



The effects of sex, gonadectomy and status on investigation patterns of unfamiliar conspecific urine in domestic dogs, *Canis familiaris*

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Little is known about social roles of urine marking and mark investigation in interpack communication in canids beyond mate acquisition, or of the influence of gonadal hormones on interpack urinary communication. We studied the responses of male and female, intact (nonoestrous) and gonadectomized Labrador retrievers to urine from unfamiliar dogs of the same four reproductive categories. We compared two measures of subject social status within subjects' home groups and measured the effect of subject status on urine investigation duration. We also compared the responses of subjects to urine from familiar and unfamiliar dogs. All subjects showed high interest in unfamiliar urine samples, but differed in their preference for particular unfamiliar urine types. Intact males, intact females and spayed females investigated urine from intact males and females equally, whereas neutered males investigated urine from intact males longer than urine from intact females. Urine from intact males and females elicited longer investigation than did urine from gonadectomized sources. Males showed no difference in investigation of familiar and unfamiliar urine, whereas females showed a nonsignificant tendency to investigate urine from unfamiliar dogs longer than urine from groupmates. Low-status subjects investigated urine longer than high-status subjects. Sex, status and familiarity patterns suggest that males and females, both intact and gonadectomized, have strong interest in unfamiliar urine and investigate urine to assess unfamiliar conspecifics in multiple social contexts, including mate and threat assessment. These results also suggest that gonadal hormones may affect urine investigation patterns both by increasing sexually motivated urine investigation in males and by creating signals in urine that allow assessment of potentially risky conspecifics.

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Scent marking serves to reduce and resolve conflict in many species, aiding both the marker and the mark investigator by allowing identification of high threat, high status or extremely fit competitors while avoiding direct confrontations (house mice, *Mus domesticus*: Gosling & McKay 1990; Hurst & Rich 1999; lobsters, *Homarus americanus*: Karavanich & Atema 1998a, b). Hormones can play complex roles in this process by contributing to scent mark composition and influencing marking and investigatory behaviours (see overview in Wyatt 2003). Androgens in particular can alter secretion composition (domestic dogs: Dunbar et al. 1980; grey wolves, *Canis lupus*: Raymer et al. 1986; meadow voles, *Microtus pennsylvanicus*: Ferkin & Johnston 1993) and may correspond to social status or competitive success, breeding status, and overall body condition (grey wolves: Asa et al. 1990; cichlid fish, *Oreochromis mossambicus*: Oliveira et al. 1996; naked mole-rats,

Heterocephalus glaber: Clarke & Faulkes 1998; California mice, *Peromyscus californicus*: Oyegbile & Marler 2005), thereby mediating chemical signals that honestly reflect these traits. Individuals in highly social species could assess hormonally mediated scent marks not only to avoid high-risk interactions, improve competitive success and choose quality mates, but also to form and maintain social groups and social hierarchies. However, the relations between hormones, scent marking and social status in species with long-term stable social groups and social hierarchies are poorly understood. Canids provide a unique model for studying the mechanisms, social roles and evolution of the relations between hormones, chemical communication and social status in a complex social system. As a whole, canids provide many examples of complex social behaviours (Asa 1997), and urine marking may mediate communication within and between social groups (Anisko 1976).

Domestic dogs provide an experimentally flexible model for studying both the social functions of urine marks and the detailed inter-relations between gonadal hormones, social status and inter- and intragroup chemical communication. Studies on dogs may

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improve our understanding of these relationships, guide and aid interpretation of similar studies in wild canids, and have direct applications for the management and understanding of domestic companion and free-ranging canids. These studies could especially complement studies of gonadal hormones and urine marking in closely related grey wolves (Peters & Mech 1975; Asa et al. 1985, 1990; Mertl-Millhollen et al. 1986; Raymer et al. 1986).

Most studies of urinary behaviours in dogs focus on the relations between mating, gonadal hormones and urinary behaviours. Urination rates increase in both sexes in oestrous seasons and with exogenous gonadal hormone administration (Beach 1974; Dunbar 1978; Pal 2003). Within established groups, urine presentation studies suggest that urine marking and urine investigation are important in mating and that males investigate and respond to urine marks more than females (Doty & Dunbar 1974; Dunbar 1977, 1978; Dunbar et al. 1980; Ranson & Beach 1985). However, urine from unfamiliar dogs may elicit different responses. Although aggression and competition occur among groupmates, established relationships, social hierarchies and appeasement behaviours decrease intragroup aggression (Scott & Fuller 1965; Schenkel 1967; Beach et al. 1982a). Along with habituation (Dunbar & Carmichael 1981), established social relationships may contribute to a decreased need for urine marking and investigation beyond a mating context among groupmates. Urine from unfamiliar conspecifics, however, may provide detailed and socially relevant information about prospective mates, playmates and potential threats. Until new relationships are established, the threats posed by unfamiliar conspecifics, as sources of possible aggression and as competitors, create an incentive for dogs to investigate their urine to identify or assess unfamiliar individuals.

Gonadal hormones may contribute to the use of urine marks in unfamiliar conspecific assessment in dogs. In grey wolves, social status, testosterone and urine-marking rates appear to be positively correlated during the breeding season (Peters & Mech 1975; Mertl-Millhollen et al. 1986; Asa et al. 1990), and exogenous testosterone administration affects volatile urine components (Raymer et al. 1986). The widespread gonadectomy of domestic dogs provides a large subject pool in which to test the effects of gonadal hormones on urine investigation patterns and thereby illuminate the effects of gonadal hormones on urine signals and signal reception and direct further study on the contributions of individual gonadal hormones.

In this study, we established the investigatory patterns of dogs to unfamiliar conspecific urine, assessed whether dogs investigate unfamiliar conspecific urine outside of an immediate mating context, and examined the effects of gonadectomy on the responses to urine from unfamiliar dogs. When possible, we also measured the investigatory patterns to urine from familiar versus unfamiliar dogs. We made the following predictions.

Both sexes have an incentive to establish relationships with unfamiliar conspecifics, so males and females presented with unfamiliar urine should spend equal time investigating samples.

Dogs are unusual among canids in that female oestrus is aseasonal and males maintain consistent testosterone levels and full breeding capability year-round (Asa 1997). Although we expected intact males to show a strong interest in unfamiliar female urine because of sexual interest, we expected that the need to evaluate and safely establish relationships with unfamiliar males would also affect males' investigation patterns. Since male–male aggression occurs more frequently than male–female aggression in dogs (Scott & Fuller 1965), and since males are more likely to successfully outcompete females for limited resources (Scott & Fuller 1965; Beach 1970; Beach et al. 1982a), unfamiliar males pose a greater threat than unfamiliar females to male dogs. We therefore expected that intact males would show strong interest in female urine because of sexual attraction and all males would display similarly

strong interest in male urine because of the potential threat posed by unfamiliar males with whom a relationship has yet to be established. If true, this pattern would differ from that seen in tests with groupmate urine in which males investigated intact and spayed female urine much longer than urine from intact males (Dunbar 1977, 1978; Dunbar et al. 1980).

We expected that gonadectomy of males would reduce males' sexual interest in female urine, an effect already supported for females (Dunbar 1978), but would not affect males' motivation to investigate urine to assess risk. Therefore, we predicted that neutered males, unlike intact males, would spend more time investigating intact male urine than intact female urine.

Observations on free-ranging dogs suggest that females prefer familiar dogs as mates (Daniels 1983), and studies on laboratory beagles showed that spayed females have little interest in urine from male groupmates until induced into oestrus (Dunbar 1977, 1978). Nonoestrous females may, however, consider mate quality when assessing unfamiliar males as well as considering the potential threats that both male and female unfamiliar conspecifics may pose. Females often lose control of limited resources when in competition with males (Scott & Fuller 1965; Beach 1970). However, observations of free-ranging dogs suggest that aggression from females may be more common than aggression from males (Pal et al. 1998). We expected spayed and nonoestrous females to spend equal time investigating urine from unfamiliar intact males and unfamiliar intact females as a reflection of the potential benefits and threats posed by unfamiliar dogs of both sexes.

Gonadectomy of urine donors could alter the response to urine by (1) reducing the ability of subjects to differentiate male and female urine, (2) reducing the sexual attractiveness of opposite-sex urine and/or (3) minimizing the chemical cues indicating potential social threat. If gonadectomy simply confuses the sexual identity of the urine source, the investigation duration of urine from spayed females and neutered males should be intermediate to or higher than the investigation durations of urine from intact males and females. If gonadal hormones contribute to the sexual attractiveness of female urine outside of oestrus, then intact males should investigate urine from spayed females less than urine from intact females. If donor gonadectomy renders urine less threatening either by creating urine similar to that of immature dogs and/or by interrupting the production of chemical indicators of social status or body condition, donor gonadectomy will reduce same-sex investigation by males and same-sex and opposite-sex investigation by females.

Since habituation and established social relationships may decrease interest in urine from groupmates, and studies of free-ranging dogs suggest that intergroup aggression is more common than intragroup aggression (Pal et al. 1998), we predicted that dogs would spend more time investigating urine from unfamiliar individuals than from groupmates.

We expected individuals of lower status to spend more time investigating conspecific urine than same-sex high-status individuals since low-status individuals may be more likely to be outcompeted for resources by unfamiliar dogs than high-status individuals, and may therefore be more likely to view unfamiliar conspecifics as a potential threat.

EFFECTS OF FROZEN STORAGE ON RESPONSE TO URINE

To determine the viability of using previously frozen and thawed urine samples in the subsequent studies, we first compared the responses of dogs to fresh and frozen, thawed urine samples. Previous studies have used frozen samples or overnight collection methods, but the effects of freezing urine on subsequent responses have not been tested relative to freshly collected urine.

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