrupted olfaction display abnormal social behaviors; male mice fail to display territorial aggression and also mount and thrust both males and females (Chamero et al., 2011; Stowers et al., 2002), and female mice fail to display maternal aggression (Chamero et al., 2011; Del Punta et al., 2002). Three areas of research regarding the chemical complexity in rodents has received particular attention: the role of the major histocompatibility complex (MHC) in the production of chemical constituents and the functions of these constituents in mate choice (Johnston, 2003; Liberles, 2014; Tirindelli et al., 2009), the use of odors in kin recognition (Hurst et al., 2001; Johnston, 2003; Liberles, 2014; Tirindelli et al., 2009), and the functions of scent marking (Arakawa et al., 2008; Johnston, 2003; Liberles, 2014; Tirindelli et al., 2009).

The importance of olfaction for rodents is evident by studies examining consequences of olfaction deficiency (Chamero et al., 2011; Del Punta et al., 2002; Stowers et al., 2002), however, it is clear that mammalian chemical communication has increasingly focused on a relatively limited number of model species, particularly mice [but see: (Drea, 2015)]. A growing number of studies employing cutting-edge techniques and gene knock-out models have revealed an incredible diversity of chemosensory systems that mediate murine signal detection and transduction and their underlying cellular and molecular mechanisms (Liberles, 2014). For example, the G protein, Gαo is vital for sensory

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responses to cues including exocrine gland-secreting peptide, and is also essential for the display of male-male territorial aggression and maternal aggression in mice (Chamero et al., 2011). Further, distinct chemical constituents that induce behaviors have been identified in mice [e.g., aggression: (Novotny et al., 1985), dominance: (Novotny et al., 1990); reproductive partner preference: (Jemiolo et al., 1991)]. Despite these and other major advances in mice, much less is known about how changes in reproductive phenotype and social behaviors influence individual chemical constituents in non-murine mammalian models.

Siberian hamsters (*Phodopus sungorus*) are well-established for studying seasonal changes in physiology and behavior (Jasnow et al., 2000; Rendon et al., 2015b; Scherbarth and Steinlechner, 2010; Soma et al., 2015), making this species an excellent model to characterize the interactions of season, sex, and behavioral context on individual chemical constituents. First, both males and females housed in short "winter-like" days exhibit gonadal regression and display *increased* territorial aggression when compared with hamsters in long "summer-like" days (Bedrosian et al., 2012; Jasnow et al., 2000; Rendon et al., 2015b; Scotti et al., 2007). This inverse relationship between gonadal steroids and aggression allows for the disassociation of the individual effects of reproductive phenotype and aggression on chemical signaling. Second, this species exhibits a polymorphism in the reproductive response to short days in that ~30% of the population does not respond to short day lengths by inhibiting reproductive physiology and behavior. These animals, called reproductive *non-responders*, maintain fully functional reproductive capacity and appear phenotypically indistinguishable from long-day hamsters (Gorman and Zucker, 1995; Lynch et al., 1989) despite maintenance in short days. This distinct polymorphism makes it possible to dissociate the direct effects of photoperiod *per se* from the indirect effects of photoperiod on reproductive phenotype and chemical signaling. Lastly, Siberian hamsters utilize a variety of chemical signaling mechanisms, including deposition of chemical constituents in feces, and urine, sacculi, and ventral glands (Burger et al., 2001a, 2001b; Burger, 2005; Ross, 1998; Soini et al., 2005).

Among the variety of signaling mechanisms in hamsters, the ventral gland chemical trails applied to ground substrate are thought to be of particular importance for territorial marking in this species (Wynne-Edwards, 2003; Wynne-Edwards et al., 1992). Observations of Siberian hamsters in the wild have demonstrated that females use scent-marking to establish boundaries between their home-ranges (Wynne-Edwards, 2003; Wynne-Edwards et al., 1992), which corroborates laboratory studies using naturalistic housing conditions (Wynne-Edwards and Lisk, 1987). Male hamsters presented with conspecific male odors (i.e., urine, bedding material, and saccular secretions) behaviorally responded by increasing ventral gland marking (Feoktistova, 1994). More specifically, male hamsters presented with ventral gland secretions display increased investigation of the secretion in short-day photoperiods when compared to long-day photoperiods (Sokolov and Feoktistova, 1997). Further, ventral gland secretions, unlike feces and urine, which are partially metabolized, are likely to change during social encounters, providing temporally salient feedback to counterparts within a social interaction. Siberian hamster ventral compounds have previously been analyzed in males, but were undetectable in females (Burger et al., 2001b). Males have larger ventral glands when compared with females, likely explaining the sex difference in the ability to detect chemical constituents previously. In the present study, however, we used a stir bar surface sampling method (Soini et al., 2006), and reached a sufficiently low detection limit to quantify female ventral gland chemical constituents, which allowed us to examine sex differences in Siberian hamsters. By identifying and quantifying specific chemical constituents, and coupling such compounds with aggression and reproductive phenotype (i.e., breeding condition and levels of the gonadal hormone testosterone), we can clarify key sex-specific and functionally relevant chemical components contributing to chemical communication in Siberian hamsters.

In the present study, we examined photoperiodic changes in the composition and quantity of volatiles within the ventral glands of both male and female Siberian hamsters during same-sex aggressive encounters, as well as aggression-induced changes in these volatiles. We also investigated the association between the gonadal steroid testosterone (T) and production of volatile compounds within individuals. We predicted that the composition of volatiles would differ photoperiodically such that specific ventral gland compounds would be present in elevated levels in short-day when compared with long-day photoperiods. We also predicted that composition of volatiles would differ with reproductive phenotype such that some ventral gland compounds would be present in greater amounts in reproductively functional hamsters (i.e., long day and short-day non-responders) compared with non-reproductively functional hamsters (i.e., short-day responders). We further predicted that changes in volatile composition would parallel photoperiodic changes in aggression (Jasnow et al., 2000; Rendon et al., 2015b), such that gonadally regressed hamsters would produce elevated levels of specific volatile compounds closely associated with aggression. Previous work in male mice identified volatile compounds that are associated with aggression in gonadally intact males with elevated levels of T (Chamero et al., 2007; Novotny et al., 1985). Using a hamster model in which functional reproductive physiology and aggression can be dissociated, we expected to identify both T-dependent and T-independent volatile compounds associated with increased aggression. To test these predictions, we sampled secretions of the ventral gland of both male and female Siberian hamsters before and after aggressive interactions, and across photoperiodic conditions that induced seasonal phenotypes.

By using a seasonal rodent, Siberian hamsters, to study how social and non-social environmental factors and endocrine status influence chemical signaling in an ecologically relevant context, our findings will complement those that have emerged from studies in laboratory mice. Such insight will also expand our largely-fragmented knowledge of the roles and mechanisms of chemical communication in mammals. Lastly, the results from this study will contribute to our understanding of the chemical ecology of mammalian communication within an aggressive context.

Material and methods

Animal housing and photoperiodic treatment

Adult (>60 days of age) hamsters were reared and maintained under long days (light:dark, 16:8 h), and group-housed at weaning (postnatal day 18). Hamsters were given *ad libitum* access to standard laboratory rodent chow (Lab Diet 5001, PMI Nutrition) and water. Ambient temperature was maintained at 20 ± 2 °C and relative humidity was maintained at $55 \pm 5\%$. All procedures were performed in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the Bloomington Institutional Animal Care and Use Committee at Indiana University.

Prior to the start of the experiment, resident hamsters were individually housed ($n = 76$; male: $n = 51$; female: $n = 20$), whereas intruder hamsters remained group-housed (3–4 animals per cage; males, $n = 25$; females, $n = 9$) in a room on a long-day light (LD) cycle for a one-week acclimation period. Subsequently, a subset of hamsters was transferred to a room on a short-day light (SD) cycle (light:dark: 8:16 h), and the remaining hamsters were relocated to a new room on a long-day light cycle (light:dark, 16:8 h). All hamsters remained in their photoperiodic regimens for eight weeks. Reproductive phenotype was determined based on *a priori* criteria previously established for Siberian hamsters (Jasnow et al., 2000; Scotti et al., 2007). Briefly, hamsters were characterized as reproductively competent if they had functional reproductive tissues (i.e., testes for males or ovaries, uterine horns, and parametrial white adipose tissue for females), displayed no significant change in body mass (<10%), and maintained a "summer brown/

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