

Some Experimental Tests of the Functional Significance of Scent-Marking by Gerbils (*Meriones unguiculatus*)

Martin Daly

University of California, Riverside
and University of Toronto, Toronto
Ontario, Canada

The functional significance of male gerbil scent-marks was investigated in four experiments. In Experiments 1 and 2, males in a novel test environment marked more, groomed more, and urinated less in the presence of odors of a strange male than in their absence. Female odors elicited male marking more than did male odors. In Experiments 3 and 4, females were selectively less aggressive toward familiar-smelling males in comparison with unfamiliar-smelling males. These results, in conjunction with field observations of related species, call into question the hypothesis that gerbil scent-marks function territorially and instead suggest that the primary targets are adult females.

Gerbils mark low objects with an odorous sebaceous substance secreted from a midventral gland, during a stereotyped species-typical marking behavior. Although much is known of the physiological and biochemical control of this scent-marking behavior (reviewed by Thiessen, 1973), its functional significance remains obscure.

We must distinguish "true biological functions" from "mere consequences" (Williams, 1966). The true functions are those results of a behavior that have been instrumental in its evolution and maintenance by natural selection. Ultimately, the function of any behavior that has evolved is reproductive, but that function may be served either directly or through more immediate short-term functions. In the case of a communicative behavior such as scent-marking, the act must serve the

sender by virtue of its influence on a receiver. But when we observe scent-marking behavior, the identity of the relevant receiver(s) is unknown (Ewer, 1968).

Discussions of male gerbil scent-marking have mostly assumed that the relevant receivers are other males. Males indeed preferentially approach and sniff other males' marks (Baran, 1973), but Thiessen, Blum, and Lindzey (1970) and Thiessen, Lindzey, and Nyby (1970) were unable to discriminate a receiver male's behavior in a marked versus an unmarked area. In Experiments 1 and 2, I present evidence that a sender male's marks indeed influence several behaviors in a receiver male.

A neglected possibility is that a male's marks directly influence females. Two lines of evidence suggest that this possibility deserves attention: evidence on the salience of females as stimuli for male marking, and field observations.

If females are important targets of male marks, one might expect stimuli from females to be important causal factors for male marking, and this expectation is confirmed. Swanson (1974) found that males marked more than twice as much in direct encounters with females than with males. Halpin (Note 1) found that intact males marked far more in the vacated cage of an intact female (20-min $M = 27.3$) than in the cages of a castrated

Experiments 1 and 3 were conducted in Toronto with support from National Research Council of Canada Grant A-140 to Jerry A. Hogan. Experiments 2 and 4 were conducted in Riverside with support from the psychology department. I thank Kelly Moore for research assistance, Zuleyma T. Halpin for permission to cite as-yet-unpublished data, and Margo Wilson and Jerry Hogan for critical comment.

Requests for reprints should be sent to Martin Daly who is now at the Department of Psychology, University of California, Riverside, California 92502.

male (13.5), a castrated female (7.3), an intact male (5.1), or a clean cage (4.6).

Relevant field observations (Daly & Daly, 1975a, 1975b) unfortunately concern other gerbil species (*Meriones libycus* and *Psammomys obesus*) rather than the laboratory species *M. unguiculatus*. It is at least plausible, however, that scent-marking functions similarly in the three species, since the behavior is identical in appearance and since the gland and behavior are similarly sexually dimorphic in the three species. In both species observed in the field, adults live alone, and one circumstance in which males mark is when visiting females, which they do day after day even outside the breeding season. The males do not maintain a territorial organization, and it must be suspected that the marks are aimed at the females.

The notion that gerbil scent-marking might have a reproductive function has hitherto been dismissed on the basis of two faulty arguments. Mitchell (1967) denied the ventral gland a reproductive role because gerbils bred successfully after it was surgically removed. Blum, Balsiger, Ricci, and Spiegel (1975) gave such evidence its proper due, however, by concluding therefrom "that ventral gland odor does not play a crucial role in the mating behavior of gerbils that are confined together indefinitely in small cages" (p. 1218). The gland may still play an important part in reproductive competition in nature. Sokolov and Skurat (1966) denied the gland a reproductive function in the great gerbil (*Rhombomys opimus*) on the grounds that it functions throughout the year. Non sequitur again. The function hypothesized in the next paragraph can be served by the male's visiting prior to the breeding season, which is just what the male *M. libycus* does (Daly & Daly, 1975b).

The visiting patterns of gerbils observed in the field, in combination with some evidence that pairs of *Meriones* require a period of individual familiarization before mating (Daly & Daly, 1975b; Norris & Adams, 1972; Renoux, 1957), suggested the following hypothesis: A male's marks during repeated visits to the female's home

bush may serve to habituate her to that individual male. This may serve to mitigate her aggressiveness and thereby gain him a mating advantage in competition with other males. The female in her turn might benefit by the selection of mates of demonstrated survival capacity and hence presumptive fitness. This hypothesis led me to investigate in Experiments 3 and 4 the responses of female gerbils to males, as a function of the female's controlled prior exposure to the odors of that particular male.

Experiment 1

This experiment investigates the behavior of male gerbils placed in a terrarium as a function of the presence of odors of another male.

Method

Subjects. Subjects were eight male Mongolian gerbils (*Meriones unguiculatus*), obtained at 5 mo of age from High Oak Ranch, Goodwood, Ontario, and individually housed for 8 wk before and throughout the experiment. Each had had a single mating experience 4 wk earlier; none had encountered a male in the previous 8 wk.

The gerbils were maintained in glass terraria, 17 × 35 × 22 cm, containing sawdust, nest paper, and Purina Laboratory Chow pellets. Some sunflower seeds and succulent vegetables were provided daily. A reversed 13:11 hr light/dark cycle prevailed. Females were housed in the same room.

Procedure. Each gerbil was observed on 28 trials in a glass terrarium. On half of the trials (designated X), the terrarium was clean, and on half (designated M), it contained the odor traces left by the male from the previous X trial. Each male received 14 X trials and 14 M trials, one trial per day over 28 days. Each was tested twice before and twice after every other subject, with running orders counterbalanced.

The test terrarium measured 25 × 50 × 30 cm, with two roughened Plexiglas pegs 2.6 × 1.2 × .7 cm (providing optimal stimuli for eliciting ventral marking, according to Thiessen, 1968) glued to the floor 12 cm from the walls and 25 cm from each other.

Trials lasted 5 min. Each M trial began about 90 sec after the end of the previous X trial. After each M trial, the terrarium and pegs were washed with water and then with a 70% ethanol solution, dried, and let stand for 20 min before a further X trial.

Testing was conducted under dim light during the first 2 hr after lights-out. The observer placed the gerbil in the center of the terrarium, seated himself 80 cm away, and began recording behavior

immediately with a 20-button keyboard connected to programming equipment which counted the number of 1-sec intervals during which each button was depressed. The behaviors thus time scored are listed in Table 1. After the trial, urination was scored dichotomously: whether or not it had occurred without regard to time or quantity.

Results

Table 1 presents the mean time spent in each activity under the two conditions. Time scores were square-root transformed for analysis of variance: two conditions (a fixed factor) by eight subjects (a random factor), with 14 scores per cell.

Significant condition effects are indicated in Table 1. The gerbils scent-marked, sniffed, and face washed more, and open reared less, in the presence of another male's odors. Subject effects were significant beyond $p < .001$ for all activities except four rare ones: scratching, stretching, side rubbing and foot thumping. No condition by subject effect was significant.

The elevation of scent-marking in the

M condition, although significant at $p < .01$, is not large. Conditions accounted for just 1% of the variance in marking, whereas subjects (stable individual differences) accounted for 51% (variance apportioned according to Vaughan and Corbally, 1969). Within subjects, marking in M trials was correlated with the amount of marking in the preceding X trial (and thus, presumably, with the strength of enduring odors). This correlation was positive in seven of eight gerbils and significantly so overall (Wilcoxon signed-ranks test, $T = 2$, two-tailed $p < .02$).

Urination occurred on 63% of X trials and 44% of M trials. In comparing each gerbil's frequency of urinating on X and M trials, this difference is significant, $t(7) = 3.55$, $p < .01$. Urination and defecation were positively related: X trials, contingency coefficient $C = .39$, $\chi^2(1) = 19.7$, $p < .001$; M trials, $C = .52$, $\chi^2(1) = 40.7$, $p < .001$; indeed, they were frequently observed to occur together with a stereotyped digging motion, as Rieder and Reynierse (1971) described. No relation between elimination and ventral marking was discernible between trials within subjects. Between subjects, urination and ventral marking were negatively related ($r = -.58$, two-tailed $p = .10$).

Systematic changes in behavior over the 28 days of testing were sought: The daily time sums for each act, in X trials, M trials, and overall, were tested for monotonic trends by rank-order correlation. Scrabbling, open rearing, freezing, and walking all increased significantly ($p < .05$) over days in both conditions and overall. Face washing and peg sniffing declined significantly in X trials and overall. No other behavior showed any monotonic trend over days.

Discussion

Urination and open rearing were the only activities significantly depressed in the soiled terrarium, while sniffing, face washing, and scent-marking were elevated. That male scent-marking was enhanced by the presence of another male's odors is consistent with results of most

Table 1
Mean Number of Seconds per Trial During Which Each Activity Occurred, with Significant Condition Effects (Experiment 1)

Behavior	Clean terrarium	Male odor	$F(1, 7)$	$p <$
Marking pegs	33.1	34.0	—	—
Marking elsewhere	3.8	5.9	7.02	.05
Total ventral marking	36.9	39.9	15.10	.01
Sniffing pegs	22.8	27.1	10.31	.05
Sniffing elsewhere	82.1	105.1	56.86	.001
Face washing	11.1	13.0	11.00	.05
Scratching	.6	.8	—	—
Body grooming	1.8	2.1	—	—
Stretching	.4	.2	—	—
Side rubbing	.4	.6	—	—
Open rearing ^a	129.7	117.4	5.86	.05
Wall rearing ^b	36.7	34.2	—	—
Scrabbling ^c	15.0	15.1	—	—
Walking	75.2	73.5	—	—
Freezing	10.3	10.0	—	—
Digging	31.9	30.3	—	—
Foot thumping	.0	.2	—	—
Defecating	.7	.7	—	—

^a Standing on the hind feet without forepaw support.

^b Similar, but with forepaw contact with the wall.

^c Upward-oriented scraping and leaping at walls.

studies of mammalian marking (Johnson, 1973; Johnston, 1975). It is evidently the first such demonstration in gerbils, however, and is contrary to Thiessen's (1968) suggestion that a male's activity may be inhibited by the presence of another male's marks.

Urination and ventral marking were oppositely affected by the persisting odors of a previous male. This result contradicts Thiessen, Blum, and Lindzey's (1970) suggestion that ventral marking, urination, and defecation constitute a causally integrated set of scent-marking behaviors. In the present study urination and ventral marking were negatively related between subjects. The above authors found a positive correlation, but this was significant only when sexes were combined, which merely reflected that males did more of both.

Behavioral changes over days also differ among studies. The present study did not find a day-to-day decrement in activity or an increase in marking, as Thiessen, Blum, and Lindzey (1970) did, but instead found systematic changes in other behavior (see also Blum et al., 1975). The several differences in the data may be due to several procedural differences, but in any case the different results are cautionary and support Thiessen's (1973) suggestion that there may be considerable plasticity in the gerbil's response to conspecific odors. Experiment 2 was undertaken to determine whether the effects of residual odors of another male would vary interactively with other variables.

Experiment 2

This experiment investigates male gerbil behavior as a function of residual odors from another male, female odors, and the time of day.

Method

Subjects. Subjects were 12 male Mongolian gerbils obtained at 2 mo of age from Tumblebrook Farms, West Brookfield, Massachusetts, and individually housed for 3 mo before the experiment. All were sexually inexperienced, and none had encountered a male since arrival in the laboratory.

The gerbils were maintained in plastic cages, 20 × 33 × 20 cm, containing dried corncob bedding and nest paper. Purina Laboratory Chow and water were available ad lib and were occasionally supplemented with vegetables. A reversed 14:10 hr light/dark cycle prevailed. The males were housed in a room containing no females.

Procedure: Phase 1. Each gerbil was observed on eight trials, one per day over 8 days. Each gerbil received two trials under each of four conditions, defined by two times of day (12th hr of the light period vs. 3 hr later in the first hour of the dark) × X versus M (clean vs. soiled terrarium, see Experiment 1). The conditions are referred to as LX, LM, DX, DM (L: light; D: dark; X: clean; M: previous male). Trials in the dark period were observed under dim red light. The 24 possible running orders for the four conditions were each used once in running two 4-day blocks for the 12 subjects. For any gerbil each M trial followed a different animal.

Test terraria measured 20 × 40 × 25 cm and contained a centrally fixed roughened Plexiglas peg 2.6 × 1.2 × .7 cm. Trials lasted 5 min. Each M trial began about 90 sec after the end of the previous X trial. Each test terrarium was used for only one pair of trials daily and was washed with water and ethanol after use.

The observer placed the gerbil in the center of the terrarium, sat 80 cm away, and began recording behavior immediately on a check sheet, counting ventral marks on and off the peg, fecal boluses, and face-washing bouts. Urination was scored dichotomously (a single yes or no for the trial).

Phase 2. The gerbils were left undisturbed for 2 wk after Phase 1 and were then run for a further 8 days. The procedure was identical to that in Phase 1, with the time-of-day variable replaced by a new one: presence or absence of female odor. The conditions were XX (clean field), FX (female odor), XM (odor of previous male), and FM (odors of female and previous male). For trials with female odor (F trials) a pinch of odorous bedding material was taken immediately before the trial from the habitual urination site in the cage of a noncycling, behaviorally anestrous, isolated, adult female and was added to the test terrarium. Trials were run within the first 2 hr of the dark period. The counter-balanced order of trials and the methods of recording behavior were as in Phase 1.

Results

Mean levels of the recorded behaviors are shown in Table 2.

Ventral marking, face-washing bouts, and fecal bolus counts were analyzed for each phase of the experiment by 2 × 2 × 12 analysis of variance (X-M × L-D or F-X × Subjects; subjects a random factor and the others fixed), with two scores per cell. "Explained" variance was approx-

Table 2

Male Behavior as a Function of Time of Day and of Residual Odors of Males and Females (Experiment 2)

Condition	M no. of ventral marks	M no. of face-washing bouts	M no. of fecal boluses	Probability of urination
Phase 1				
LX (light; clean terrarium)	20.0	.7	4.5	.92
LM (light; male odor)	24.8	2.0	4.3	.79
DX (dark; clean terrarium)	23.0	.9	5.2	.88
DM (dark; male odor)	27.5	2.0	3.0	.67
Phase 2				
XX (neither odor)	20.5	1.0	2.9	.88
XM (male odor only)	23.7	1.5	2.0	.71
FX (female odor only)	29.9	1.9	2.4	.71
FM (both odors)	37.2	1.8	3.0	.79

tioned according to Vaughan and Corballis (1969).

Three variables (X-M, X-F, and subjects) influenced the behaviors measured; time of day and interactions produced no significant effects.

Male marking increased in the presence of another male's odors: Phase 1, $F(1, 11) = 10.00$, $p < .01$; Phase 2, $F(1, 11) = 31.30$, $p < .001$, but the X-M variable accounted for just 5% of the variance in scent-marking in both phases. Female odors also enhanced male marking, $F(1, 11) = 49.61$, $p < .001$, and accounted for 26% of the variance in Phase 2. A planned comparison of the separate influences of the odors of the two sexes (i.e., FX vs. XM) confirmed a greater effect of the female odor, $t(11) = 3.28$, $p < .01$. Subject effects accounted for 57% of the variance in Phase 1, $F(11, 48) = 15.97$, $p < .001$, and for 39% in Phase 2, $F(11, 48) = 11.16$, $p < .001$. Time of day accounted for 2% in Phase 1, $F(1, 11) = 3.61$, $.05 < p < .10$. No interaction approached significance or accounted for more than 1% of the variance.

Urination was more frequent in a clean terrarium than in a soiled one. This comparison was significant only in Phase 1, $t(11) = 2.60$, $p < .05$.

Face washing was elevated in the soiled terrarium in Phase 1, $F(1, 11) = 5.08$, $p < .05$. In Phase 2, only subject effects were significant.

In both phases, defecation varied significantly only between subjects.

In both Experiments 1 and 2, it was noted that scent-marking elevation in the

M condition was slight but significant and that the effect was greatest early in the experiment. Only on each subject's first trial was the test situation completely novel: First trial data were therefore examined separately from data for subsequent trials, and Figure 1 presents these scent-marking comparisons. (For purposes of comparison, the time scores from Experiment 1 were converted to frequencies by multiplying by .6, a factor determined from test trials in which both measures were taken.) In a novel test situation, scent-marking was more than doubled by the presence of odors of a previous male, $t(9) = 5.13$, $p < .001$; the X-M variable (absence vs. presence of another male's odor) accounts for 62% of the first-trial variance.

Discussion

The hypothesis that the influences of male odors upon another male's behavior would interact with other variables was not supported. Experiment 2 replicated the effects of scent-marks upon marking, urinating and face washing but did not demonstrate interactive effects with other variables. The first variable, time of day, was ineffective. The second, female odor traces, was highly influential, but its effects were additive with those of male odors rather than interactive.

Odor of a strange male was a most salient cue on the first test trial (Figure 1), that is, when a naive gerbil was first placed in a novel testing environment. In

particular, such odors elicited a high level of "counter-marking" (cf. Roper & Polioudakis, in press). As a male was repeatedly exposed to the test situation, sometimes in the presence of another male's odor and sometimes not, but in neither case ever encountering another male, then the reaction to the odor declined. This change is not surprising: The gerbil apparently learns to ignore a cue that predicts nothing. In this sense the response to the odor is indeed plastic.

The remaining experiments investigate effects of male odors on females.

In a pilot study eight opposite-sex pairs of individually housed gerbils were made olfactorily familiar with one another by daily cage switching. Behavior of such olfactorily familiar pairs during encounters in a neutral arena was then compared with that of olfactorily unfamiliar pairs (made up from the same 16 gerbils). Sexual behavior did not occur in these tests, but the olfactorily unfamiliar partners fought significantly more than familiar pairs, and females were responsible for a larger proportion of the total aggressive acts and scent-marked more when they were paired with an unfamiliar-smelling male partner.

These pilot results supported the hypothesis that olfactory familiarity of a par-

ticular male can function to mitigate a female's aggressiveness. However, the cage-reversal procedure in the pilot experiment resulted in each member of the pair being olfactorily familiar to the other; observed effects on behavior could not be ascribed solely to the responses of either sex. In Experiments 3 and 4, odor was transferred only from males to females so that any discriminatory behavior during encounter tests must reside initially with the female, and transferred odors were restricted to those from the ventral gland.

Experiment 3A

Method

Subjects. The subjects were eight male and eight female Mongolian gerbils, obtained from High Oak Ranch, Goodwood, Ontario. The sexually experienced 11-mo-old males had been housed individually in the laboratory for 6 mo. The 15-wk-old virgin females were newly arrived in the laboratory. The gerbils were individually maintained in glass terraria, 17 × 35 × 22 cm, containing sawdust, nest paper, and Purina Laboratory Chow pellets. Some sunflower seeds and succulent vegetables were provided daily. A reversed 13:11 hr light/dark cycle prevailed. Gerbils of each sex were randomly assigned numbers 1 to 8, so that each had a same-number partner.

Procedure. Each female was exposed to the odor of her same-number familiar-smelling (FS) male partner by the following procedure: The female was

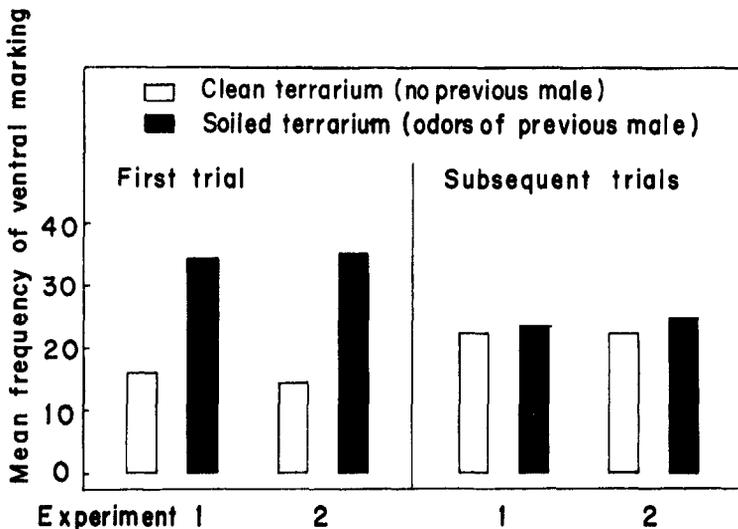


Figure 1. Scent-marking by males on first and subsequent trials as a function of the presence of male odors.

presented in her home cage with a strip of absorbent paper that had just been rubbed three times across the midventral sebaceous gland of her FS male. This odor-transfer procedure was carried out once daily throughout the 51-day experiment. (Females always shredded the scent-bearing paper and incorporated it into their nests.)

Estrous cycles were monitored by vaginal smearing on Days 15–51. Smears were taken daily 30–60 min before lights-out, with cotton swabs moistened in distilled water. The vaginal smears were stained by the quick-staining procedure of Shorr (1941) and examined immediately. The estrous cycle was characterized from the smears, and each female was tested on a day of apparent vaginal estrus (minimal leukocyte count).

Females were tested separately with one FS and one UFS (unfamiliar-smelling) male on the same day. Tests entailed two 15-min encounters, one with each male, at 30–45 min and 60–75 min after lights-out. Tests were conducted in an alcohol-washed glass terrarium, 25 × 50 × 30 cm, containing a roughened Plexiglas peg, 2.6 × 1.2 × .7 cm, glued to the floor. Each female was tested on one day only, between Day 36 and Day 46. Half were tested first with the FS male and half first with the UFS. Each male served once as FS male, once as UFS.

The male and female were simultaneously placed in opposite corners of the test terrarium. The observer sat down 60 cm away and immediately began recording behavior with a 20-button keyboard which recorded activity-time data as in Experiment 1. Trials lasted 15 min, after which the gerbils were returned to their home cages. Behaviors recorded were the following: (a) fighting, (b) mutual sidling and boxing, (c) male chase female, and (d) female chase male. No other button was depressed simultaneously with any of the above four. The remaining 16 buttons were used to record eight further behaviors separately for the two gerbils: (e) unilateral aggressive upright posture, (f) cut off (low freezing posture with eyes shut), (g) sniffing partner's head, (h) sniffing partner's body, (i) grooming self, (j) ventral rubbing (ventral gland scent-marking), (k) freezing (sitting still with eyes open), and (l) other nonsocial behavior (walking, rearing, digging).

Results

A regular estrous cycle was manifest in the vaginal cytology of five females, while three cycled irregularly. All eight were tested with males on a day of apparent vaginal estrus (minimal leukocyte count).

Two females, both irregular cyclers, copulated during the test encounters, each with both test males. Both females sometimes failed to hold lordosis long enough to permit intromission, and both held lordosis longer for the FS than for the UFS male; this difference was apparent to the observer, but lordosis durations were un-

fortunately not timed. One UFS male ejaculated extravaginally as the female suddenly moved away from him and never achieved intravaginal ejaculation. Neither female became pregnant.

Table 3 presents the mean number of seconds spent in each push-button-recorded behavior. Correlated *t* tests were used to compare the responses of females to FS and UFS males. Females sniffed the FS partner more than the UFS partner, both his head, $t(7) = 3.80, p < .01$, and body, $t(7) = 4.73, p < .01$. Each of the six females that did not copulate scent-marked more in the presence of the FS male than the UFS, $t(5) = 3.71, p < .02$, but the two that copulated both marked more with the UFS male.

The proportion of total aggressive behavior (fighting, chasing, and upright threat) that was performed by the animal of each sex was determined for each trial. Females were responsible for 65.5% of aggressive acts in FS trials, 78.1% in UFS trials. The difference is significant when correlated for females, $t(7) = 2.42, p < .05$, but not for males. Males froze (a response to female threats) significantly more in UFS trials than in FS trials, $t(7) = 3.62, p < .01$.

The behaviors that were scored separately for the two sexes were square root

Table 3
Mean Number of Seconds Spent in Each Behavior (Experiment 3A)

Behavior	FS trials		UFS trials	
	FS	UFS	FS	UFS
Fighting	6.9		6.3	
Mutual sidling and boxing	24.0		24.1	
	Females		Males	
Chase partner	3.0	6.8	2.0	0.1
Unilateral aggressive upright posture	71.7	101.0	7.9	1.6
Cut off	7.5	8.6	11.4	11.4
Sniff partner's head	106.3	72.5	62.5	45.6
Sniff partner's body	40.9	19.6	109.5	102.9
Groom self	34.5	33.5	57.8	78.8
Freeze	32.0	32.8	58.0	106.3
Scent-mark	27.9	24.3	41.4	35.3

Note. Abbreviations: FS = male olfactorily familiar to female; UFS = male not olfactorily familiar to female.

transformed to reduce positive skew and analyzed by a 2×2 (sex by olfactory familiarity) analysis of variance, with repeated measures on the second variable (Winer, 1962, pp. 302-307). Overall main effects of familiarity were not significant for any behavior. The Sex \times Familiarity interaction was significant for the aggressive upright posture, $F(1, 14) = 4.86$, $p < .05$; females exhibited the posture more in UFS trials and males more in FS trials (Table 3). Sex differences (Table 3) were significant ($p < .01$) for freezing, aggressive upright, and sniffing the partner's body.

Discussion

This experiment confirms that females behave differently toward familiar-smelling and unfamiliar-smelling males. Moreover, this discrimination can be made by females on the basis of male ventral gland odors alone. As in the pilot study, females were responsible for a larger proportion of the aggressive behavior in UFS trials than in FS trials, and freezing by males was more frequent in UFS than FS trials. These results support the notion that females will be relatively tolerant of males that smell familiar to them.

It remains plausible, though speculative, that the familiar-smelling male will thus gain a competitive advantage in mating. In this experiment only two females mated, and they did so with both males. Observations of the matings indicated some continuing discrimination in favor of FS males, particularly in the duration of lordosis, but this cannot be stated with confidence. In order that a familiar-smelling male enjoy a competitive mating advantage, the female need not absolutely refuse copulation with all others; it is likely that any mating advantage to the FS male in the natural situation would result not simply from selective receptivity in the estrous female but from a reduced vigor of repelling him before estrus.

Experiment 3B

If females are more tolerant of FS males, they may prefer the FS males' odors to

those of strange males. This experiment tests for such a preference in the absence of direct encounters.

Method

The experiment is a continuation of Experiment 3A. The subjects were the same. The procedure of transferring the FS male's scent to the female's home cage was continued through Day 51, and each female was given choice tests on Days 50 and 51.

For choice tests, females were introduced singly into an alcohol-washed glass terrarium, $25 \times 50 \times 30$ cm, divided visually into two halves, $25 \times 25 \times 30$, by a line of tape on the outside of the terrarium, with a roughened Plexiglas peg, $2.6 \times 1.2 \times 0.7$ cm, fixed to the floor in the center of each half. One peg was smeared with the ventral gland odor of the FS male, the other with that of the UFS male that the female had encountered on a single occasion between 4 and 14 days previously in Experiment 3A. Male odor was placed on the pegs with a cotton swab rubbed over the male's ventral gland. The spatial positions of the two males' odors were reversed on the two days.

Choice tests lasted 10 min and were conducted within the first 2 hr after lights-out. Ten behaviors were recorded separately for the two halves of the terrarium with the 20-push-button system: total time in that half, wall rearing, open rearing, scrabbling, digging, grooming, scent-marking on the peg, scent-marking elsewhere, sniffing the peg, and sniffing elsewhere. Counters tallied the time scores separately for each 2-min interval.

Results

Females spent an average of 52% of their time in the FS side of the terrarium, 48% in the UFS side. This difference did not approach significance. In the first 2-min period of the first test, females spent 57% of their time on the FS side, 43% on the UFS side, $t(7) = 2.08$, one-tailed $p < .05$.

Females sniffed more in the area marked with the FS male's odor, both at the peg itself (M : FS, 30.4 sec and UFS, 23.4 sec), $t(7) = 2.83$, $p < .05$, and elsewhere (M : FS, 85.4 sec and UFS, 59.7 sec), $t(7) = 2.42$, $p < .05$. Other behaviors did not differ significantly between the two halves of the terrarium.

Discussion

The FS males' odors were initially more attractive than the UFS males', but the preference did not persist over the total

test time. Such an initial preference might be important in the natural habitat where a female's choice behavior can lead to direct encounters. (Since the UFS male was not entirely unfamiliar at the time of the preference test, female discrimination between FS and UFS odors may already have been mitigated, but the functional hypothesis suggests that the effects of familiarity should depend upon repeated exposures.)

Females sniffed more in the FS area than in the UFS area, even as they sniffed the FS male himself preferentially in Experiment 3A. This result is especially interesting since one might have anticipated that novel odors would provoke greater interest. Halpin (1974) found that a test male A that was allowed to sniff the odor of another male B would then prefer to sniff the odor of novel male C in preference to the now familiar odor of B. This "habituation preference test" was used to demonstrate the individuality of male odors, and the preference for the novel male's odor was strong and consistent. In the present experiment, by contrast, females sniffed preferentially at the familiar male's odor. This sex difference may have an adaptive explanation as follows: While males should be primarily interested in investigating the odors of novel (intruder) males, females may be expected to prefer to approach familiar-smelling males, in accord with our original hypothesis.

Experiment 4

Females are relatively less aggressive to a male if he is olfactorily familiar, a result consistent with our hypothesis that male scent-marks serve a courtship function, perhaps appeasing the female. Appeasement was not complete, however. Females were aggressive to both FS and UFS males, the difference being one of degree. Pairs evidently were not together long enough to establish really amicable relations.

Male Saharan gerbils (*Meriones libycus* and *Psammomys obesus*) observed in the field repeatedly visited females at their home burrows despite rebuffs (Daly &

Daly, 1975a, 1975b). In an attempt to simulate this pattern of encounters and to assess the effects of the male's marks, a series of daily encounters was run in Experiment 4. Groups differed in whether the particular encountered male's marks were also presented in the female's home cage. Predictions were made that the UFS males would be met with greater aggressiveness than the FS males and that FS males would be permitted to mate sooner in the series of daily encounters.

Method

Subjects. The subjects were 12 female and 12 male sexually inexperienced Mongolian gerbils obtained as juveniles from Tumblebrook Farms, West Brookfield, Massachusetts, and maintained individually as in Experiment 2. The sexes were housed in separate rooms, separated by several doors and a ventilated hallway. The 12 gerbils of each sex were randomly assigned numbers 1 to 12.

Procedure. Scent transfer. Scent was transferred to each female from her same-number male as in Experiment 3, on 36 consecutive days: 26 days before testing and 10 test days (see below).

Test pairs. Gerbils were assigned to one of two testing groups. In six same-number pairs, the males were familiar-smelling (FS) to the females. The other six were unlike-number pairs, so males were unfamiliar-smelling (UFS) to the females. This defined FS-tested and UFS-tested groups, and these same groups and test pairs were retained through the 10 test days. Thus, for a female in the FS-tested group, her test male and her odor-donor male were the same, and for a female in the UFS-tested group, they were different individuals.

Test procedure. Fifteen-minute male-female encounter tests were conducted daily for each test pair for 10 days. A test pair was simultaneously introduced into an alcohol-washed terrarium, 20 × 40 × 25 cm. Behavior of the two gerbils was recorded on a check-sheet divided into fifteen 1-min intervals. Behaviors scored were scent-marking, fighting, mutual and unilateral sidling, boxing, chasing, and upright aggressive posture as well as any sexual behaviors. All tests were conducted during the first 2 hr after lights-out.

Results

Aggressive behavior tended to increase over test days, and no copulation occurred. For these reasons testing was discontinued after 10 days.

Five females exhibited some "subreceptive" behavior, i.e., sexual approaches and partial lordoses (cf. Burley, Note 2), but

the few resultant male mounting attempts never resulted in intromission and, instead, evoked aggressive female responses. The five that exhibited such behavior did so on 1, 2, 3, 3, and 5 of the 10 test days, with no apparent cyclicity of recurrences. All five subreceptive females were in the UFS-tested group (Fisher exact probability test, two-tailed $p = .015$).

For simplification of presentation, a compound aggression score was computed by summing points as follows: 1 point for each upright aggressive posture, 2 for sidling, boxing, or chasing, and 2-5 to each participant in a fight according to its severity. The differences and trends presented below for these aggression scores are similar in each measure separately.

Aggression scores over trials are presented in Figure 2. A proportion-of-aggression score for each trial was computed for each actor from the points assigned. Over all trials females perpetrated 70% of the aggression in UFS-tested pairs and 59% in FS-tested pairs, $t(10) = 2.35$, $p < .05$. On Day 1 (on which no female was yet subreceptive) females performed 79% of the aggressive behavior in UFS pairs and 64% in FS pairs, $t(10) = 1.96$, one-tailed $p < .05$.

Table 4 presents mean aggression scores and scent-marking over all trials. There

were large sex differences: Females were more aggressive than males in all 12 test pairs, and males marked more than females in 11 of the 12. Females were initially more aggressive in UFS pairs than in FS pairs (Figure 2); by separate t tests for each day, UFS females were significantly more aggressive ($p < .05$) on Days 2, 4, and 5.

Discussion

It has often been assumed that male gerbil scent-marks serve a "territorial" function. This ambiguous term needs clarification. It is clear that marks are attractive rather than repulsive to other males (Baran, 1973; Baran & Glickman, 1970; Thiessen, Lindzey, & Blum, 1970), and this is generally true in mammals (Johnson, 1973). We now find (Experiments 1 and 2) that the presence of male marks in a novel situation elicits further marking, as it does in most mammals, a result that is at best anomalous under the territorialism hypothesis.

In an attempt to salvage that hypothesis, it has been suggested that the territorial defense function of the marks might depend on previous encounters between intruder and marker. This hypothesis also

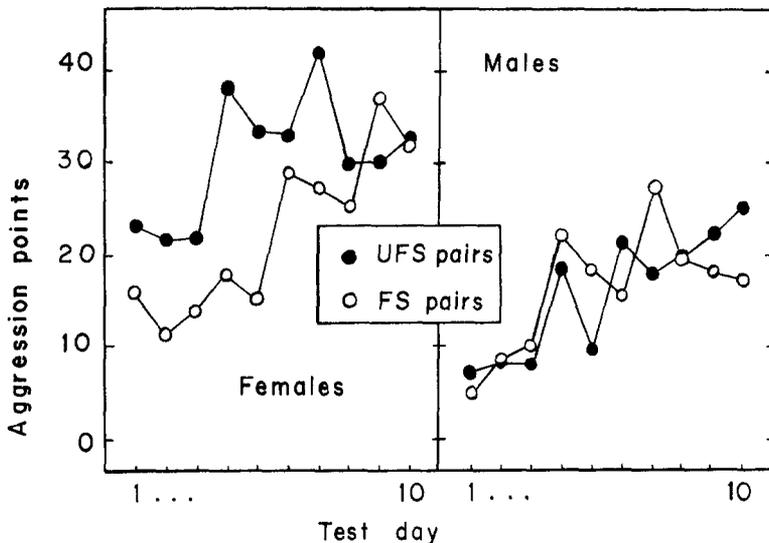


Figure 2. Aggressive behavior in opposite-sex encounters as a function of the olfactory familiarity of the male to the female (Experiment 4). (Abbreviations: UFS = unfamiliar smelling; FS = familiar smelling.)

Table 4
Mean Aggression and Scent-Marking per 15-Min Test Trial (Experiment 4)

Variable	FS pairs		UFS pairs	
	Male	Female	Male	Female
Aggression points	16.1	22.5	16.4	30.7
Scent-marking	19.0	.6	20.2	3.3

Note. Abbreviations: FS = male olfactorily familiar to female; UFS = male olfactorily unfamiliar to female.

lacks support. Although defeat suppresses marking (Nyby, Thiessen, & Wallace, 1970; Thiessen et al., 1971), attempts to show that defeat leads to avoidance of the victor's scent have not succeeded (Thiessen & Dawber, 1972; Thiessen et al., 1971). In fact, evidence for a repulsive function of mammalian scent-marks, so widely assumed, is surprisingly scanty (Johnson, 1973; but see Jones & Nowell, 1973; Peters & Mech, 1975).

In several species of Saharan gerbils (*M. libycus*, *M. crassus*, *P. obesus*) identical scent-marking behavior occurs. In these species, as in *M. unguiculatus*, males have a larger gland and mark a novel terrarium more than do females (unpublished data). Nevertheless, males do not exhibit a territorial organization; defended areas of exclusive use are maintained only by females (Daly & Daly, 1974, 1975a, 1975b). These observations cast considerable doubt on the assumption of a territorial function of marking. It remains possible that there are more subtle effects on receiver behavior, such as increased wariness (cf. Mykytowycz, 1965; Platt, 1976), and that such effects might serve to defend a resource, such as mating opportunities, for the sender, thus functioning "territorially" in a special sense. Even this sort of defense function seems unlikely in view of the countermarking observed in Experiments 1 and 2 and in view of Roper and Polioudakis' (in press) observation that gerbils in a seminatural environment did not defend areas or other gerbils that they marked; instead, a male protected mating rights by attacking another male that was otherwise tolerated. In nature,

M. libycus males actively guard estrous females (personal observations).

If there are any such intrasexual functions of scent-marking in male gerbils, they might better be construed as related to dominance structures, a social method of resolving competition that can be viewed as an alternative to territorialism (Davis, 1958). Group-maintained gerbils exhibited a male dominance hierarchy (Gallup & Waite, 1970; but see Roper & Polioudakis, in press, who doubt that this phenomenon is meaningful). Future experiments might investigate the ventral gland's role in achieving and maintaining high status.

We must also call into question the notion that scent-marking is a unitary phenomenon. Thiessen, Blum, and Lindzey (1970) suggested that ventral marking, urination, and defecation are marking behaviors with similar causation and functions. Their causation is distinct: Ventral marking was elevated in the presence of another male's odors (and in proportion to their magnitude), while urination was depressed by the same stimuli. Their communicative functions are surely also distinct: In Experiments 1 and 2, ventral marks influenced the behavior of a subsequent male, whereas no effects of urine or feces could be discerned.

On the basis of Experiments 3 and 4, an adaptive function of male scent-marking behavior can be proposed. A female that has been olfactorily familiarized with a particular male through exposure to his ventral marks reacts less aggressively to that male than to an olfactorily unfamiliar male. Such an effect would benefit the male in nature if the mitigation of female aggressiveness permitted the familiar-smelling male to maintain proximity to the female through proestrus and hence be first on the scene during estrus. Direct effects of ventral gland odors upon reproduction were not detected, but the possibility deserves further study.

The above studies demonstrate that ventral gland scent-marking is capable of selectively mitigating female aggressiveness. Its true biological functions, which are those selective (reproductive) conse-

quences relevant to the behavior's evolution and persistence in natural populations (Williams, 1966), cannot be conclusively determined by laboratory studies alone. Confirmation from experimental work in the field is necessary.

Reference Notes

1. Halpin, Z. T. Personal communication, July 1976.
2. Burley, R. A. *Role of hormones in the patterning of oestrus behaviour in the Mongolian gerbil (Meriones unguiculatus)*. Paper presented at the International Ethological Conference, Parma, Italy, September 1975.

References

- Baran, D. Responses of male Mongolian gerbils to male gerbil odors. *Journal of Comparative and Physiological Psychology*, 1973, *84*, 63-72.
- Baran, D., & Glickman, S. E. "Territorial marking" in the Mongolian gerbil: A study of sensory control and function. *Journal of Comparative and Physiological Psychology*, 1970, *71*, 237-245.
- Blum, S. L., Balsiger, D., Ricci, J. S., & Spiegel, D. K. Effects of early exposure to ventral gland odor on physical and behavioral development and adult social behavior in Mongolian gerbils. *Journal of Comparative and Physiological Psychology*, 1975, *89*, 1210-1219.
- Daly, M., & Daly, S. Spatial distribution of a leaf-eating Saharan gerbil (*Psammomys obesus*) in relation to its food. *Mammalia*, 1974, *38*, 591-603.
- Daly, M., & Daly, S. Behavior of *Psammomys obesus* (Rodentia: Gerbillinae) in the Algerian Sahara. *Zeitschrift für Tierpsychologie*, 1975, *37*, 298-321. (a)
- Daly, M., & Daly, S. Socio-ecology of Saharan gerbils, especially *Meriones libycus*. *Mammalia*, 1975, *39*, 298-311. (b)
- Davis, D. E. The role of density in aggressive behaviour of house mice. *Animal Behaviour*, 1958, *6*, 207-210.
- Ewer, R. F. *Ethology of mammals*. New York: Plenum Press, 1968.
- Gallup, G. G., & Waite, M. S. Some preliminary observations on the behavior of Mongolian gerbils (*Meriones unguiculatus*) under semi-natural conditions. *Psychonomic Science*, 1970, *20*, 25-26.
- Halpin, Z. T. Individual differences in the biological odors of the Mongolian gerbil (*Meriones unguiculatus*). *Behavioral Biology*, 1974, *11*, 253-259.
- Johnson, R. P. Scent marking in mammals. *Animal Behaviour*, 1973, *21*, 521-535.
- Johnston, R. E. Scent marking by male golden hamsters (*Mesocricetus auratus*): I. Effects of odors and social encounters. *Zeitschrift für Tierpsychologie*, 1975, *37*, 75-98.
- Jones, R. B., & Nowell, N. W. Aversive effects of the urine of a male mouse upon the investigatory behaviour of its defeated opponent. *Animal Behaviour*, 1973, *21*, 707-710.
- Mitchell, O. G. The supposed role of the gerbil ventral gland in reproduction. *Journal of Mammalogy*, 1967, *48*, 142.
- Mykutowycz, R. Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit, *Oryctolagus cuniculus* (L.). *Animal Behaviour*, 1965, *13*, 400-412.
- Norris, M. L., & Adams, C. E. Aggressive behaviour and reproduction in the Mongolian gerbil (*Meriones unguiculatus*), relative to age and sexual experience at pairing. *Journal of Reproduction and Fertility*, 1972, *31*, 447-450.
- Nyby, J., Thiessen, D. D., & Wallace, P. Social inhibition of territorial marking in Mongolian gerbil (*Meriones unguiculatus*). *Psychonomic Science*, 1970, *21*, 310-312.
- Peters, R. P., & Mech, L. D. Scent-marking in wolves. *American Scientist*, 1975, *63*, 628-637.
- Platt, W. J. The social organization and territoriality of short-tailed shrew (*Blarina brevicaudata*) populations in old-field habitats. *Animal Behaviour*, 1976, *24*, 305-318.
- Renoux, G. About *Meriones*. *Science*, 1957, *125*, 314.
- Rieder, C. A., & Reynierse, J. H. Effects of maintenance condition on aggression and marking behavior of the Mongolian gerbil (*Meriones unguiculatus*). *Journal of Comparative and Physiological Psychology*, 1971, *75*, 471-475.
- Roper, T. J., & Polioudakis, M. The behaviour of Mongolian gerbils in a semi-natural environment, with special reference to ventral marking, dominance and sociability. *Behaviour*, in press.
- Shorr, E. A new technic for staining vaginal smears: III. A single differential stain. *Science*, 1941, *94*, 545-546.
- Sokolov, W., & Skurat, L. A specific midventral gland in gerbils. *Nature*, 1966, *211*, 544-545.
- Swanson, H. H. Sex differences in behaviour of the Mongolian gerbil (*Meriones unguiculatus*) in encounters between pairs of same or opposite sex. *Animal Behaviour*, 1974, *22*, 638-644.
- Thiessen, D. D. The roots of territorial marking in the Mongolian gerbil: A problem of species-common topography. *Behavior Research Methods & Instrumentation*, 1968, *1*, 70-76.
- Thiessen, D. D. Footholds for survival. *American Scientist*, 1973, *61*, 346-351.
- Thiessen, D. D., Blum, S. L., & Lindzey, G. A scent marking response associated with the ventral gland of the Mongolian gerbil (*Meriones unguiculatus*). *Animal Behaviour*, 1970, *18*, 26-30.
- Thiessen, D. D., & Dawber, M. Territorial exclusion and reproductive isolation. *Psychonomic Science*, 1972, *28*, 159-160.
- Thiessen, D. D., Lindzey, G., & Nyby, J. The effects of olfactory deprivation and hormones on territorial marking in the male Mongolian gerbil (*Meriones unguiculatus*). *Hormones and Behavior*, 1970, *1*, 315-325.
- Thiessen, D. D., Owen, K., & Lindzey, G. Mechanisms of territorial marking in the male and female Mongolian gerbil (*Meriones unguiculatus*).

- Journal of Comparative and Physiological Psychology*, 1971, 77, 38-47.
- Vaughan, G. M., & Corballis, M. C. Beyond tests of significance: Estimating strength of effects in selected ANOVA designs. *Psychological Bulletin*, 1969, 72, 204-213.
- Williams, G. C. *Adaptation and natural selection*. Princeton, N. J.: Princeton University Press, 1966.
- Winer, B. J. *Statistical principles in experimental design*. New York: McGraw-Hill, 1962.

Received September 23, 1976 ■