TERRITORIAL BEHAVIOR
OF THE KANGAROO RAT,
Dipodomys ordii richardsoni

A Thesis

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INTRODUCTION

Most mammalian orders have evolved acute olfactory faculties which are utilized for communication purposes. Chemical signals derived from urine, feces, or cutaneous scent glands are deposited in the environment through the employment of specialized action patterns. The ethological implications of these action patterns in connection with glandular sites associated with olfactory communication are of particular importance in individual identification within many mammalian groups. Among territorial and asocial species the need for such individual identification mechanisms is crucial.

Within the sciuromorph rodent family Heteromyidae, Dipodomys, the kangaroo rat, possesses a mid-dorsal, holocrine skin gland composed of enlarged and modified sebaceous gland units. Conflicting reports attributing gland function to both pelage dressing and scent responses have been recorded (Bailey, 1931; Tappe, 1941; and Quay, 1953). Although the genus is characterized by high intraspecific aggressiveness, there are also conflicting reports of territoriality (Fitch, 1948; Eisenberg, 1963; and Garner, 1974).

The existing disparities concerning both territoriality and dorsal gland function prompted this study. Research was conducted with the kangaroo rat, Dipodomys ordii richardsoni (Setzer, 1949), to determine if territoriality exists as a behavioral phenomenon, and if the dorsal gland functions as a scent marker for individual identification.

The investigation was conducted in three phases:

1. Determination of territoriality within a naturally-occurring population.
2. Identification of behavioral marking action patterns.
3. Histological comparison of glandular regions within the continuous epidermis.

Literature Review

Territorial studies have been conducted on a number of mammalian species. Such studies have also demonstrated the existence of specialized odoriferous glands for territorial marking among mammals. Mykytowycz (1965) reported the presence of such odoriferous glands in all species of mammals whose behavior has been carefully studied. Burt (1943) stated that the territorial trait is not developed to the same degree in all species known to possess it but its wide distribution among the vertebrates supports the theory that territoriality is a basic characteristic of animals. Eibl-Eibesfeldt (1970) agrees that many animals defend against other members of their species a particular area of their habitat as a territory and often mark this territory in a specific manner.

The simplest form of territorial organization, according to Ewer (1968), occurs among those species which are solitary, each individual occupying its own territory. Eisenberg (1963) referred to a "closed" social system characterized by a narrow range of tolerance for conspecifics. Among solitary species the predominant function of the territory is to space the individuals adequately in order to provide sufficient living space. Eisenberg (1963) also suggested that the exploitation of arid lands necessitated behavioral adaptations

promoting dispersion and some form of territoriality because of the strict limitations the more arid habitats present on the density at which a population can successfully utilize a given area.

The rodent family Heteromyidae exemplifies the asocial, dispersed type of social system tending toward adult isolation. Within the Heteromyidae, Dipodomys has a reputation for intense intraspecific aggressiveness, with only one individual kangaroo rat occupying a given burrow site (Bailey, 1931; Fitch, 1948; Reynolds, 1960; and Eisenberg, 1963). The range for Dipodomys extends throughout the semi-arid and arid regions of western North America, where they show a highly dispersed pattern of spatial distribution (Dale, 1939; and Eisenberg, 1963). Dale (1939) characterized the species D. ordii as being the most widespread in distribution of any of the members of the genus. The geographic range of the 35 subspecies of Dipodomys ordii extends from southern Canada south through the Mexican Tableland and from Nevada east to the Great Plains in Nebraska, Kansas, and Oklahoma (Fig. 1), (Setzer, 1949).

Fitch (1948) reported an absence of true territoriality among kangaroo rats. Eisenberg (1963) concluded from his study of heteromyid rodent behavior that territorial defense for Dipodomys seemed to be restricted to the limited area in the vicinity of and including the burrow. Garner (1974) also concluded that D. ordii exhibits a degree of territoriality.

Montagna (1962) described the histology and histochemistry of mammalian unmodified sebaceous glands. The dorsal, holocrine skin gland of the kangaroo rat has been described by Quay (1953). Tappe (1941) proposed that the dorsal gland in the Tulare kangaroo rat,

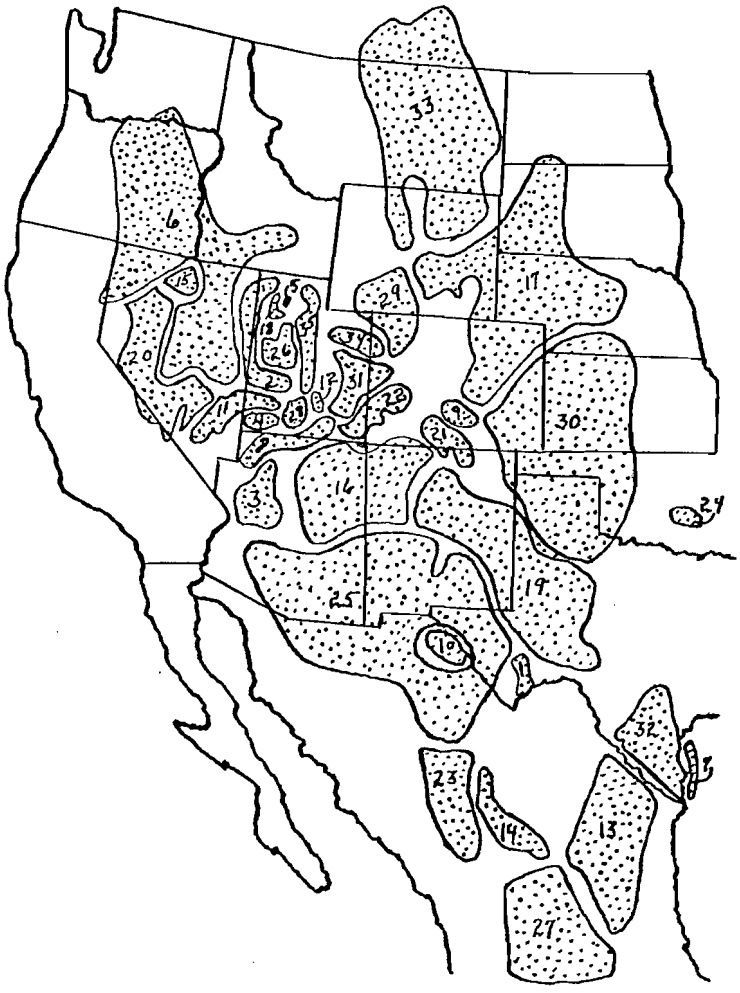

Figure 1. Distribution of subspecies of Dipodomys ordii (Setzer, 1949).

1. D. o. attenuatus
2. D. o. celeripes
3. D. o. chapmani
4. D. o. cinderensis
5. D. o. cineraceus
6. D. o. columbianus
7. D. o. compactus
8. D. o. cupidineus
9. D. o. evexus
10. D. o. extractus
11. D. o. fetosus
12. D. o. fremonti
13. D. o. fuscus
14. D. o. idoneus
15. D. o. inaquosus
16. D. o. longipes
17. D. o. luteolus
18. D. o. marshalli
19. D. o. medius
20. D. o. monoensis
21. D. o. montanus
22. D. o. nexilis
23. D. o. obscurus
24. D. o. oklahomae
25. D. o. ordii
26. D. o. pallidus
27. D. o. palmeri
28. D. o. panguitchensis
29. D. o. priscus
30. D. o. richardsoni
31. D. o. sanrafaeli
32. D. o. sennetti
33. D. o. terrosus
34. D. o. uintensis
35. D. o. utahensis

D. heermanni tularensis, was important for hair and skin conditioning in response to the arid environment. Quay (1953) rejected this proposal both on the assumption that active sebaceous glands are probably distributed through nearly all of the skin, with their secretions functioning as a pelage dressing, and because the dorsal gland is a localized structure. Concerning scent function, there are no sexual differences in secretory activity of the dorsal gland in D. ordii. The functional significance of the gland appears to concern scent responses (Quay, 1953).

Eisenberg (1963) studied the behavior of Dipodomys and identified belly-rubbing and side-rubbing as components of a single behavioral movement--sandbathing. Sandbathing was credited with the dual function of chemical communication and pelage dressing. The perineal drag was also credited with individual marking in Dipodomys.

Description of the Study Area

Field research was conducted at the Sandhills Game Management Area, Pratt County, Kansas. This region of low, undulating hills encompasses an area of approximately seven square miles in north-west Pratt County in south-central Kansas (Fig. 2). Field studies were restricted to Section 31 within the Game Management Area. Except for the water discharge from one windmill, there was no natural source of free water present within this section.

Annual rainfall averaged approximately 22 inches. Soil composition throughout the study area was predominantly sand. Vegetation density was greatest in the depressions between the low hills, with the slopes of the hills being only sparsely vegetated (Fig. 3). The

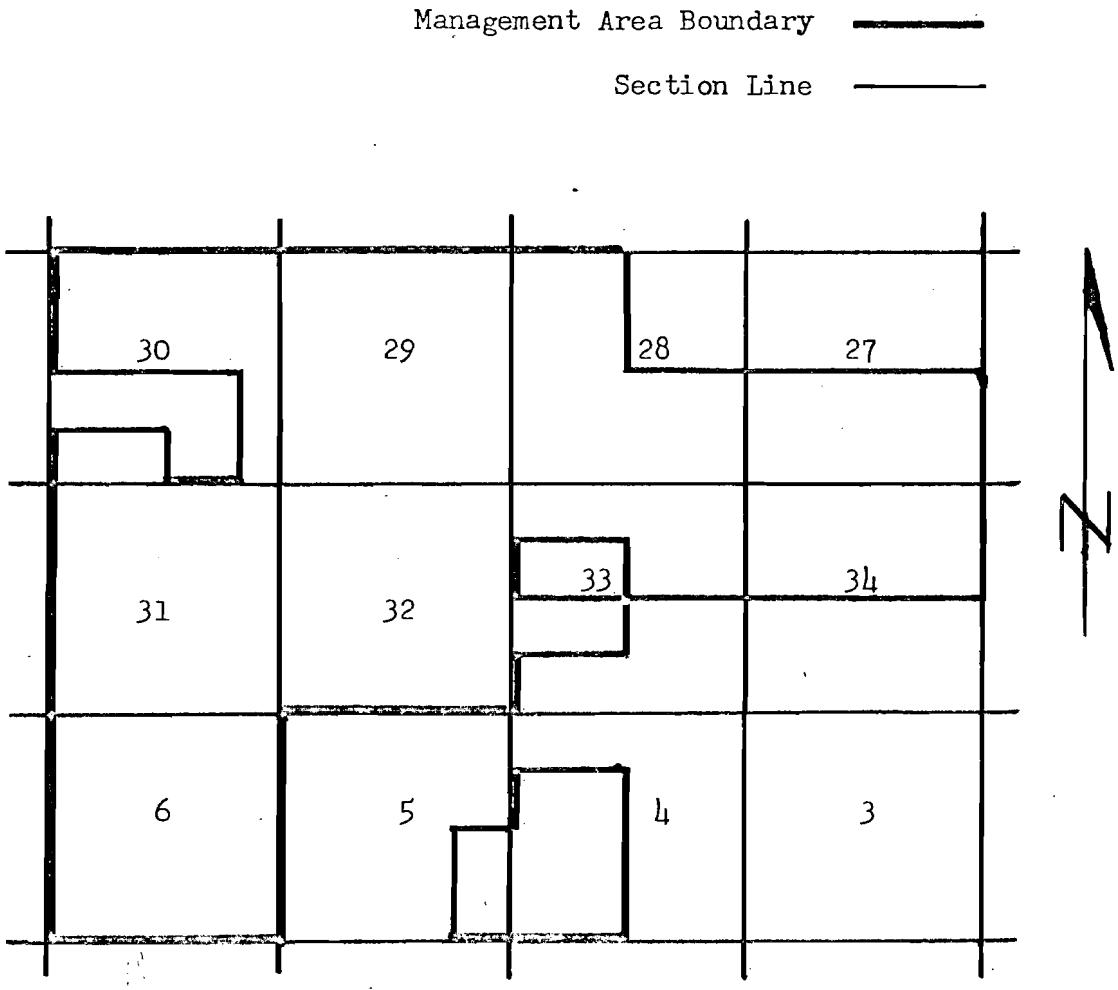

Figure 2. Pratt Sandhills Game Management Area, Pratt County, Kansas. Field study site was restricted to Section 31.

Figure 3. Surface view of typical study plot terrain at the Sandhills Game Management Area, Pratt County, Kansas.

vegetation throughout the area was composed of forbes interspersed among clumping-type grasses among which were Triplasis purpurea (sandgrass), Sporobolus pyramidatus (dropseed), Andropogon scoparius (little bluestem), Bouteloua curtipendula (sideoats grama), Panicum virgatum (switchgrass), and Cenchrus pauciflorus (sandbur), (Gates, 1937).

Throughout those areas of meager vegetation with exposed sandy soil there was much evidence of kangaroo rat activity, exemplified by the presence of runways and burrow sites. The surface area in the immediate vicinity of a burrow entrance was usually free of vegetation. Virtually all movement of D. ordii in the study area was restricted to runways which were maintained throughout the vicinity of the burrow site. Runways averaged 15.0 cm. in width and were maintained vegetation free.

METHODS AND MATERIALS

Burrow sites in the Pratt Sandhills Game Management Area were situated throughout the study area primarily in areas of sparse vegetation and exposed sand. A systematic survey was made of the study area to locate all burrow sites. Each site was then marked with an identifying marker. Occupancy of each burrow site was determined by a series of live trappings. A Sherman live-trap, baited with a standard grain mixture of sunflower seeds, milo, millet, wheat, and hulled oats, was positioned at each burrow entrance for three consecutive nights. Each morning during the trapping period captured rats were sexed and toe clipped for identification. Toe clipping was restricted to the hind feet. The appropriate toe was amputated with surgical scissors at the most proximal possible location and the wound was coated with an antiseptic iodine solution. Consecutive nights of trapping served to confirm burrow occupancy. Seven days after the initial trapping period an additional three consecutive nights of live trapping was carried out to substantiate further burrow occupancy.

All runways visibly associated with each burrow site were charted and measured. The straight line distance between adjacent burrow sites was also measured. On 15 randomly selected nights during the period May, 1974, to August, 1974, runways associated with each of the marked burrow sites were swept clear of all tracks. The following morning at 0600 hours runways were checked for tracks made by toe-clipped kangaroo rats. The maximum distance of an individual kangaroo rat's travel on the runways associated with its burrow site was charted.

Kangaroo rats not utilized in the tracking study were trapped during August, 1974, from the same study area. Sherman live-traps, baited with the standard grain mixture, were utilized. Captured rats were maintained individually in glass aquaria measuring 50 x 27 x 30 cm. Each aquarium was provided with a sand covering on the bottom and a metal nesting can. A grain mixture of sunflower seeds, wheat, milo, millet, and hulled oats was provided daily. Lettuce was added on alternating days. A supply of free water was not available to captive rats. Rats were maintained either exposed to a light cycle of natural sunlight or in the laboratory without regard for the natural light cycle.

Observations were initiated in September, 1974, for the purpose of identifying potential marking behaviors. Rats used for this study were exposed to the natural light cycle. Observation enclosures were designed with an artificial burrow system having one burrow entrance. The enclosure surface was covered with sand. A daily ration consisting of the standard grain mixture and lettuce was provided at a given feeding locus on the surface. A total of 10 rats (five males and five females) was retained in such artificial burrows. Visual observations began at dusk each evening and continued for two hours. One rat was randomly selected for each night's observation. There was a total of 22 observation nights during which each rat was observed at least once and no single rat was observed more than three times. Minimal illumination was provided by a 25 watt red incandescent light. All rat behavior which was visibly observed on the surface area outside the burrow was recorded.

Captured kangaroo rats kept without regard to the natural light cycle received 12 hours of light followed by 12 hours of dark. These rats were observed in situations specifically designed to examine potential marking functions of previously observed behavior patterns. Six male and four female rats were placed in individual observation pens, each with a sand-covered surface measuring 50 x 30 cm., for three consecutive nights in order to define marking behaviors exhibited when encountering a neutral area. The one centimeter deep surface covering of sand within each enclosure remained unchanged during these three nights. A rat was introduced into an observation pen illuminated by incandescent red light for 15 minutes. All observable behaviors were recorded on a 20-column Esterline polygraph event recorder.

Individual rats were introduced into one another's resident pens to determine if marking behavior exhibited in a neutral area was altered within the territorial area of another rat. Eleven males and five females were used. Under red light illumination, an "intruder" rat was placed into the pen of another rat for a 15 minute interval while the "occupant" rat was removed. All observable behavior was recorded on the polygraph event recorder. After removal of the "intruder" rat, the "occupant" rat was replaced and its behavior was recorded for 15 minutes. This procedure was repeated for three consecutive nights. Such "intruder" to "occupant" combinations consisted of male to male, female to female, male to female, and female to male combinations.

In order to delimit the pheromone source associated with the observed marking behavior, a fourth group of rats (five males and three females) was confined in metabolism cages. These cages allowed for

controlled food and water input and collection of urine and feces output. A sand substrate was not available to the rats retained in these metabolism cages. Three test groups and a control group, each consisting of two rats, were maintained for 10 day testing intervals under standard temperature, humidity, and light conditions. A total of five testing periods was conducted. Each test group received an unlimited quantity of Purina Laboratory Chow but with controlled water input. Group I received a water supply restricted to 1.0 ml. per 24 hours. Group II was restricted to 0.5 ml. of water per 24 hours. Group III did not have an access to a source of free water, while the Control Group received an unlimited water supply. Commercial laboratory chow was substituted for the standard grain mixture, since such pellets would have a negligible water content. Every 24 hours water consumption and urine output were recorded and the rat was removed to a sand substrate observation pen measuring 50 x 30 cm. for a 15 minute period. Observation pens were illuminated by incandescent red light and all observed behavior was recorded on the polygraph event recorder.

Histology

Preparations of the specialized dorsal sebaceous gland and dermal tissue from the dorsum of the head, ventral body surface (submandibular, thoracic, and abdominal), perineal region, inner thigh region, and lateral hip were made in order to determine the distribution of unmodified sebaceous glands as compared to the component modified sebaceous glands of the dorsal glandular area. Snap-trapped kangaroo rats were placed in a 10 percent formalin solution immediately upon being removed from the traps. Dermal tissue samples 0.5 cm. in area were taken

from a shaved surface and fixed in Bouin's Fixative. Dehydration was then achieved by immersing the tissue in a series of aqueous ethyl alcohol solutions. The alcohol series changed through solutions of 50, 70, 95 percent and absolute alcohol. "Clearing" of tissues was accomplished by passing them through a xylene bath. Paraffin, with a melting point in the 54^{o} to 56^{o}C range, was used for infiltrating the tissues; sections were then embedded.

Following embedding, blocks were sectioned either longitudinally or transversely at 10 microns thickness using a Spencer 820 microtome. Tissue ribbons were mounted on slides as serial sections. Sections were deparaffinized using xylene as the solvent. This was followed by removal of the xylene with absolute alcohol. The slides were then hydrated through a series of decreasing alcohol/increasing aqueous solutions of 95 and 70 percent alcohol. Staining was with Delafield hematoxylin and eosin counterstain.

Slides were observed with a light microscope in order to survey the unmodified sebaceous glands distributed throughout the dermis and to compare them with the modified sebaceous elements of the dorsal gland. This comparison was based on a determination of mean alveolar volume for the dermis of the dorsal head, venter, perineal region, lateral hip, inner thigh region, and the dorsal sebaceous gland. Each glandular alveolus was measured at its widest point with a calibrated ocular micrometer by observing the serial section showing maximum surface area. All diameter measurements for a particular somatic region were averaged in order to obtain a mean alveolar width per body region for each rat. Since most glandular alveoli were spherical in shape, alveolar volume was computed according to the geometric formula for

the volume of a sphere. Dermal samples were taken from 11 specimens of D. ordii. All rats, five males and six females, were adults collected at the same time from the same population.

RESULTS

Territoriality

The burrow sites of *Dipodomys ordii* contained from one to four burrow entrances in close proximity to one another. Generally, two entrances of a given burrow site were not separated by a distance of more than one meter. Essentially, all movements of *D. ordii* were confined to runways which were maintained free of obstructing vegetation in the vicinity of the burrow site (Fig. 4). Three fundamental purposes appeared to be served by the runways: (1) they led to areas of extensive vegetation which served as feeding sites; (2) they led to areas of open sand used for sandbathing; and (3) neighboring burrow sites were interconnected to a limited extent by runways. Runways at the study site averaged 15.0 cm. in width and extended from the burrow entrance into the surrounding environment an average of 7.72 m. The mean distance separating adjacent burrow sites was 24.82 m. Since the mean distance for a runway associated with any of the observed burrow sites was 7.72 m., the minimal spacing of 24.82 m. between burrows would appear to provide some isolation among conspecifics.

Utilization of the runway is presumably necessary to accommodate the adaptation of the kangaroo rat to bipedal locomotion. This type of locomotion is most efficient on an open surface unencumbered by vegetation. Captured rats released in areas of dense vegetation were observed to be impeded in their escape movements when compared with rats released on a runway. Rats which were released on a runway (associated with their burrow site) and pursued always followed a course fixed on

Figure 4. Runways of D. ordii as they progress through the surrounding vegetation providing an unobstructed surface area for maximum mobility.

the runway until reaching a burrow entrance or escape tunnel. This rigid adherance to the runway and avoidance of random movement throughout the general area of the burrow site would seem to indicate that movement was limited to the runways.

Subsidiary escape tunnels were located throughout the runway system. The entrance to an escape tunnel was of approximately the same dimensions as the entrance of a burrow. However, escape tunnels extended into the soil a mean distance of only 23.0 cm. These escape tunnels were frequently located at either the termination of a runway or at a curve in the runway and provided a source of protection for the rats during nocturnal forays.

Certain runways were designated as being associated with feeding sites (Fig. 5). These runways either terminated in an area of dense vegetation or the runway was bordered by such dense vegetation. In either situation, the runway provided the occupant rat with access to a food supply of seeds and succulent vegetation. It was observed on several occasions, when a runway was bordered by an area of much vegetation, that the surface of the runway would become strewn with seeds from surrounding grasses. This would supply the occupant rat with an abundant and readily obtainable food supply. When such a situation existed, which was rather frequent, it was observed on the following morning that the runway had been cleared of seeds, presumably by the occupant rat.

Occasionally, a runway would terminate in an open area of loose sand or a runway would be extensively widened and provide an exposed area of sand. Such areas, designated as sandbathing sites, showed evidence of the body drags associated with the sandbathing behavior.

Figure 5. Runway bordered by dense vegetation and used as a feeding area.

Not all of the runways associated with a burrow site were traveled during any one night's activity. In locations where runways interconnected neighboring burrow sites there was an absence of any indication of travel into the vicinity of the neighboring burrow site. On only limited occasions did the tracks of two different kangaroo rats overlap on these interconnecting runways. On the occasions where this trespassing existed there was seldom an indication of an altercation between the two rats. It would appear that movements of individual rats occurred at different times during the night. Generally, however, if the interconnecting runway between neighboring burrow sites was traveled, neither of the rats traveled the central portion of the runway midway between their respective burrows. It appeared that the distance traveled on such a connecting runway did not greatly exceed the average length of a typical runway.

During the four month period (May, 1974, to August, 1974) in which field studies of D. ordii occurred, the established burrow sites were continually occupied by their resident, and the associated runways were maintained without appreciable expansion or deletion. Utilization of the habitat for burrow sites was so extensive that sub-adult rats could only establish themselves in vacant burrow systems. Surface area was not available to accommodate new burrow systems with sufficient runway space. During this four month study only two sub-adult rats established themselves in previously abandoned burrows. It was intended that this field study would be continued over a one year period in order to monitor the stability of burrow occupancy. However, rains during the final week of August, 1974, caused such frequent flooding of the study site that an excessive proportion of the kangaroo rat population was

destroyed, resulting in termination of the study at that time. From information accrued during the initial four months of periodic live-trapping, it would seem that the range occupied by an individual rat, once established and assuming the continuation of favorable ecological factors, remained relatively stable.

From observations of the release of captured kangaroo rats on runways, compared with individuals released into the surrounding vegetation, there seemed to be a physical advantage complementing bipedal locomotion obtained through the use of an obstacle-free runway. This close association between bipedal locomotion and the runway system has evolved into a rigid adherance to the runway and avoidance of random movement throughout the general area of the burrow site. Restriction of movement to the established runways coupled with D. ordii's relatively stable home range and asocial behavior would seem to indicate an adaptive value in territorial behavior.

Marking Behavior

Initial unstructured observations were undertaken in observation enclosures for the purpose of defining behavioral action patterns that might be of importance as potential territorial marking mechanisms. For example, after making a cautious exit from the burrow, characterized by a detailed olfactory scrutiny of the environment, the rat advanced to a sandbathing site. This sandbathing site was a distinctly defined locus within the environment and was unobstructed by vegetation or other physical objects, allowing unencumbered sandbathing behaviors.

Sandbathing was an activity involving two distinct action patterns; the lateral hip drag and the ventral drag. Both types of dragging

behavior were preceded by pushing or digging at the sand with the forepaws. If a series of drags occurred in rapid succession, the introductory digging component was not repeated prior to each drag. In a series of drags, the digging phase was a precursor for the entire series. The lateral hip drag action pattern consisted of turning the side of the body toward the substrate, lowering the flank and hip surface to the substrate, and extending the body forward. The thrust for this gliding movement came from the hind limbs, which were laterally compressed and extended away from the body to the side opposite the dragging surface at approximately 45°, while the sides of the feet were braced against the substrate (Fig. 6). Because the hind limbs were pressed together in the lateral hip drag, the perineal region did not come into contact with the substrate. In the ventral drag the ventrum was pressed against the substrate while the body was extended forward (Fig. 7). Impetus for the ventral drag was also in the hind limbs, although in this action pattern the limbs were retained directly under the body with the pad of the foot braced against the substrate. With the pad of the foot being used as a brace against the substrate the perianal region tended to be held above the substrate. A perineal drag was observed on limited occasions in which the perianal region was pulled forward while in contact with the substrate. On the few occasions in which it was displayed, the perineal drag was added as a terminal phase of a ventral drag.

Sandbathing, consisting of both lateral drag and ventral drag action patterns, was restricted to specific dusting sites and appeared to function as pelage grooming. However, as a kangaroo rat commenced exploring the home range it randomly engaged in one or several lateral

Figure 6. Lateral hip drag. Left hip is being dragged against the substrate while the hind limbs are extended to the opposite side and used to propel the animal forward.

Figure 7. Ventral drag. Ventrum is being dragged against the substrate as the animal is extended forward by the hind limbs which are arched under the rat.

hip drags and/or ventral drags throughout the range. Observation revealed that the majority of this type of behavior was limited to the lateral hip drag. The purpose of this behavior did not appear to include grooming, especially since the animal had previously completed an elaborate series of drags and pelage grooming at the sandbathing site. It seems plausible to conclude that this behavioral action pattern might be a potential source of individual identification.

During the series of initial observation, rats were presented with a new environmental situation in order to analyze any behavioral modifications induced by the new environmental conditions. Prior to observation, all of the sand was removed from the rat's pen, except for that at the sandbathing locus, and fresh sand was added to the remainder of the pen. Upon emerging from the burrow, the rat became markedly wary, and quickly and cautiously surveyed the entire surface of the pen. The animal maintained an elongate, horizontal posture with the ears widely spread while engaged in this exploration. When the sandbathing site was determined to be familiar, the rat based itself at the site and made brief exploratory investigations into the unfamiliar area, frequently returning to the familiar sandbathing area. Upon completing its investigation of the new substrate, the rat assumed the normal foraging posture characterized by a more rounded contour and a higher profile from the substrate. In this posture the animal would move about the entire pen engaging in an excessive number of lateral hip drags. During such a movement over fresh sand, ventral drags were seldom performed. There were no sexual distinctions in the manner in which these behaviors were manifested.

Once these potential marking behaviors were described as a result of the primary observations, structured testing situations were devised to examine further these behavioral mechanisms. When rats were observed individually in a neutral pen for three consecutive nights, a definite behavioral pattern was revealed (Table I). On the first night of exposure the animal maintained the elongate, horizontal posture of quadruped locomotion with slow and deliberate movements. Lateral hip drags and ventral drags were displayed as the rat proceeded to explore the unfamiliar pen. Lateral hip drags greatly exceeded ventral drags; the ratio of lateral drags to ventral drags was 5:1. On the second night of exposure, the animal initially assumed the elongate, horizontal posture with extremely deliberate movements. During this period lateral drag and ventral drag behavior occurred. However, the dragging action pattern occurred less frequently than on the first night, the cautious, elongate posture phase was of shorter duration and the rat soon assumed an upright posture of more rounded contours and actively explored the environment without the deliberate movements of the previous posturing. On the third night the period of elongate, horizontal posturing and the accompanying lateral drag and ventral drag action pattern was markedly abbreviated. After a brief introductory period with only a minimum of dragging behavior, the rat assumed the upright and exploratory posture.

A significant difference ($P > 0.01$) in the quantity of dragging action patterns occurred as days progressed on the neutral sand substrate of the observation pens. Among the kangaroo rats observed, no added variance component was demonstrated ($P < 0.05$).

Table I. Total number of body drags during a 15 minute period each night for three consecutive nights in a neutral pen. Total number of drag action patterns is a composite of lateral hip drags and ventral drags. (M) male; (F) female.

RAT	DAY 1	DAY 2	DAY 3
1A (M)	37	13	7
1B (M)	25	20	7
1C (F)	20	11	5
1D (M)	11	4	0
1E (F)	27	18	8
1F (F)	15	13	6
1G (M)	16	9	5
1H (M)	16	10	8
1K (M)	15	11	4
1L (F)	20	9	7

On the fourth night, feces from another rat were added to the observation pen. The feces were collected from metabolism cages so that the fecal material would not be exposed to urine or the external body surface of the rat which could potentially alter any olfactory response. In order to determine more accurately if the observed rat was reacting to the introduced fecal matter, it was distributed in a pattern on the sand substrate. Responses were recorded on a polygraph event recorder only if the response was exhibited in association with the fecal pattern. In each test situation the animal did not show any response to the introduced feces except for occasional olfactory investigation. The rats, however, did not follow the patterned arrangement of the fecal material and no behavioral responses, i.e. dragging behaviors, were displayed as a direct response to the presence of this foreign material.

Individual kangaroo rats were introduced into the "home" pens of other kangaroo rats for the purpose of determining if the dragging action pattern would be influenced by factors from the "home" area of another rat. If the dragging action pattern was altered as compared with the pattern exhibited on a neutral substrate, it could possibly contribute substantial credence to the dragging action pattern as the component of individual territorial marking by D. ordii.

An "intruder" rat, defined as the rat placed in the "home" pen of another rat, immediately assumed the elongate, horizontal posture and became extremely rigid when first placed in the pen of another rat. (The occupant rat was removed during the test period.) The eyes were opened widely and the pinnae were erect and widely spread. As the intruder slowly began exploring the substrate it utilized quadruped

locomotion and maintained a low body profile. If startled by a sound or sudden movement, the animal "froze" in the horizontal position and pressed flat against the sand with eyes open wide. Before the animal returned to exploring it assumed an upright stance with its head extended in order to scrutinize the environment olfactorily. Again, the elongate, horizontal posture was taken and the rat continued its investigation of the sand. This was the general pattern of behavior for the intruding rats during each test period.

With only three limited exceptions, the intruder rat did not exhibit lateral hip drags or ventral drags while in the pen of another rat. The exceptions involved three separate intruding rats; one rat displayed a lateral hip drag twice and the other two introduced animals each displayed one lateral hip drag (Table II).

During 36 test sessions, intruder rats urinated three times in the "home" pen of another animal. The urinating animals were both male and female and the occupant rats were both male and female. All possible sexual combinations of exposure to urine occurred except female to female. During urination, the animal maintained a quadruped position, with the body elevated above the substrate in a rigid stance. Upon completion, the animal turned and sniffed the urine spot then turned facing away from the urine spot and kicked sand over the spot before moving away. During these and other urinating incidents, a rat was never observed depressing its perineal region against the urine spot.

The "occupant" rat, defined as the rat inhabiting the observation pen, initially assumed the elongate, horizontal posture when returned to its pen immediately after the removal of the intruder rat. Soon the animal was engaged in investigatory, upright posturing while scru-

Table II. Comparison of the number of dragging action patterns for "intruder" and "occupant" rats during 15 minute observation periods. Dragging action patterns are given as a composite of both lateral hip drags and ventral drags. Sexual combination of each test situation is given in the order of Intruder/Occupant; (M) male; (F) female.

	NUMBER OF DRAG ACTION PATTERNS					
	DAY 1		DAY 2		DAY 3	
TEST SERIES	INTRUDER/OCCUPANT		INTRUDER/OCCUPANT		INTRUDER/OCCUPANT	
2A (M/M)	0	11	0	10	0	11
2B (F/M)	0	10	0	16	0	12
2C (M/F)	0	21	0	16	0	12
2D (F/F)	0	4	1	12	0	8
2E (M/F)	0	16	0	7	0	10
2F (F/M)	2	8	0	8	1	13
2G (M/M)	0	8	0	10	0	7
2H (M/F)	0	9	0	14	0	12
2I (F/F)	0	10	0	10	0	7
2J (F/M)	0	12	0	12	0	11
2K (M/M)	0	7	0	15	0	13
2L (F/F)	0	9	0	14	0	10

tinizing olfactorily the environment, and it moved rapidly about the pen in biped fashion. Lateral hip drags and, to a limited extent, ventral drags were displayed first in the area about the burrow. Then, the dragging action pattern was extended throughout the pen (Table II). Ventral drags comprised only five percent of all dragging action patterns displayed by the occupant rat (Table III).

If the intruding rat had performed any dragging behaviors in the occupant's "home" pen, the occupant rat engaged in lateral hip drags on the exact site of the intruder's drag. This dragging over the sand on which the intruder had exhibited dragging behaviors superseded the performance of all other dragging action patterns by the occupant rat. Urination spots deposited by the intruding rat were not observed by the occupant rat when surveying the substrate. No behavioral response was directed at the urine spot by either male or female rats.

There was no significant difference ($P < 0.05$) in dragging behavior among the three test days for either the "intruder" group or the "occupant" group. There was also no significant difference ($P < 0.05$) among the individual kangaroo rats sampled for dragging behaviors. Since these test situations showed that dragging action patterns were displayed on a neutral substrate and that they were also exhibited within the "home" pen, but not in the range of another rat, the conclusion that the dragging behavior, when used outside the sandbathing site, is an individual territorial marker appears appropriate. Because there was such a consistently small percentage of ventral drags, compared with the lateral hip drags, the marking behavior should essentially be limited to the lateral hip drag.

Table III. Comparison of the number of ventral drag and lateral hip drag action patterns for the "occupant" kangaroo rat after removal of the intruding rat. (M) male; (F) female.

	NUMBER OF DRAG ACTION PATTERNS					
	DAY 1		DAY 2		DAY 3	
TEST SERIES	LATERAL DRAG	VENTRAL DRAG	LATERAL DRAG	VENTRAL DRAG	LATERAL DRAG	VENTRAL DRAG
2A (M)	11	0	10	0	11	0
2B (M)	9	1	16	0	11	1
2C (F)	20	1	16	0	10	2
2D (F)	4	0	12	0	8	0
2E (F)	15	1	7	0	10	0
2F (M)	8	0	8	0	13	0
2G (M)	8	0	9	1	7	0
2H (F)	7	2	14	0	12	0
2I (F)	10	0	9	1	7	0
2J (M)	12	0	11	1	9	2
2K (M)	6	1	15	0	13	0
2L (F)	9	0	14	0	9	1

Pheromone Source

Since the dragging action pattern has been indicated as a means of individual identification, it becomes necessary to define the pheromone source. Results obtained from the confinement of rats of either sex in metabolism cages were significant in this respect. Kangaroo rats were maintained at 10 day intervals in four different metabolic conditions dependent upon water consumption. Within the parameters of this situation, the potential pheromone source in urine could be scrutinized, leaving sebum as the remaining pheromone possibility.

Once every 24 hours each rat retained in a metabolism collecting cage was placed in an observation pen for a 15 minute period in which the behavioral responses were recorded. Principal behavior responses were limited to the dragging action pattern consisting of both lateral hip drags and ventral drags. Other behaviors exemplified were restricted to the realm of exploratory behaviors and grooming behaviors. Table IV is a summary of the mean values for metabolic measurements and the number of marking responses for each test group. There was no significant difference ($P < 0.05$) within each experimental group for water consumption, urine output, or marking behaviors.

Rats in test groups where water availability was restricted always consumed the entire daily water quota. As the water intake was reduced, the urine output was reduced until reaching the minimum output value in Group III. A direct relationship existed between water intake and urine output under standardized conditions (Fig. 8).

Marking behavior, expressed as the dragging action pattern, did not correlate with urine output (Fig. 9). With the exception of Group I, the dragging action pattern remained quantitatively consistent

Table IV. Mean values for water intake and urine output in milliliters (ml.); and the mean number of lateral hip drags, ventral drags, and total mean of all body drags. Each experimental group was a composite of both male and female D. ordii.
Control - 20.0 ml. water per day.
Group I - 1.0 ml. water per day.
Group II - 0.5 ml. water per day.
Group III - 0.0 ml. water per day.

	MEAN WATER INTAKE (ml.)	MEAN URINE OUTPUT (ml.)	MEAN NUMBER OF LATERAL DRAGS	MEAN NUMBER OF VENTRAL DRAGS	TOTAL MEAN FOR DRAG BEHAVIORS
Control	6.24	2.83	20.49	3.16	23.65
Group I	1.00	0.37	6.72	0.55	7.27
Group II	0.50	0.17	16.50	2.38	18.88
Group III	0.00	0.13	17.75	2.06	19.81

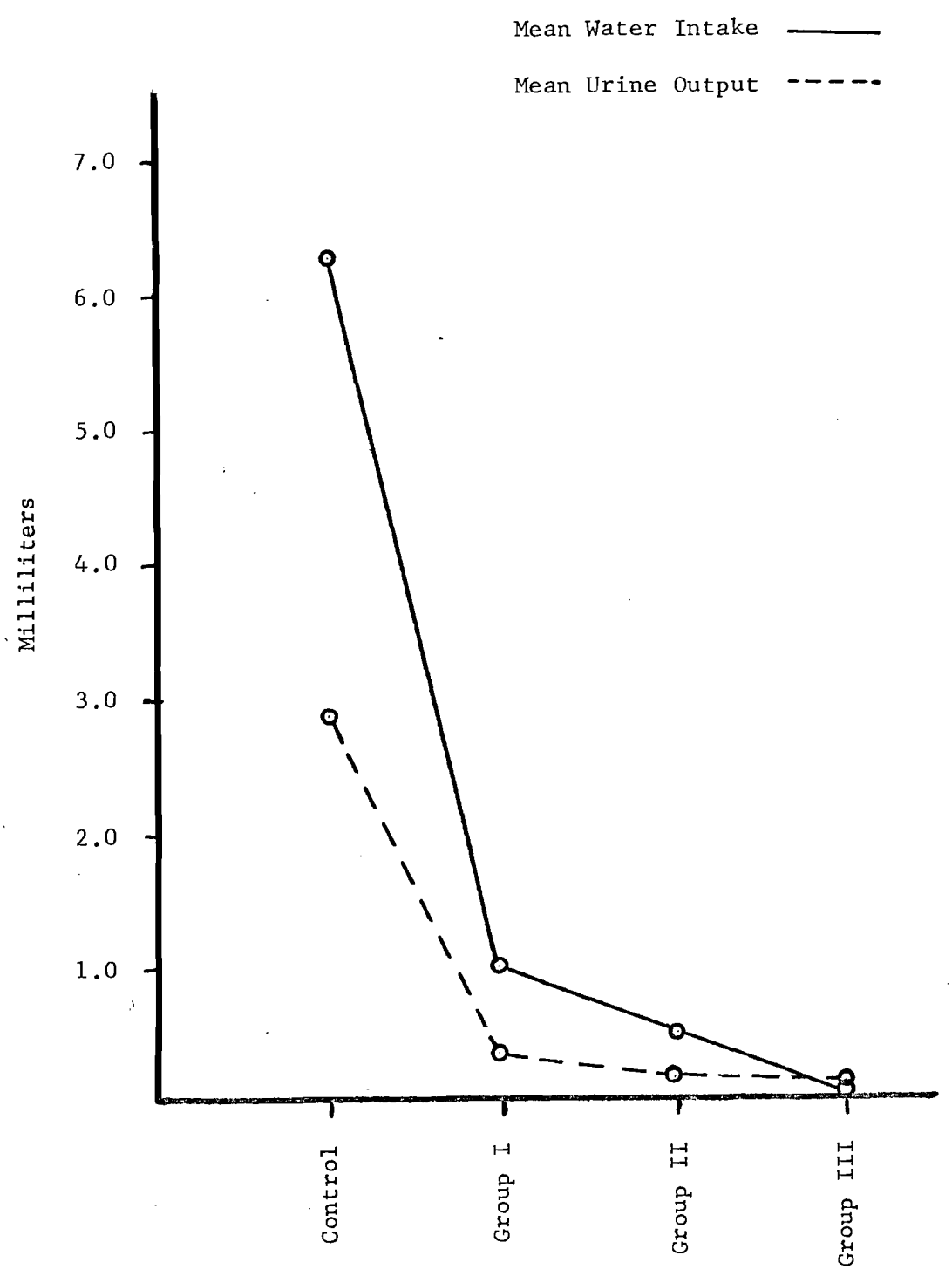

Figure 8. Relationship of mean water intake to mean urine output in 20 male and female D. ordii.
Control - 20.0 ml. water per day.
Group I - 1.0 ml. water per day.
Group II - 0.5 ml. water per day.
Group III - 0.0 ml. water per day.

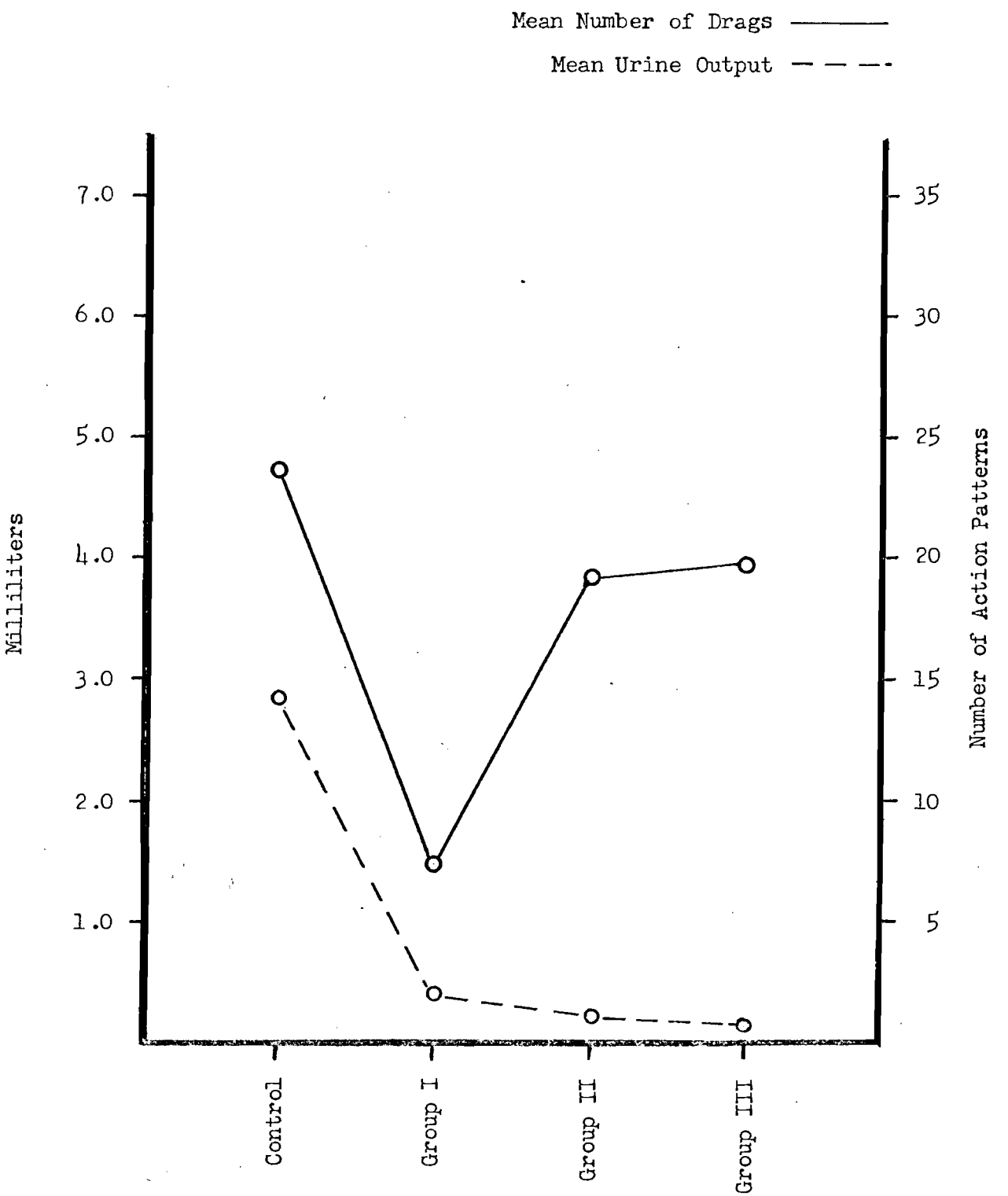

Figure 9. Relationship of mean urine output to the average number of dragging action patterns in 20 male and female D. ordii.

irrespective of urine production. Group I was not consistent with the other groups for the number of dragging action patterns due to the death of one animal on the third day of testing and a consistently inhibited response of a second rat when under observation. If a pheromone source for the marking behavior of the dragging action pattern was associated with the urine, a direct correlation would be expected to exist between dragging behavior and urine availability.

Histology

Observation of transversely sectioned dermis revealed that a sebaceous gland consisted of a cluster of glandular alveoli (acini) converging into a central duct which led to the dermal surface (Fig. 10). Examination of longitudinal tissue sections indicated that a sebaceous gland was composed of an average of five glandular alveoli (Fig. 11). An individual alveolus is composed of holocrine cells, with the more mature cells being situated toward the center of the sphere. Centrally positioned mature cells rupture, releasing their component sebum into the neck of the gland and out to the epidermal surface. This is consistent with Quay's findings (1954).

From longitudinally prepared serial sections, measurements of the diameter of glandular alveoli for the dermis of the dorsal head, venter, perineal region, lateral hip, inner thigh region, and the dorsal sebaceous gland were made. Alveolar volumes for each tissue section were calculated from the diameter measurements for each sampled animal. A mean alveolar volume for each tissue area was then computed (Table V).

A significant difference ($P>0.001$) existed among the sebaceous alveoli for the dermal regions sampled. Repeated analyses among

Figure 10. Transverse section of an adult male dorsal gland (100X). D, duct; A, alveolus.

Table V. Mean alveolar volume in cubic microns calculated from alveoli diameter measurements at 100X magnification. Tissue samples represent 11 adult specimens of *D. ordii* (five males; six females).

DERMAL REGION	MEAN ALVEOLAR VOLUME
Dorsal gland	155,870.04 microns^3
Dorsal head	53,354.82 microns^3
Lateral hip	52,147.28 microns^3
Perineal region	46,207.75 microns^3
Venter	41,757.43 microns^3
Inner thigh surface	21,849.97 microns^3

tissue sites indicated that the significant variance component was attributable to two dermal areas, the dorsal sebaceous gland and the inner thigh area. Mean alveolar volume of the modified dorsal sebaceous gland proved to be significantly greater than the alveolar volume of other dermal regions. The mean alveolar volume of the inner thigh was significantly less than that of other regions sampled. Figures 11, 12, and 13 illustrate the significant difference in diameter of glandular alveoli and the variation in sebaceous gland density for the dorsal gland, ventral tissue, and inner thigh tissue.

The data indicate that there was uniform distribution of unmodified sebaceous glands throughout the dermis of D. ordii. This complement of sebaceous glands undoubtedly functioned in pelage maintenance. Two exceptions occurred to this rather uniform glandular distribution. One was on the surface of the inner thigh, the other was in the modified dorsal sebaceous gland. The integument covering the inner surface of the thigh was a region of sparse pelage and, therefore, would not require the normal aggregation of sebaceous material for pelage dressing. The second exception, the dorsal gland, occurred as an area of modified sebaceous glands along the anterior portion of the mid-dorsal line. The area was discernible by a thickening of the skin and an absence of hair follicles. Glandular acini were both more abundant and of a significantly greater volume in the dorsal gland than in any other region of the dermis. This study also revealed that there was no significant difference in the component alveolar volume among male and female kangaroo rats.

The relatively consistent distribution of sebaceous glands throughout the dermis of the animal seemed to indicate that glands function as

Figure 12. Longitudinal section from the inner thigh region of an adult male D. ordii (100X). A, alveolus; SG, sebaceous gland.

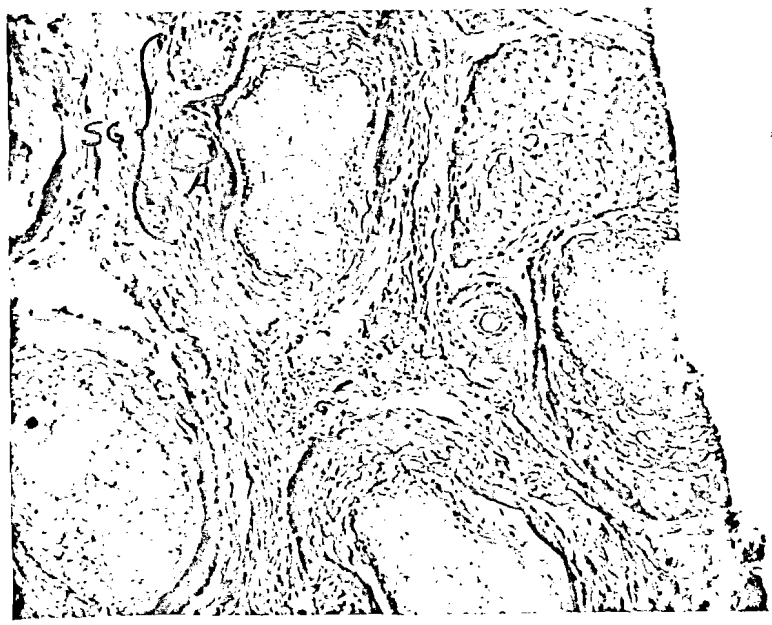

Figure 13. Longitudinal section of the modified dorsal sebaceous gland of an adult male D. ordii (100X). A, alveolus; SG, sebaceous gland.

the source of sebum for pelage dressing. This consistent abundance of sebaceous glands precluded the need for a supplemental source of sebum from the dorsal gland. Within four days, kangaroo rats confined to cages without a sand substrate to accommodate dragging behaviors showed a discernible flow of sebum from the dorsal gland posteriorly following the curvature of the spine. As this sebum flow reached the hip region it descended laterally, covering the external surface of the hind limbs. This was the region that was brought in contact with the substrate during the dragging action pattern which has been implicated with individual territorial marking.

DISCUSSION

Scent Marking

An animal's home range inevitably becomes saturated with its own scent due to the dispersion of urine, feces, and scent gland secretions as a result of its movements. However, random methods of scent distribution are not characteristic of most mammalian species which have evolved distinctive behavior patterns permitting the marking of their home range by depositing their appropriate scent upon suitable environmental objects (Ewer, 1968). These scent marks function as chemical property signs. Familiar scent marks increase an animal's confidence, while an unfamiliar marking decreases confidence and stimulates an escape response. Certain mammalian species also respond to foreign scent markings with increased aggression. In many solitary dwelling species a foreign scent mark can also relay information without constituting a threat.

Most mammalian species have highly developed olfactory processes which are employed in a communicative context. Chemical signals are derived from urine, feces, or dermal scent glands. Many species have evolved toward a dependence on specialized scent glands for producing pheromone substances rather than relying on urine or feces. Frequently, specialized motor patterns are utilized for depositing scent markings in the environment with the advantage that these signals can be restricted to situations when marking is necessary. According to Hinde and Tinbergen (1958), such communicative movements conceivably had their origins in more simple reflex movements constituting the repertoire of

general maintenance behavior. In such mammalian situations, natural selection simultaneously functioned to intensify odor production in those somatic regions corresponding to the evolving communicative movements. Once elaborate structures had been developed and behavioral movements had been modified to complement this structuring, there remained the severing of the evolving structure and accompanying behaviors from the primal motivational state.

According to Eisenberg (1963) the kangaroo rat employed side rubbing as a comfort movement which was transformed to a pelage dressing movement as the increased sebaceous gland secretions were favorably selected as the species adapted to the arid environment or as a selective complement for a dense pelage. Following the theory of Hinde and Tinbergen, the dorsal sebaceous gland presumably continued evolving as an aggregate of sebaceous units functioning in the auxiliary production of sebum distinct from the somatic sebaceous glands utilized for pelage maintenance. Lateral flank drag movements, originating as comfort movements, were modified for the dispersal of sebum, complementing the development of the specialized dorsal sebaceous gland.

Territoriality

Ralls (1971) postulated that marking behavior occurred in stimulus situations which were either known or theorized to give rise to aggressive motivation. One such stimulus situation was the possession of a territory. Numerous accounts attest to the solitary dwelling habits and the intraspecific aggressiveness of Dipodomys (Bailey, 1931; Fitch, 1948; Reynolds, 1960; Eisenberg, 1963). Ewer (1968) identified the simplest form of territorial organization as one in which the animals

were solitary, each holding its own territory. The territory served the principal function of spacing individuals which insured adequate resources for the survival of the individual. In kangaroo rats, the territorial concept appeared credible as an adaptation supporting the solitary dwelling habit, intraspecific aggressiveness, and the restrictive environmental limitations of an arid habitat.

Burt (1943) theorized that territoriality was a basic characteristic of animals. He did not contend that this trait was present in all species nor that it was developed to the same degree in all species. But, the existence of territorial behavior even among some invertebrate groups, as well as being widely distributed among the vertebrates, lends support to a theory of territoriality as a diffuse behavioral trait throughout the animal kingdom. Mykytowycz (1965), applying this generalization of territoriality to mammals, stated that the presence of specialized scent glands for territorial marking was now well substantiated and had been demonstrated in all mammalian species whose behavior had been carefully studied. The literature concerned with the potentiality of this territorial trait for Dipodomys has been inconsistent. Fitch (1948) acknowledged intraspecific hostility and mutual avoidance as a generic trait of Dipodomys but negated indications of true territoriality. Eisenberg (1963) continued to emphasize the excessive conspecific intolerance within the genus and from this proposed the feasibility of territorial defense restricted to the burrow and a limited area adjacent to the burrow. In a study undertaken by Garner (1974), the behavior of D. ordii indicated that there was mutual exclusiveness at the burrow sites and the associated surface areas. This restriction of activity centers suggested that D. ordii exhibited

a measure of territoriality.

The initial phase of this study was designed to provide indication of the extent of the territorial condition of Dipodomys ordii. Working within the restrictions of the habitat of a naturally occurring species and with the nocturnal mannerisms of Dipodomys, the observer is limited to the realm of indicators of behavior rather than direct evidence of behavior. To substantiate better the observed indicators, a second phase of study was later conducted in the controlled confines of the laboratory.

Field observation substantiated the work of previous investigations which defined the activity areas of the kangaroo rat to the pathways of its runway system. Locomotor association with the runway system has become so selective that bipedal locomotion now restricts the animal to its runway for maximum efficiency of movement. Both feeding sites and sandbathing areas are associated with the runways. Alliance of these activity centers with the runway system and the bipedal habit has served to limit the species mobility to the runway system or open areas free of vegetation.

During the four month period encompassing this field study, the established burrow sites were immutably maintained and there was no appreciable expansion or deletion of the associated runways; nor did the population density experience any notable change. New burrow sites were not added. Only by occupying abandoned burrows did new residents enter the population. This was consistent with Garner's (1974) finding that the density of a resident population did not change substantially throughout the year. His trapping results also revealed that the natural distribution of kangaroo rats was patterned. All trapping

situations revealed that each burrow's occupancy was restricted to a solitary rat. Bailey (1931) Fitch (1948), Reynolds (1960), and Eisenberg (1963) were in agreement in verifying this isolated asocial pattern within the genus Dipodomys.

The restriction of movement to established runways coupled with D. ordii's stable burrow occupancy and its solitary intraspecific aggressive behavior would appear to indicate a territorial need.

Territorial possession necessitates a marking method to reduce intraspecific encounters which would otherwise require the continual physical defense of the territory by the possessor. Fitch (1948) in his negation of the territorial concept for Dipodomys contended that the animal could not maintain exclusive surface area rights to the degree required to constitute a territory because of the limited time spent above ground. A scent communicator would serve to delimit the territory from adjacent conspecifics during the physical absence of the possessor from the surface area.

Eisenberg (1963) concluded his study of heteromyid behavior noting that sandbathing served the dual function of chemical communication and pelage dressing. The present study supports the theory of sandbathing as a method of pelage grooming. However, results obtained indicate a disparity between sandbathing and chemical (scent) communication. In all experimental situations, sandbathing consisted of both lateral drag and ventral drag action patterns performed in approximately equal proportions only at specific dusting (sandbathing) sites. As a kangaroo rat explored its territory, it periodically engaged in the performance of lateral hip drags with only an occasional ventral drag. This behavior was not identified as grooming since the animal had

previously completed elaborate pelage grooming activity at the sandbathing site. Rather, this behavioral action pattern was labeled as a potential method of territorial marking. In succeeding test situations kangaroo rats presented with a neutral substrate were stimulated to comply with the lateral hip dragging response. In other observations, exposure to the "marked" substrate of another rat's territory decreased the confidence of the test animal which did not then engage in dragging behavior in this already occupied territory. Return of the territorial owner resulted in a response of lateral hip dragging behavior as the animal was reacting to the presence of an unfamiliar conspecific in its territory. In all of these responses the displayed behavior consisted essentially of lateral hip drags. In only 20 percent of the responses did a kangaroo rat display a ventral drag action pattern as opposed to approximately equal display of ventral drag and lateral drag responses during previously identified sandbathing.

It would appear that the marker substance must be associated with the lateral hip drag as this was the behavioral response repeatedly stimulated in all of the testing situations warranting a territorial marker. Sebum appeared to be the logical pheromone source attached to a response such as a dragging action pattern involving the pelage. However, fecal matter and urine which impart distinctive odors also required consideration. Feces, collected from metabolism cages so as to be minimally exposed to any other odor source associated with the rat, were distributed in a pattern on the substrate of other rat's pens. Responses of the "occupant" animal were neutral. These rats did not demonstrate any behavioral response except for indiscriminant olfactory investigation. In test situations where an "intruder" rat was placed in

the home pen of another rat, urination by the intruding animal occurred on three occasions. Observed behavior of the urinating rat offered no credence to the theory that urine might be associated with the perineal region and used as a territorial marker. Urine loci were not discriminatingly observed by the "occupant" rat nor did it direct any behavioral responses at the urine spot. There was no sexual distinction made in any of the test situations for potential fecal or urine marking behavior.

Further examination of urine as a pheromone source was conducted on kangaroo rats retained in metabolism cages. Urine output was shown to be in proportion to water intake until achieving a minimal level of metabolically necessary urine output. Irrespective of urine output, marking behavior, exemplified as lateral hip drags and ventral drags, remained consistent among all rats under observation. If a pheromone source associated with the marking behavior of the dragging action pattern was to be found in urine a direct correlation should exist between dragging behavior and urine availability. This correlation did not exist. Because of this correlation discrepancy, it was therefore concluded that urine did not function as the primary pheromone source. Since previous observations had also eliminated fecal material as a potential pheromone source, inductively sebum would appear to satisfy the criterion as a territorial marking substance transmitted via the lateral hip drag.

Histology

Two sources of sebum were recognized; sebum from the somatic regions underlying the pelage, and sebum from the specialized dorsal gland. Was there a distinction between these sources or did they

simply complement one another providing sebum for both pelage dressing and scent communication? Following Hinde and Tinbergen's (1958) theory for the origins of display behavior, structure elaboration derived from primary somatic components would be expected. The aggregations of specialized sebaceous units into the dorsal sebaceous gland would be such a structural elaboration. Histological examination indicated a significant difference in alveolar volume between sebaceous glands of the somatic dermal regions and the modified dorsal gland. Throughout the dermis of D. ordii, however, the distribution of unmodified sebaceous glands remained relatively uniform. The purpose of this uniform distribution of sebaceous glands was undoubtedly for pelage maintenance.

The dorsal gland, distinguished by a thickening of the dermis and an absence of hair follicles, existed as a region of modified sebaceous glands along the anterior portion of the mid-dorsal line. No appreciable difference could be found in the component alveolar volume of the dorsal gland between male and female kangaroo rats. With a complement of unmodified sebaceous glands associated with the integument for pelage maintenance, the question of a dorsal gland's function remained. It would not appear to be necessary as a supplemental source of sebum for grooming purposes. Kangaroo rats confined for several days to cages without a sand substrate to accommodate dragging behavior began to show a discernible posterior flow of sebum from the dorsal gland following the curvature of the spine. Montagna (1962) had identified the movement of sebum along a gradiant from areas of high sebaceous secretion to areas of lower secretion. This appeared to be the current situation as the dorsal gland had been recognized as a region

of greater alveolar volume than the other dermal areas. Upon reaching the hip region the sebum flow descended laterally over the external surface of the hind limbs. This surface area corresponded to the region that was brought into contact with the substrate during the dragging action pattern which has been defined as the behavioral movement responsible for territorial marking by D. ordii, distinguishing the sebaceous flow from the dorsal gland as the territorial marker.

Although indications are that the dorsal gland has evolved as an elaboration of specialized dermal sebaceous glands for scent communication, the present lack of distinction between dragging behavior for marking purposes and dragging behavior for pelage grooming suggests that the marking behavior has not yet achieved evolutionary emancipation from the original grooming reflex (Hinde and Tinbergen, 1958). A comparative study of the composition of sebum from both the unmodified somatic glands and the modified dorsal gland is needed. Identifying chemical differences might indicate possible pheromone composition and could also be of further value in determining possible differences between sebum used for marking purposes and sebum used for pelage grooming.

Quay (1953) found that there was no sexual difference in the secretory activity of the dorsal gland in D. ordii, although there were seasonal differences. This study substantiated Quay's results concerning the absence of sexual distinction in gland activity. But, it also presented the need for a distinct form of reproductive marking which would be necessary in such a solitary and aggressive species as ordii. Though not included within the scope of the present study, it would seem feasible that urine might be a potential reproductive marker since it is intimately associated with reproductive hormones through their

elimination which could also function as a pheromone component. Such a consideration demands the attention of a separate study.

The initial portion of this study was based on a four month field study of burrow occupancy. Even though that study was substantiated by the results of previous workers a four month period is not adequate for determining stability of burrow occupancy and population density. Further field work designed specifically for gathering extensive data on burrow occupancy and population density among distinct populations of D. ordii is needed. From such a study more reliable and definitive conclusions could be formulated on the population patterns of this species.

SUMMARY

1. A study of the territorial behavior in Dipodomys ordii richardsoni was conducted from May, 1974, through April, 1975. Because of the disparity in the literature from previous studies of behavior and territoriality in the genus Dipodomys, this study was undertaken to ascertain the territorial habits of the species, D. ordii.

2. A field study was made of burrow occupancy, habitat utilization, and population movements. Observations were conducted under structured conditions to identify territorial marking behaviors and delimit the pheromone source. Histological comparisons between the dorsal gland and the somatic dermal regions were made to substantiate the pheromone source.

3. Movement was restricted to the runways established in connection with the burrow site which was found to be stably maintained. The solitary asocial condition, an adaptation of survival value in an arid habitat, and the stably maintained home range indicated a territorial need.

4. Sandbathing was identified as a grooming behavior for the purpose of pelage maintenance. It consisted of lateral and ventral dragging of the body along a sand substrate to remove excess sebum. A dragging behavior essentially restricted to the lateral hip region was observed being performed outside the sandbathing site under stimulus situations warranting the need for an individual marking behavior. This lateral hip drag action pattern was identified as an individual territorial marking behavior. Both male and female rats displayed this

behavior.

5. Marking behavior expressed as the dragging action pattern did not correlate with urine output. If a pheromone source for the marking behavior of the dragging action pattern was associated with the urine, a direct correlation should have existed between dragging response and urine availability. No indication was found favoring fecal material as a source for discriminate individual marking.

6. It was found that there was a representatively uniform distribution of unmodified sebaceous glands throughout the dermis. This complement of sebaceous glands functioned in pelage maintenance. The dorsal gland, an aggregation of modified sebaceous glands along the anterior portion of the mid-dorsal line, was discernible as a thickening of the dermis and an absence of hair follicles. Both male and female kangaroo rats showed a discernible flow of sebum from the dorsal gland posteriorly following the curvature of the spine. Reaching the hip region, the sebum descended laterally covering the external surface of the hind limbs. This is the anatomical region involved in the performance of the lateral hip dragging action pattern identified as the territorial marking behavior. Sebum, originating from the dorsal gland, was determined to be the pheromone source for territorial marking.

7. It was concluded that D. ordii maintained a surface territory confined to the limits of the runway system in association with the burrow site as an assurance against excessive aggressive encounters in its solitary asocial living pattern. Since it is a totally asocial species, both males and females maintain a territory which is chemically marked by a pheromone constituent of the sebum exuded from the dorsal

sebaceous gland. Distribution of this sebum in the environment is accomplished by the lateral hip dragging behavior.

LITERATURE CITED

LITERATURE CITED

Bailey, V. 1931. Mammals of New Mexico. North Amer. Fauna, 53:1-412.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mamm., 24:346-352.

Dale, F. H. 1939. Variability and environmental responses of the kangaroo rat Dipodomys heermanni saxatilis. Amer. Mid. Natl., 22:703-731.

Eibl-Eibesfeldt, I. 1970. Ethology - the biology of behavior. Holt, Rinehart, and Winston, New York, 530 pp.

Eisenberg, J. F. 1963. The behavior of heteromyid rodents. Univ. of Calif. Press, Berkeley, 114 pp.

Ewer, R. F. 1968. Ethology of mammals. Plenum Press, New York, 418 pp.

Fitch, H. S. 1948. Habits and economic relationships of the Tulare kangaroo rat. J. Mamm., 29:5-35

Garner, H. W. 1974. Population dynamics, reproduction, and activities of the kangaroo rat, Dipodomys ordii, in Western Texas. Texas Tech. Press, Lubbock, 28 pp.

Gates, F. C. 1937. Grasses in Kansas. Kansas State Board of Agriculture, Topeka, 349 pp.

Hinde, R. A. and N. Tinbergen. 1958. The comparative study of species-specific behavior: Behavior and evolution. Yale Univ. Press, New Haven, Chpt. 12.

Montagna, W. 1962. The structure and function of skin. Academic Press, New York, 454 pp.

Mykytowycz, R. 1965. Further observations on the territorial function and histology of the submandibular cutaneous glands in the rabbit, O. cuniculus. Anim. Behav., 13:400-412.

Quay, W. B. 1953. Seasonal and sexual differences in the dorsal skin gland of the kangaroo rat, Dipodomys. J. Mamm., 34:1-14.

_____. 1954. The dorsal holocrine skin gland of the kangaroo rat, Dipodomys. Anatomical Record, 119:161-176.

Ralls, K. 1971. Mammalian scene marking. Science, 171:443-449.

Reynolds, H. G. 1960. Life history notes on Merrians kangaroo rat in southern Arizona. J. Mamm., 41:48-58.

Setzer, H. W. 1949. Subspeciation in the kangaroo rat, Dipodomys ordii. Univ. of Kansas Publ., Museum of Natural History, Lawrence, 1:473-573.

Tappe, D. T. 1941. Natural history of the Tulare kangaroo rat. J. Mamm., 22:117-147.