SCENT COMMUNICATION IN THE
SOUTHERN PLAINS WOODRAT
(NEOTOMA MICROPUS)

by

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CHAPTER I

INTRODUCTION

Olfactory communication plays an integral role in the biology of mammals. Odor stimuli mediate a diversity of behavioral and physiological responses (Gleason and Reynierse, 1968; Bronson, 1971; Eisenberg and Kleiman, 1972; Johnson, 1973; Schultz and Tapp, 1973). Behavioral functions include territorial marking (Mykytowycz, 1968), individual recognition (Bowers and Alexander, 1967), social status recognition (Ralls, 1971), recognition of homo- and hetero-specifics (Doty, 1972), and sex recognition (Dagg and Windsor, 1971). Physiological responses to odor stimuli include the "Whitten effect," where estrous is induced in female mice after exposure to male mouse urine (Whitten, 1956); and the "Bruce effect," where pregnancy in a female mouse is terminated upon exposure to the odor of a strange male other than the mating partner or of a different laboratory strain (Bruce and Parkes, 1960; Bruce and Parrot, 1960; Parkes and Bruce, 1962).

The majority of experimental research in olfaction has been with laboratory strains of mice and rats. At least one investigator has questioned the validity of generalizing from inbred laboratory rodents to their wild counterparts (Doty, 1974). There is a paucity of information on the importance of scent communication in wild small mammals.

Urine and feces are used as chemical signals in many mammals (Eisenberg and Kleiman, 1972). Mykytowycz (1970) recently reviewed

the importance of specialized skin glands in scent communication. Male woodrats possess such a gland and it has been suggested that this ventral sebaceous gland plays a role in pheromonal production (Clarke, 1973).

Presumed scent marking behavior has been documented in woodrats (Poole, 1940; Linsdale and Tevis, 1951; Egoscue, 1962), but the source and function of these markers remains obscure. The objectives of this research were to determine if urine, feces, and sebum from the ventral gland carry olfactory signals and if so, in what way do woodrats utilize these messages.

CHAPTER II

MATERIALS AND METHODS

Forty-five southern plains woodrats (Neotoma micropus) were live-trapped 1.6 kilometers (km) south and 3.2 km east of Wink, Winkler County, Texas (elevation 853 meters). Vegetation of the area has been described by Wiley (1972), climatology by Tinkle et al. (1962), and soils by Garner (1974). Woodrats were captured with specially designed traps (Wiley, 1971) baited with rolled oats.

All woodrats were housed in wooden cages (46 X 20 X 20 centimeters, cm) in the laboratory. Woodshavings were provided as bedding material. All animals were maintained on a diet of Purina Lab Chow and water ad libitum. Animals and bedding were dusted with flea powder (Hartz Mountain Co. and Sevin) upon arrival to the laboratory. The animal room was kept on a 11D:13L photoperiod.

The olfactorium used in the study was constructed of resined plywood painted neutral gray and was similar to that described by Moore (1965). Two chambers, each measuring 39 X 60 X 58 cm, were separated by a partition. A passageway 10 X 10 cm was cut into one corner of the partition allowing access to both compartments. A treadle mechanism (see Martin, 1974) was placed in the passageway. When an animal tilted the treadle (by passing through the passageway) a mercury switch was activated, registering on a twenty channel event recorder (Esterline Angus Co.). Passes were recorded on chart paper moving at a speed of 7.5 cm per hour.

Urine was collected by placing a donor animal in a wire mesh holding cage (1.25 cm mesh, 30 X 15 X 15 cm) set over a bowl of heavy mineral oil (Squibb Co.). Fecal pellets were caught on a fine mesh screen (0.15 cm mesh) placed above the oil tray to prevent contamination of urine samples. Urine droplets were withdrawn from the oil with a syringe and a twenty gauge needle. Approximately one milliliter (ml) of urine was immediately placed on a 2.5 cm² piece of absorbent paper. The urine soaked paper was set in a round tray (4.5 cm diameter) and covered with hardware cloth. This prevented subjects from using gustatory cues to determine the contents of the scent tray. Plastic gloves were worn at all times when handling urine samples or scent trays to reduce contamination of the odor source with human scent.

Feces were collected by placing the donor animal in the holding cage that was suspended over a slanted fine mesh screen. Fecal pellets were caught on the screen, while urine passed through, thus minimizing fecal pellet contamination by urine. Approximately six to eight fecal pellets were placed in the scent trays as an odor source.

Sebum, from the ventral sebaceous gland of male woodrats, was collected by an extraction technique similar to that described by Müller-Schwarze (1969). To ensure glandular activity, donor rats were injected daily, for two weeks, with 0.8 milligrams of testosterone propionate (Sigma Chemical Co.) in sesame oil (Clarke, 1975). Ventral glands were then excised and homogenized in petroleum ether. The glandular material was filtered out and one milliliter of extract was

randomly placed in a chamber ten minutes before each experiment so that the ether would evaporate before the experiment began.

Before each experiment, a scent tray was randomly placed in each chamber. When only one chamber was scent marked (scent versus, vs., air trials), a placebo tray was placed in the other compartment. In tests with urine as the odor source, the placebo was an identical scent tray, but the paper insert was saturated with one milliliter of water. When feces were used as the odor source, the placebo was a scent tray containing dark stones the same size and shape as fecal pellets. This minimized the possibility that subjects employed visual cues. After an olfactorium was properly marked, a subject was randomly placed in one of the compartments.

When all animals were in the olfactoria (generally, six were run simultaneously), the event recorder was started and the room left dark and undisturbed for the duration of the ten hour trial. Upon completion, the animals were returned to their cages and the olfactoria thoroughly washed with hot water and detergent (Vestapol and Lysol).

Scent donor animals and subjects were rotated so that no animal was used in two consecutive experimental sets. All male subjects used in the study had scrotal testes. Attempts to determine estrous stages in female subjects using the vaginal smear and temperature techniques were unsuccessful (see Wiley, 1972, and Chapman, 1951, for discussion of problems in determining estrous in woodrats).

Data taken from the event recorder printout were number, time, and duration of chamber visits. All time measurements were analyzed

in millimeters of chart printout then transformed to percent units for clarity in presentation.

A total of 379 trials were run. Of these, 110 were control trials and 269 were experimentals. In controls, neither compartment was scent marked. These were done in order to determine handedness or side preference in subjects. In experimental trials, male and female subjects were tested for preference to male urine, male feces, male sebum, female urine, female feces, male urine and feces mixed together, and female urine and feces mixed. When only one odor was used, the time a subject spent on the scented side of the olfactorium was measured. In trials where two odors were used (e.g., male urine vs. female urine), the time a subject spent on the homo-sex scented side was measured. The time spent in the left compartment of the olfactorium was measured in control trials.

A set of control experiments was performed to determine if subjects responded differently to urine collected in mineral oil and urine collected in a beaker from a metabolic chamber. Six female woodrats were tested 23 times for responses to urine collected in oil (N=12) and air (N=11).

In all experimental and control sets, a Wilcoxon sign rank test was used to determine the probability that subjects spent equal time in each chamber. Nested analysis of variance was used to determine the relative amount of variation between sexes, scent stimuli, individual subjects, and repetitions within subjects.

CHAPTER III

RESULTS

Responses of male and female woodrats to odor stimuli are presented in Table 1. In the scent vs. air trials (forced approach-avoidance paradigm), male woodrats showed an attraction to female urine, spending 58 percent of the time in the scented chamber. Female woodrats showed a strong attraction response to male sebum. In this set, females spent 68 percent of the experimental time in the compartment marked with sebum. Neither males nor females showed any response to the other odor stimuli. Although females spent 62 percent of the experimental time in the compartment marked with female feces, this response was not considered a significant attraction because of the high variance, low sample size, and non-significant probability of chance occurrence.

In the scent vs. scent trials (approach paradigm), both male and female woodrats showed significant responses to odor stimuli. Female rats spent 63 percent of the time in the chamber marked with male urine. The other scent in this set was female urine. Females showed no response in the sets: male feces vs. female feces, and male feces-urine mixed vs. female feces-urine mixed. Male woodrats were attracted to female urine-feces mixed and spent 64 percent of the experimental time in this chamber. In the male feces vs. female feces set, male subjects spent 58 percent of the time in the female scented side. Male rats did not show a response in the male urine vs. female urine trials.

Table 1.--Responses of woodrats to odor stimuli. The percent time (mean $\pm$ 1 SE) spent in the scented side (in scent vs. air trials) or homo-sex scented side (in scent vs. scent trials) is given. The probability (P) represents the probability that the total time spent in the scented chamber equals 50 percent, indicating random choice. The number of repetitions of each trial is given as well as the number of subjects used (in parentheses).

SCENT TRIAL	SUBJECT	
	MALE	FEMALE
Male feces vs. air	53.77 $\pm$ 8.29 P = 0.28 18(6)	46.23 $\pm$ 8.82 P = 0.34 16(6)
Female feces vs. air	46.71 $\pm$ 6.55 P = 0.25 25(4)	62.80 $\pm$ 9.73 P = 0.10 8(2)
Male urine vs. air	48.67 $\pm$ 7.82 P = 0.50 16(5)	49.27 $\pm$ 9.53 P = 0.50 7(3)
Female urine vs. air	58.50 $\pm$ 6.14 P = 0.07 22(6)	53.62 $\pm$ 5.46 P = 0.30 25(6)
Male urine vs. female urine	53.70 $\pm$ 6.45 P = 0.22 18(3)	36.41 $\pm$ 6.07 P = 0.02 17(3)
Male feces vs. female feces	42.09 $\pm$ 6.86 P = 0.14 21(3)	49.92 $\pm$ 8.93 P = 0.47 20(3)
Male vs. female urine and feces mix	35.48 $\pm$ 7.77 P = 0.02 17(3)	52.89 $\pm$ 8.92 P = 0.30 15(3)
Male sebum vs. air	44.73 $\pm$ 11.05 P = 0.37 13(3)	68.00 $\pm$ 6.67 P = 0.01 11(3)

Female woodrats were attracted to male ventral gland sebum (Fig. 1A) and male urine (Fig. 1B). In both cases, the attraction response was consistent over the ten hour experimental period. Male woodrats showed strong attraction to the female urine-feces mixture (Fig. 2C) and less attraction to female urine (Fig. 2A) and female feces (Fig. 2B).

The results of the control experiments showed neither male nor female woodrats preferred either side of the olfactorium. Responses of both male and female controls did not differ significantly from 50 percent (Wilcoxon sign rank; male Ss, $T=665.5$, $P > 0.1$; female Ss, $T=550.5$, $P > 0.2$).

No portion of the experiments was highly correlated with total time spent in a single chamber. Correlation matrices of time spent in the scented chamber for all hours (one through ten) for males (Table 2) and females (Table 3) reveal adjacent hour times are highly correlated but distant hour times less so. No one hour was especially good as a predictor of total time.

The method of urine collection did not affect responses of subjects. The Mann-Whitney U statistic was used to test the null hypothesis that females responded the same to urine collected in oil and air. There was no difference in responses to the two sources of urine ($U=76.5$, $P > 0.2$).

The analysis of variance revealed that 92-97 percent of the total variance was in replicates within individuals. There was no variance between subjects in all analyses. The remainder of the

Fig. 1--Attraction responses of female woodrats. The mean (± 1 S. E.) percent time a subject spent in a given chamber is plotted for each hour. The dashed horizontal line represents 50 percent the total experimental time. The probability (P) represents the probability that subjects spent equal time in both chambers.

A-- Male sebum vs. air trial. The time a subject spent in the scented chamber was measured. B-- Male urine vs. female urine trial. The time a subject spent in the female scented chamber was measured.

Fig. 2--Attraction responses of male woodrats. Symbols same as in Fig. 1. A-- Female urine vs. air trial. The time a subject spent in the female urine marked chamber was measured. B-- Male feces vs. female feces trial. The time a subject spent in the male marked chamber was measured. C-- Male urine-feces mix vs. female urine-feces mix trial. The time a subject spent in the male scented chamber was measured.

Table 2.--Correlation matrix of responses of male subjects over ten hour experimental period. Note that adjacent hour times are highly correlated but distant times are less so.

	HR. 1	HR. 2	HR. 3	HR. 4	HR. 5	HR. 6	HR. 7	HR. 8	HR. 9	HR. 10
HR. 1	1.00									
HR. 2	0.69	1.00								
HR. 3	0.60	0.78	1.00							
HR. 4	0.44	0.59	0.74	1.00						
HR. 5	0.40	0.52	0.65	0.76	1.00					
HR. 6	0.32	0.46	0.57	0.64	0.75	1.00				
HR. 7	0.38	0.44	0.60	0.66	0.69	0.72	1.00			
HR. 8	0.35	0.37	0.51	0.58	0.62	0.66	0.76	1.00		
HR. 9	0.30	0.32	0.43	0.51	0.52	0.67	0.69	0.79	1.00	
HR. 10	0.37	0.38	0.44	0.48	0.46	0.57	0.59	0.61	0.82	1.00
TOTAL	0.61	0.71	0.80	0.82	0.81	0.82	0.84	0.81	0.79	0.75

Table 3.--Correlation matrix of responses of female subjects over ten hour experimental period. Note that adjacent times are highly correlated but distant times are less so.

	HR. 1	HR. 2	HR. 3	HR. 4	HR. 5	HR. 6	HR. 7	HR. 8	HR. 9	HR. 10
HR. 1	1.00									
HR. 2	0.63	1.00								
HR. 3	0.55	0.80	1.00							
HR. 4	0.39	0.59	0.68	1.00						
HR. 5	0.48	0.53	0.62	0.66	1.00					
HR. 6	0.44	0.54	0.52	0.58	0.79	1.00				
HR. 7	0.51	0.46	0.49	0.41	0.53	0.66	1.00			
HR. 8	0.49	0.47	0.48	0.39	0.44	0.56	0.74	1.00		
HR. 9	0.39	0.39	0.44	0.44	0.42	0.55	0.63	0.69	1.00	
HR. 10	0.37	0.31	0.32	0.44	0.43	0.50	0.58	0.59	0.82	1.00
TOTAL	0.69	0.75	0.77	0.73	0.77	0.81	0.79	0.78	0.77	0.72

variation was between sexes or scent types. Male and female responses were highly variable in repeated trials but all behaved similarly. Response patterns indicative of habituation were not noted in repetitions within individuals.

CHAPTER IV

DISCUSSION

Several variables have been used in the assessment of preference response in approach or forced approach avoidance paradigms (Doty, 1975). Doty (1972) used mean time spent in a selected chamber for 15 minute blocks of a 1-1/2 test period. He found average time spent in a scented chamber significantly different between two experimental groups; but activity was not significant when measured by the number of crosses from one chamber to the other. He reported a significant inverse correlation between activity and time spent in one chamber. Martin (1974) found positive or no correlation between time and activity. As a measure of preference, he used activity totals and did not consider time. Martin (1974) considered ten minute trials adequate to determine preference, based upon Doty's (1972) suggestion that preferences were initiated early in the trials. Later, Doty (1973) reported that freezing and exploratory behavior in the early portions of a trial may bias true preference responses. Therefore, he considered only the second half of a one hour experiment in analyses.

Because of the problems associated with the use of activity data as a measure of preference, I have restricted analyses to time data. All portions of each ten hour trial were considered equally and early or late responses were not weighted. No portion of the experiment was highly correlated with total time spent in one chamber.

The results indicate that Neotoma micropus discriminate and respond to odor stimuli. Female woodrats were attracted to male urine

and male ventral gland sebum. Male woodrats showed a strong attraction to female urine and feces in combination and less attraction to urine and feces individually. No avoidance or homo-sex responses were observed. Bowers and Alexander (1967) have shown that lab strain Mus musculus can identify the sex of a conspecific on olfactory cues alone. Dagg and Windsor (1971) reported that gerbils (Meriones unguiculatus) have similar discriminative powers.

The ability of woodrats to identify sexes with olfactory cues has definite selective advantages in reproduction. Sexual recognition by scent facilitates mate location and mobilization, increasing reproductive efficiency (Bowers and Alexander, 1967; Bronson, 1971; Eisenberg and Kleiman, 1972; Doty, 1974). There is adequate field evidence to support the contention that woodrats can and do utilize scent messages.

A unique characteristic of members of the genus Neotoma is their dens. Woodrats construct conical "houses" usually supported by trees, rock outcrops, or shrubs. Depending on the availability of local vegetation (Cornely, 1975) and debris, these nests are constructed of sticks, cactus, dung, and rocks (English, 1923; Linsdale and Tevis, 1951; Rainey, 1956, 1965; Finley, 1958; Johnson, 1966; Raun, 1966; Cameron and Rainey, 1972). Dens are large and conspicuous, with reported heights of eight feet (Vestal, 1938). Generally, one rat or one mother with young will occupy a nest (Linsdale and Tevis, 1951).

Raun (1966:45) emphasized the importance of the den in woodrat communities. In his study of the ecology of N. micropus in south

Texas, he stated that "houses are probably the most important single factor limiting the population." Brown (1968) gives a thorough discussion of the protective function of dens. The importance of home site availability to woodrat communities may be appreciated when population numbers are compared to nest density. Box's (1959) estimates of the average number of woodrat dens per acre (12.4) in a prickly pear-short grass community correspond well to Raun's (1966) peak population density estimates (12.6) for the same community type.

Typically, woodrat dens are constructed at the base of a tree, shrub, or in a rock crevice. Each den has a number of openings leading to the interior, which contains food caches, one or two nesting chambers, and passageways. The outside of the den is usually littered with fecal pellets (Rainey, 1965) and in some cases fecal pellets carpet the interior portions, except the nest chambers (Linsdale and Tevis, 1951; Rainey, 1956; Raun, 1966).

Woodrats do not maintain a large territory but will aggressively defend the den against an intruder (Linsdale and Tevis, 1951). Numerous authors have commented on the antisocial behavior of woodrats (Wood, 1935; Vorhies and Taylor, 1940; Poole, 1940; Hamilton, 1953; Rainey, 1956; Raun, 1966). Poole (1940) and Raun (1966) both noted that female woodrats are generally more aggressive than males.

Olfaction may play a prominent role in woodrat life history during the breeding season. There is little information on which sex is the active mate seeker. Movement data show male woodrats to be more motile than females (Linsdale and Tevis, 1951; Fitch and Rainey,

1956; Smith, 1965; Raun, 1966; Classen, 1968). Linsdale and Tevis (1951:384) noted that "during the breeding season the males move about, changing houses in search of sexually receptive females." Fitch and Rainey (1956) and Rainey (1965) also observed that male woodrats moved much more than females in the reproductive season. It would be advantageous for a breeding male to discriminate between male and female dens. Linsdale and Tevis (1951) have observed male woodrats sniffing the area around the nest of females prior to entering. If the occupant is of the same sex, a hostile interaction will likely follow when the breeding male enters. This is an unnecessary waste of energy for a breeding individual. If the occupant is a receptive female, reproductive energy may be channeled into courtship and copulation.

It is difficult to study the natural breeding behavior of nocturnal rodents, such as woodrats. There is a limited amount of information on courtship behavior. Spencer (1968) observed that prior to copulation, woodrats engaged in mutual sniffing and sparring bouts. He suggested these behaviors were associated with sex recognition. Close contact sniffing would give the female rat opportunity to perceive male ventral gland odors (Clarke, 1973). Spencer (1968) also noted that male woodrats were frequently observed dragging their venters after a female rat had been placed in the same enclosure. It is possible that this courtship behavior permits females to play a significant role in mate selection (Doty, 1974).

Female woodrats actively seek mates during the breeding season (Clarke, 1973), sometimes visiting a number of unoccupied dens (Linsdale and Tevis, 1951). Spencer (1968) noted that male woodrats are frequently observed rubbing their venters in the vicinity of their dens. It seems probable that dens of male woodrats do have a sex specific odor and may serve as an attractant for wandering females. This is supported by Vestal's (1938) observation that the houses of male woodrats were especially odorous to the investigator during the breeding season. Again, mate selection efficiency is increased by reducing the number of hostile homo-sex encounters.

Ecological observations of woodrats are consistent with the present experimental results. Woodrats may utilize olfactory cues in a sex recognition context. Male woodrats increase mate-seeking efficiency by discriminating nests of females and males through olfactory detection of urine and feces deposited outside the houses. Female woodrats seeking mates likely identify nests of males from females on perception of urine and ventral gland sebum deposits outside the houses. Females possibly detect and select potential mates while engaged in courtship ritual. The selective advantage of such a system lies in the saving of energy by avoiding agonistic encounters with members of the same sex.

Another possible use of olfactory discrimination in woodrats may be related to the maintenance of species identity. Numerous authors have found olfaction to mediate reproductive isolation in closely related taxa (Godfrey, 1958; Moore, 1965; Doty, 1972; Martin, 1974).

Neotoma micropus, N. albigula, and N. floridana are phylogenetically close. All three taxa occur in sympatry or parapatry and hybridize in the laboratory. Possible natural hybrids have been detected by means of multivariate statistical analyses on sympatric populations (Spencer, 1968; Birney, 1974, 1976), however, the extent of interbreeding and its effect on the genetic integrity of these taxa is difficult to assess.

Clarke (1973) proposed that the ventral gland of male woodrats may function as a reproductive isolating mechanism. Doty and Kart (1972) found well developed ventral glands in seven of eight taxa within the Peromyscus maniculatus species group. P. polionotus leucocephalus, an insular form, did not possess such a gland. Doty (1974) suggested this may be evidence in support of the tenet that secondary sexual characters mediate reproductive isolation.

Wiley (1972), in a study of the reproductive biology of the same deme of N. micropus utilized in this study, noted that ventral glands, although present, were never exceptionally active in male rats. No other species of woodrat occurs in the area. Spencer (1968), in a study of sympatry in Neotoma micropus and N. floridana, observed that N. micropus had very active ventral glands, much more so than N. floridana. It is clear that activity in these specialized sebaceous glands is variable from population to population and may have a species recognition role. More research is needed to determine the importance of olfaction in contact zones of closely related woodrat taxa.

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