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BRIEF REPORT

The Effects of Exposure to Conspecific Urine on Urine-Marking in Male and Female Degus (*Octodon degus*)[1]

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The urine-marking, defecation rates, and urine-sniffing behavior of male and female degus (*Octodon degus*) were recorded in an open field whose substrate was clean (Control Tests) or covered in conspecific urine (Experimental Tests). Animals were exposed to these conditions intermittently over a 3-mo period. Males urine-marked more than females. Both sexes exhibited increased levels of urine-marking and defecation during Control Tests as time passed. Males showed decreased urine-marking and defecation rates when exposed to the urine of conspecific males, but no changes in these behaviors with female urine. Females increased urine-marking rates when exposed to female urine, but exhibited no changes with male urine. The results are discussed with reference to degu social organization and the factors influencing scent-marking behavior.

The degu (*Octodon degus*) is a little known rat-sized South American rodent (Caviomorpha) which is diurnal and highly social. We have been studying several aspects of its social behavior, including olfactory communication (Kleiman, 1974; Wilson and Kleiman, 1974). Male and female degus scent-mark with urine using two methods. The first involves urination on inanimate objects (e.g., a rock or the substrate). The animal will depress the hindquarters while reducing forward movement, and, as the urine is expelled, the hindquarters may move from side to side. The resultant urine spot often looks like a long wavy line. In normal urination, shown especially by females, urine is excreted copiously which results in a small pool of urine. The second method of urine-marking (termed enurination) occurs during social investigation, usually when two animals are in an antiparallel position (Kleiman, 1974). One individual will spray urine on the partner's flank using a leg-lift posture; enurination often precedes separation of the pair. Urine odors are also

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transferred from individual to individual through dust-bathing in sand which contains urine.

The use of urine in scent-marking behavior has long been recognized in carnivores, such as canids (Berg, 1944; Kleiman, 1966). In rodents, however, most research on scent-marking has involved species which use secretions from specialized glands, e.g., the gerbil (ventral gland), *Meriones unguiculatus* (Thiessen *et al.*, 1970; Thiessen, 1973), and the hamster (flank gland), *Mesocricetus auratus* (Johnston, in press a,b). Urine-marking has been almost ignored, except in species exhibiting special postures for urine deposition on conspecifics (e.g., the caviomorph rodents; Kleiman, 1974). Urine-marking in more common laboratory rodents, such as mice, has only recently been investigated (Reynolds, 1971; Desjardins *et al.*, 1973; Maruniak *et al.*, 1974). Despite the relatively few investigations ot urine-marking itself, there is considerable literature on the physiological and behavioral effects of urine and other biological scents (see Eisenberg and Kleiman, 1972; Johnson, 1973; Mykytowycz, 1970).

In this study, the urine marking and urine sniffing of male and female degus were compared and the responses of animals to urine from conspecifics of the same and opposite sexes were examined. The effect on urine marking of intermittent exposure to a test cage over several months was also studied. Data were collected on defecation rates in order to determine whether defecation frequencies also altered in response to repeated testing, and the urine stimuli from conspecifics.

The degus used in these experiments were all laboratory-reared animals bred at the National Zoological Park or obtained from the University of Vermont; the colony was derived from animals brought to the Massachusetts Institute of Technology from Chile in 1964. Seven males and seven females, ranging in age at the start of testing from 10 to 16 mo (except for two older males of unknown age), were used. During the test series, males were housed singly and females as pairs in standard laboratory rabbit cages.

For testing, each individual was removed from its home cage and placed in a Plexiglas test chamber measuring 149 X 55 X 53 cm, whose floor was completely covered with a strip of corrugated cardboard. We had previously found that the cardboard absorbed the urine, but left a visible urine stain. Tests lasted 15 min, and an observer recorded the urination latency, the number of urine marks, number of fecal boluses, and the number of sniffs and total time spent sniffing urine-marks. The number of urine-marks immediately following a bout of urine-sniffing was later computed.

Tests were conducted over a 3-mo period from August to October 1972. Females were not tested during periods of vaginal opening when they might have been in estrus. Individuals were exposed to the test chamber several times a week, encountering either an unsoiled cardboard substrate (Control Tests) or a substrate which had been urine-marked by a single male or female

during a Control Test within the previous 5 hr (Experimental Tests). Feces were removed from the Control Test cardboard substrate prior to an Experimental Test.

All tests were run between 0900 and 1500 hours; the degus were on a light cycle of 12 hr of day and 12 of night, with darkness beginning at 1530 hours.

Individual degus were tested between 14 and 23 times. The minimum number of Control Tests per individual was six, and each animal was exposed to the urine of the same and the opposite sex a minimum of four times. Females were not exposed to the urine of cagemates.

During the early part of the test series, individuals were exposed mainly to heterosexual urine odor. Due to the changes in urine-marking behavior as the test series progressed (see below), it became impossible to compare directly the behavior of animals exposed to heterosexual urine with the same-sex urine. Thus, for purposes of analysis, the results of each Experimental Test have been paired with the results from a Control Test occurring within the week *prior* to the Experimental Test. For each animal, the results of at least three tests per condition have been averaged and these figures used for computing group means. The effects of frequent but intermittent exposure to the testing chamber have been analyzed by comparing the results from the first three Control Tests with the final three Control Tests for each individual. Statistical analysis was done using the two-tailed Walsh Test (Siegel, 1956) unless otherwise stated.

Table 1 presents the mean sniffing duration, urination latency, and number of urine-marks and fecal boluses for male and female degus during the initial and final three Control Tests. For both males and females, there was a significant decrease in the latency to urinate and increased urine-marking. Defecation rates also increased although the difference in these measures was only significant for females. Neither males nor females significantly increased the time spent sniffing their own urine marks.

Table 1 also indicates the degree to which degus are sexually dimorphic in these scent-marking related behaviors. However, a comparison of the mean frequencies revealed that only the differences in urine-marking behavior were significantly different ($P = .036$; Mann-Whitney U Test).

Table 2 summarizes the scent-related behaviors observed in male and female degus in response to conspecific urine. Males appeared to be most responsive to the urine of other males, exhibiting a decrease in the frequency of urine-marking and defecation and an increased urination latency. Sniffing duration significantly increased in response to both male and female urine.

Like males, the females appeared most responsive to the urine of conspecifics of the same sex, but urine-marking rates increased instead of decreasing, as with males. Females significantly increased urine-sniffing time when exposed to both male and female urine, and exhibited increased defecation rates with exposure to male urine.

TABLE 1

Mean Rates of Sniffing, Urination, and Defecation in Male and Female Degus During Habituation to an Empty Test Cage

	Urination latency (sec)	Number of urine marks	Number of fecal boluses	Sniffing time (sec)
Males				
First three tests	288.4 [a]	6.5 [a]	6.2	3.8
Last three tests	43.4 [a]	14.6 [a]	10.1	11.1
Mean	165.8	10.6	8.1	7.5
Females				
First three tests	237.5 [a]	3.3 [b]	6.7 [b]	4.1
Last three tests	59.8 [a]	5.8 [b]	12.3 [b]	5.7
Mean	148.7	4.6	9.5	4.9

[a] $P = .016$.
[b] $P = .047$.

During the testing series, it was noticed that individuals often urinated following a bout of sniffing urine deposited by themselves, or a previous animal. Calculations of the percentage of marks which followed within 10 sec of sniffing urine revealed that both males and females significantly increased the frequency of marking following a sniff in Experimental versus Control Tests (Fig. 1). However, whereas females did not appear to differentiate between male and female urine in the frequency of "sniff-marking," males tended to mark following sniffing male urine more frequently than female urine. Indeed, about 50% of urine marks were deposited after sniffing the urine of males versus 25% after sniffing female urine.

This study was conducted as part of a larger investigation of social behavior in the degu and was meant to produce baseline data on degu urine-marking to compare with data collected from more naturalistic observations. Such a combined approach is important for an understanding of the motivation and function of scent-marking behavior.

Degu males urinate more frequently than females. This dimorphism in marking is observed in young animals before 60 days of age (Wilson, unpubl.) and is common in many other mammalian species (Eisenberg and Kleiman,

TABLE 2

Mean Rates of Sniffing and Urine and Feces Deposition in Male and Female Degus in a Test Cage When Exposed to no Odor, Heterosexual Urine, and Same-Sex Urine

	Urination latency (sec)	Number of urine marks	Number of fecal boluses	Urine sniffing time (sec)	No. of subjects
Males					
Controls	17.9	17.2	12.1	8.2	6
With ♂ urine	28.4	13.3	10.4	33.1	6
Controls	255.8	7.0	7.1	6.8	7
With ♀ urine	252.3	7.9	9.5	26.7	7
Females					
Controls	63.4	5.1	11.6	5.0	7
With ♀ urine	45.9	6.7	13.0	32.0	7
Controls	135.0	4.7	6.8	5.3	7
With ♂ urine	126.3	5.0	10.7	22.7	7

[a] $P = .016$.
[b] $P = .031$.
[c] $P = .047$.
[d] $P = .062$.

1972; Johnson, 1973). That such urination in indeed scent marking is suggested by (1) the small quantity of urine released each time, (2) the fact that urination occurred in response to sniffing conspecific odors, and (3) that urine was often deposited near the marks of conspecifics.

Theissen, Blum, and Lindzey (1970) report an increase in male and female gerbils' ventral gland marking, urination, and defecation during a

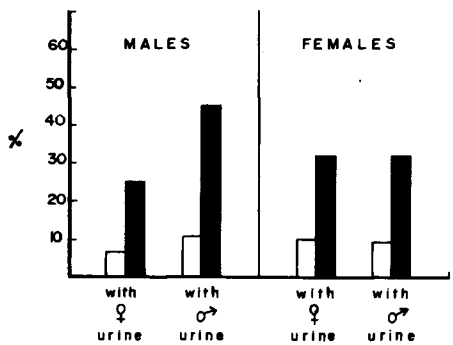

Fig. 1. Percentage of urine-marks which followed urine-sniffing within 10 sec during Control (open bars) and Experimental (closed bars) Tests in male and female degus.

testing series lasting 11 days; this change is similar to what was found for degus over a 3-mo testing period. In both species it would appear that increasing frequencies of urination and defecation may not indicate higher levels of "emotionality" as might be assumed from reports of studies of open-field behavior (Archer, 1973), since the increases occurred as the animals became more familiar with and presumably less fearful of the test cage. In fact the increasing frequencies of urination were associated with the deposition of smaller quantities of urine, greater exploratory activity, and fewer escape attempts while during the earliest tests, animals urinated infrequently and copiously as well as attempting to escape or sitting frozen in a corner. Individuals who were immobile appeared more stressed than individuals who moved around. Archer (1973) already has criticized the behaviors used as measures of "emotionality," and these findings further indicate that the results and assumptions of open-field tests must be reevaluated, especially when species are studied which may use urine and feces in the context of communication, e.g., rats and mice (Calhoun, 1963; Reynolds, 1971; Maruniak *et al.*, 1974).

Degu males exhibited an increased urination latency and a decreased urination frequency in response to the urine of other males. This is one of few recorded cases of behavioral inhibition in response to conspecific scent in mammals (Eisenberg and Kleiman, 1972; Johnson, 1973). However, although urination was inhibited, other behavioral measures suggest that the degus were highly responsive to the conspecific male urine. Sniffing rates increased significantly and the tendency to urine-mark after sniffing was enhanced. In the analysis of behaviors involved in olfactory communication, it appears that multiple measures must be taken to accurately assess the individual's response to any experimental situation.

The results of this study differ from several others (e.g., mice, Maruniak *et al.*, 1974; Desjardins *et al.*, 1973; dogs, Hart, 1974; marmosets, *Callithrix jacchus*, Epple, 1970; hamsters, Johnston, in press a, b), where exposure to conspecifics or their odor greatly increased scent-marking levels. Except for Epple (1970), the above studies used only males as subjects.

The contrasting results for the degu males may be due partly to different experimental techniques. For example, Epple (1970) and Maruniak *et al.* (1974) tested animals in what was essentially a home cage situation, while the degus were in a relatively unfamiliar cage which did not resemble the home environment. Presumably, the response to conspecific odor should depend on where it is encountered.

There should also be species differences in the responses of individuals to conspecific odor, which are dependent upon the social and spatial organization of a species. Degus are colonial and highly social. Neighboring males within a large colony commonly show mild forms of aggressive behavior toward each other and many such encounters involve direct tactile contact

(Fulk, 1974). An encounter with urine from an alien male in a relatively unfamiliar environment probably occurs rarely for a degu. This may be one explanation of the observed inhibition of urine-marking in males exposed to conspecific male odor. By contrast, hamsters, marmosets, and dogs, being less colonial and more territorial, commonly encounter the scent marks of absent male conspecifics, both familiar and unfamiliar.

The differences in the responses of male and female degus to conspecific urine were surprising but may relate to the more social nature of females. Although unfamiliar males will fight when introduced (Davis 1975), females typically exhibit more amicable behaviors during encounters both with other females and with males (Kleiman, unpubl.). Thus, a female may be less fearful and inhibited in the presence of conspecific odor. Of course, a confounding factor was the difference in housing of males and females during the study. A further series of tests where males and females are maintained in isolation is necessary to confirm this sexual difference in responsiveness.

This study is only a starting point for the analysis of the factors influencing degu urine-marking behavior, and it would not be useful to generalize from the results, especially concerning the "motivation" to urine-mark. Further studies in which marking levels are monitored in a variety of social and non-social conditions are needed both for degus and other mammals before conclusions concerning motivation can be drawn. Recent attempts to ascribe simple motivational explanations to scent-marking in mice (Maruniak *et al.*, 1974) do not consider that scent-marking levels are going to be influenced by the interaction of a variety of factors, such as age, sex, reproductive status, and social experience, as well as by immediate external stimuli.

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