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Review

The response of rodents to scent marks: Four broad hypotheses

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ABSTRACT

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

Many terrestrial mammals must be able to distinguish between the myriad of scent marks they encounter in order for them to facilitate or deter direct interactions with their scent donors. I review studies that examine how rodents, mainly meadow voles (*Microtus pennsylvanicus*), respond when they encounter the scent marks of conspecifics and heterospecifics, and how context, as well as the age and condition of senders and receivers, affect their responses. The review uses four broad hypotheses to discuss the response of rodents to scent marks. The four hypotheses are as follows: 1) Scent marks convey accurate information to the receiver about the sender's state and phenotype and genotype. 2) Scent marks are individually distinct. 3) The response of receivers to scent marks is flexible and would be modulated by the cognitive abilities of receivers. 4) Receivers respond to the information contained or conveyed by the scent mark in a manner that will increase their survival and fitness. The studies cited in this review show that scent marks signal accurate information about the sender's phenotype, genotype, and condition, which receivers use to distinguish among the scent marks of different conspecifics and heterospecifics, and by doing so, receivers tailor their response accordingly to increase their survival and fitness. Thus, the four broad hypotheses may serve as guide to increase our understanding of the response of receivers to scent marks and provide a conceptual framework for future research and the development of additional hypotheses.

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Introduction

Many terrestrial mammals live in a world that is inundated with odors and scent marks (Brown and Macdonald, 1985; Wyatt, 2014). Thus, these animals must be able to distinguish between the myriad of scent marks they encounter as they move their habitat to find mates, secure resources, and avoid predation (Johnston, 1983, 1990; Roberts, 2007; Thiessen and Rice, 1976). The response of animals to scent marks remains of interest to researchers (Bossert and Wilson, 1963; Wyatt, 2014). Gosling and Roberts (2001) provided an excellent schema for the processing of scent marks in house mice (*Mus* spp.). I have extended this schema to also include the cognitive processing that animals may use to choose the appropriate response when they encounter scent marks (Franklin and Ferkin, 2006, 2008). The first step in the schema involves the detection of the scent mark, which involves sensory processes. After the scent mark is detected, it must be attended to. This involves cognitive processes that underlie or mediate the interpretation of the scent mark by the individual. Interpreting the scent mark will involve discrimination, perceptual, procedural and episodic memory, categorization, and the weighting or assessment of valence that may be attached to the sender (donor) of the scent mark by the receiver. At this

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point, the receiver may choose whether to respond to the scent mark. If the scent mark induces a response, the simplest response may depend on the receiver's determination of whether the scent mark provides information about the sender posing some type of threat or a mating opportunity (Franklin and Ferkin, 2006, 2008). If the scent mark is from a potential mate, the response would likely be to scent mark or over-mark and seek out the donor (Ferkin and Pierce, 2007; Johnston, 2003; Roberts, 2007). If the scent mark is from a familiar same-sex conspecific, it may be ignored (Hurst et al., 1993). If, however, the scent mark is from an unfamiliar same-sex conspecific, it may be investigated (Gosling, 1982). If the scent mark is from a heterospecific, the response would depend on whether or not the donor was perceived as a threat (Vlautin et al., 2010). If the threat is such that it is too costly for the individual to be detected, it would avoid scent marking or seeking out interactions with the particular donor (Apfelback et al., 1991), or it may shift its nest or area of activity away from that donor (Jedrzejewski et al., 1993). If a receiver chooses, it may deposit its own scent mark and become a sender (Ferkin and Pierce, 2007; Johnston, 2003; Wolff et al., 2002). This action would return us to the first step of the schema.

The schema provides a strong theoretical framework to examine the responses of conspecifics to scent marks. From this framework, four broad hypotheses can be derived. 1) Scent marks convey accurate information to the receiver about the sender's state, phenotype and genotype to receivers. Thus, scent marks are honest and cheat-proof signals from senders. 2) Scent marks are individually distinct. Thus, receivers will discriminate between the scent marks of different same-sex conspecifics as well as those of different opposite-sex conspecifics. 3) The response of receivers to scent marks is flexible and would be modulated by the cognitive abilities of receivers. Thus, receivers do not respond in the same manner when they encounter the scent marks of different conspecifics. Multiple responses are likely, which requires aspects of cognition. 4) Receivers respond to the information contained or conveyed by the scent mark in a manner that will increase their survival and fitness. Thus, receivers should respond in an appropriate manner to the information conveyed in the scent mark, which should also provide benefits to the receiver and potentially the sender.

I will use these four hypotheses as the focal point to discuss the response of rodents to scent marks. I have chosen studies that examined how the response of receivers to scent marks depends on their age, sex, reproductive condition, nutritional status, as well as those of senders. I will also highlight the influence of cognitive abilities such as memory and discrimination in facilitating an individual's response to scent marks. This is important because the studies I review demonstrate that an individual's response is not fixed, but it is flexible and context-dependent. I will focus on selected studies of rodents. Many of the cited experiments come from studies using meadow voles, *Microtus pennsylvanicus*, as the focal species in an attempt to include the range of situations that these animals may find themselves when they encounter the scent marks of conspecifics. The use of meadow voles was intentional because of the vast and growing knowledge of scent marking and responses to scent marks in this species (Ferkin, 2011), and because it will allow me to discuss in some detail the design, results, and interpretations of findings of some of these experiments. I try to use direct comparisons between studies of voles and other species of rodents facing similar behavioral and ecological challenges when they need to respond to scent marks of conspecifics. My approach, however, is not to be encyclopedic and comprehensive; it is much narrower and focused by using the four broad hypotheses mentioned above as the framework. My goal is to test the value of using these four broad hypotheses as a guide to increase our understanding of the responses of receivers to scent marks as well as using them as a starting point to develop and test alternative hypotheses.

Four broad hypotheses

Hypothesis 1. Scent marks convey accurate information to the receiver about the sender's state, phenotype and genotype.

Are scent marks honest signals? The answer appears to be yes. The fundamental support for this view is based on studies showing that scent marks are often products of digestion and metabolism (Albone, 1984). Thus, scent marks from sources such as the urine, saliva, and feces (Block et al., 1981; Drickamer, 1995; Zala et al., 2004), and those from specialized glands and the integument accurately reflect the sender's diet and nutritional status (Sabau and Ferkin, 2013a). Scent marks from these multiple sources likely provide unique and overlapping information about the sender (Ferkin and Johnston, 1995a; Johnston, 1990, 2008). For example, meadow voles have a highly localized pattern of sexual information on their bodies during the breeding season (Ferkin and Johnston, 1995a). The feces, anogenital area, and urine scent marks of meadow voles are attractive to opposite sex conspecifics but not to same-sex conspecifics. However, saliva/mouth scent marks of female voles were attractive to male but not to female conspecifics, whereas the posterolateral region scent marks of male voles were attractive to both male and female conspecifics. For meadow voles, the scent marks from the mouth and posterolateral region likely provide different information than that from the scent marks from feces, anogenital area, and urine (Ferkin and Johnston, 1995a).

The attractiveness of scent marks from these different sources will also vary temporally. For example, the diet and reproductive condition of senders can induce changes in the sender's hormonal milieu (Boonstra and Youson, 1982; Ebling, 1972; Johnston, 1983; Natynczuk, 1990), which are reflected in the attractiveness of its scent marks to receivers. Several studies have shown that the attractiveness of the scent marks of spontaneous ovulators varies temporally (Brown and Macdonald, 1985). The changes in the attractiveness of a sender's scent mark appear to be concomitant with changes in the responses of receivers to such marks (Ferkin, 2011; Johnston, 2008; Roberts, 2007). The scent marks of female house mice and golden hamsters may only be attractive to male conspecifics when the female is in estrus (delBarco-Trillo et al., 2009; Johnston, 1983; Kavaliers et al., 1994). Interestingly, male house mice that had their vomeronasal organs removed no longer maintained a preference for the urine marks of a female house mouse that was in estrus (Pankevich et al., 2004). It seems that without a vomeronasal organ male mice were no longer able to detect proteinaceous compounds associated with scent marks such as lipocalins and major urinary proteins, such as Darcin, Aphrodisin and Aphrodisin-like compounds, which provide accurate information about the reproductive condition of the sender to the receiver (Hurst and Beynon, 2004; Stopková et al., 2010; Roberts, 2007). Recent work on house mice has reported that major urinary proteins of conspecifics are also detected by the receiver's vomeronasal organ and the major olfactory system in a combinatorial manner (Kaur et al., 2014).

Scent-marks also provide honest signals of health (Zala et al., 2004) and nutritional status of the sender to receivers (Pierce et al., 2005). Studies have also shown that food availability during postpartum estrus and lactation affects the response of receivers to scent donors. As females enter late gestation they become relatively sedentary (Madison, 1980, 1985) and may be limited to the forage that is available in their territory (Batzli, 1985). Consequently, females during late gestation may become food restricted or food deprived. Food deprivation for 12–18 h can bring about changes in energy availability in female voles (Mustonen et al., 2012), which may affect their behavior during postpartum estrus. Nutritional stresses such as food deprivation and food restriction are an ecological challenge faced by small herbivores that live in transitional grasslands, where food sources are patchy and vary in quality across the territories of female conspecifics (Bergeron and Jodoin, 1987, 1989; Bergeron et al., 1990; Bronson, 1989; Getz, 1985).