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Title: THE INFLUENCE OF BEHAVIOR AND WATER REQUIREMENTS ON THE DISTRIBUTION AND HABITAT SELECTION OF THE GRAY-TAILED VOLE (MICROTUS CANICAUDUS) WITH NOTES ON MICROTUS TOWNSENDII

Abstract approved: Redacted for Privacy
David H. Milne

Microtus canicaudus Miller, the gray-tailed vole, was studied in the field and laboratory in order to clarify aspects of the relationship of this species to its habitat. All trapping and sampling was done on permanent pasture land in the William L. Finley National Wildlife Refuge 12 miles south of Corvallis, Oregon. Vole runway systems were mapped. Sampling of quarter-acre plots revealed 373 vole holes per acre arranged into 39 complexes of approximately nine holes each. Complexes were located 8 feet apart and were occupied by 1.5 animals each. Trapping success for a 1-year period showed peaks of activity in February, June and October, probably associated with breeding and the dry season.

Food consumption rates while eating air-dried food pellets was

4.4 grams per day or 15% of body weight per day. A seasonal difference in food consumption rates was noted. The average daily water consumption was 11.7 cc. Consumption of water per gram of body weight was 0.4 cc/g/day. The ability to undergo dehydration and withstand a reduced net water ration was also measured.

Intraspecific behavior experiments suggested that there is a marked social dominance by one male over another and a high frequency of animals nesting separately, indicating a lack of gregariousness.

This animal's potential as a competitive force with domestic stock and potential threat to their food source was examined. Results indicated that the gray-tailed vole, at present population levels, may be a significant competitor with domestic stock but is not a threat to its own food resources.

Water availability is postulated to be a major factor in this animal's habitat selection and may limit them to more mesic areas. Extended dry periods may be critical to their survival. However, behavioral characteristics resulting in relatively solitary lives may guarantee an adequate supply of succulent plants and dew for each individual during the driest period of the year.

Limited data on water uptake, food consumption and behavioral characteristics for *Microtus townsendii* are also presented. Townsend's vole may be more gregarious than the gray-tailed vole and more limited by water requirements. _M. townsendii_ may be dominant over _M. canicaudus_ where their ranges overlap.

The Influence of Behavior and Water Requirements on the Distribution and Habitat Selection of the Gray-tailed Vole (*Microtus canicaudus*) with Notes on *Microtus townsendii*

by

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Assistant Professor of Biology
in charge of major

Redacted for Privacy

Chairman of Department of General Science

Redacted for Privacy

Dean of Graduate School

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INTRODUCTION

The gray-tailed vole (*Microtus canicaudus* Miller) is an unfamiliar animal whose potential for agricultural damage is currently unknown. Little is known of the habits and ecology of this localized West Coast species; the following summarizes most of the available information on it.

The gray-tailed vole is found only in Clark County, Washington and the lower elevations of the Willamette Valley, Oregon (Anderson, 1959) and is most commonly associated with areas in which the predominant vegetation is grass. It is found in croplands, in pasture lands and along fence rows (Goertz, 1964). Bailey (1936, p. 206) referred to this species as being "long known in the lower Willamette Valley in the open country where there were originally grassy prairies but now are fields and the best of the farming land. . . ." Goertz (1964, p. 847) stated that ". . . It may well be that agricultural land use has favored this species, since few of these voles were taken beyond farmland." Storm (1941, p. 68) stated that ". . . meadow mice (*Microtus*) are not extremely numerous in the Willamette Valley, but are probably doing well under a condition of more agriculture and less predators."

Presence of this vole species, like that of many others, is indicated by intricate and extensive runways resembling tunnels beneath the vegetation. These runways frequently have piles of feces at intersections and numerous holes leading to underground tunnels (Maser and Storm, 1970). Other voles, such as M. montanus, and presumably M. canicaudus, are most active during daylight hours and thus depend upon vegetative cover to provide concealment from mammalian and avian predation (Spencer, 1959).

Gray-tailed voles sometimes build nests of grasses under boards, hay bales and other debris left in fields. However, subterranean nests are most commonly constructed (Maser and Storm, 1970). Nests are usually found 6-12 inches below the surface with several entrances going from the surface to the nest (Goertz, 1959). Voles do not hibernate but are active throughout the entire year (Spencer, 1959).

In some areas, during the winter months, the water table rises to or above the ground surface. Though not aquatic, voles are excellent swimmers. High water, or irrigation, if not too high or prolonged, does not seem to disturb them (Spencer, 1959). Their subterranean nest cavities apparently trap and hold air but the burrows leading to the nest may become flooded. Thus, the voles must "dive" in order to reach their nests (Maser and Storm, 1970). On occasion, voles are routed by high water.

Owls, hawks, foxes, skunks and snakes are the principle wild predators of the gray-tailed vole. Domestic and feral cats also kill them. Man destroys numerous voles each year by burning and plowing fields or through poisoning programs. Winter flooding also takes its toll (Maser and Storm, 1970). Spencer (1959), referring to *M. montanus*, indicated that overwinter mortality may amount to 50% of the population.

The gray-tailed vole breeds throughout the year. Litter sizes range from two to eight but usually consist of four to six offspring (Maser and Storm, 1970).

Bailey (1936, p. 206) stated ". . . These little gray-tailed mice are so scarce and local that few specimens have been taken and little is known of their habits. . . ." At a later time, Goertz (1964, p. 847) found substantial numbers of voles on croplands. Goertz further stated that the "voles were experiencing a high in population density" during the term of his study and indicated that this high coincided with the *Microtus montanus* irruption that occurred in parts of southeast Oregon in 1957 and 1958. Goertz (1964, p. 847) stated that ". . . In the Willamette Valley gray-tailed vole numbers were of such proportions that poisoning was deemed necessary during 1957 and 1958 on various Oregon State University experimental farm plots." However, Lee W. Kuhn (1971) remembers no such irruption in the Willamette Valley, although he did say that a poisoning program on University farm plots has been in practice for over 15 years.

The food of M. canicaudus is the vegetation in which these voles live. During high density of the population, the gray-tailed vole does considerable damage to crops such as pastures, grasses grown for seed, and grains (Goertz, 1964). Spencer (1959, p. 15) stated that ". . . the common meadow mouse (Microtus) and its close relatives are the most destructive group of mammals in the United States." He further stated that ". . . each day they consume approximately their body weight of succulent green herbaceous plants, roots, and tubers." Goertz (1964, p. 847) indicated that during the high density of the population in 1957 and 1958 ". . . I found the greatest damage to be in permanent pastures of clover and grass as well as in the small grains."

Hall and Kelson (1951) considered M. canicaudus to be a subspecies of M. montanus (Peale). Hsu and Johnson (1970), Johnson (1968), and Maser and Storm (1970) disagreed with this proposal and considered M. canicaudus to be a separate species based upon field characteristics, the separated ranges of the two taxa, blood protein electrophoretic studies and cytological distinctions. However, none of these authors had conducted breeding trials or could cite evidence of such to support their views, thus not fulfilling the rigorous customary definition of species.

The preceding review represents the full extent of the information, located by the author, about the ecology of this animal. Most is based upon field observations with little actual experimentation. Little quantitative information regarding the animal's requirements is available. The purpose of this research was to attempt to determine the factors responsible for M. canicaudus' habitat selection and distribution, to assess its potential as a competitor with livestock and to investigate some factors which may affect the densities of its populations. In view of its periodic abundance there was also a need to investigate its potential for damage to agricultural crops.

Several factors, used in shaping the direction of this study, have been implicated by the following authors in explaining the occupation of a particular habitat by an animal. Calhoun (1941) and Jameson (1952) mention an understanding of food requirements as essential to understanding a species' habitat preference. Differences in the ad libitum rate of water consumption in several species of Peromyscus were reported by Ross (1930) as being a determining factor in explaining their distribution. The ability of an animal to withstand periods of water stress were discussed by Bartholomew and Hudson (1959), Brown (1964), Chew (1965), Hudson (1962) and Lindeborg (1952) as being an important factor in a species' ability to occupy a particular habitat. Intraspecific tolerance or aggression was emphasized by Brown (1964), Harris (1952) and King (1957) as a factor in ecological distribution.

All of the above mentioned factors were examined in the current study in order to determine the reasons for M. canicaudus' habitat preference. Runway systems were subjected to trapping and mapped in order to estimate the density of the population and the number of feet of runways available to each vole. Food consumption was measured and related to the estimated vole density in order to determine the degree of potential crop damage and livestock competition. Artificially constructed "societies" of these voles were studied to determine whether or not aggression might play a role in spacing mice in the field. Water consumption and water stress measurements were studied to determine whether or not a moist habitat was necessary for fulfillment of physiological requirements.

MATERIALS AND METHODS

Site Description

All trapping and sampling was done between May 1970 and July 1971 on permanent pasture land 12 miles south of Corvallis, Oregon, in the William L. Finley National Wildlife Refuge (Figure 1). The primary species of grasses occurring in the study area are listed in Table 1. The weather conditions for the study period along with the average weather conditions for the area are presented in Figure 2.

Table 1. Primary species of grasses found on the permanent pasture land in the William L. Finley National Wildlife Refuge (Krueger, 1971).

Common name	Scientific name
Dogtail	*Cynosurus echinatus*
Soft Chess	*Bromus mollis*
Tall Fescue	*Festuca arundinacea*
Orchard Grass	*Dactylis glomerata*
Kentucky Bluegrass	*Poa pratensis*
Silver Hair Grass	*Aira caryophyllea*
Annual Fescue	*Festuca* sp.
Bentgrass	*Agrostis* sp.

Field Techniques

Vole runway systems were mapped to show the physical arrangements of burrows and runways in the field. This was

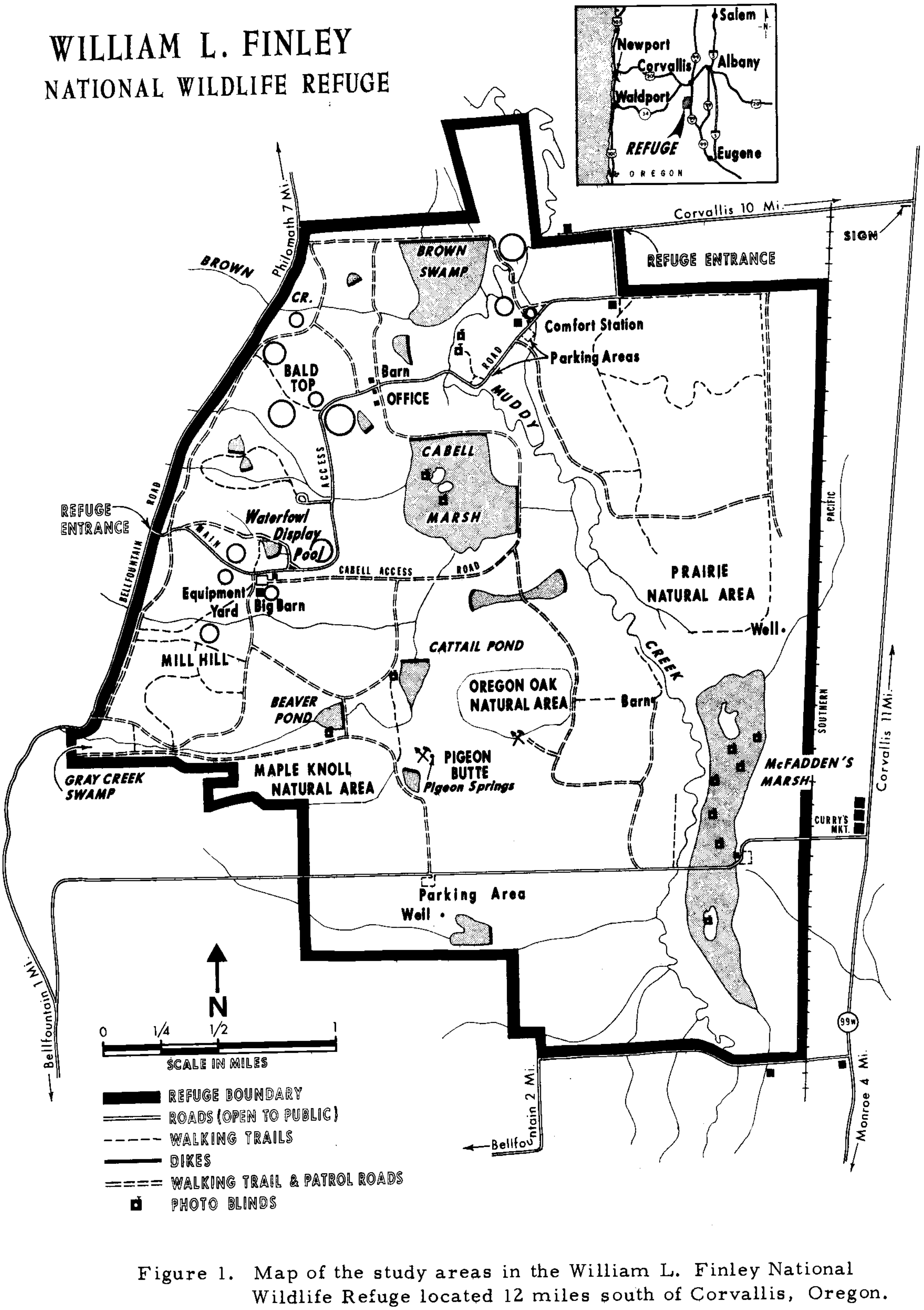


Figure 1. Map of the study areas in the William L. Finley National Wildlife Refuge located 12 miles south of Corvallis, Oregon. Areas subjected to trapping are circled.

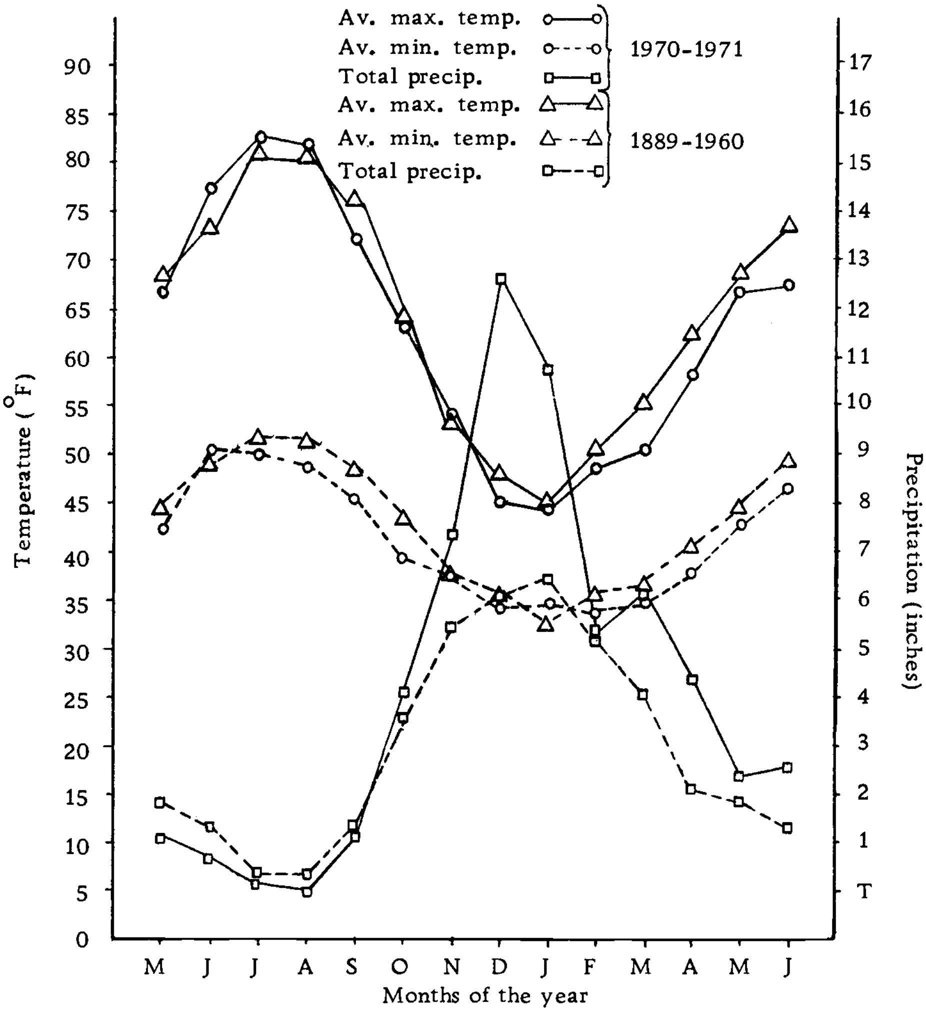


Figure 2. Monthly temperature and precipitation for the study period 1970-1971 (U. S. Weather Bureau, 1970, 1971) with the average temperatures per month and the average monthly precipitation for the period 1889-1960 (Calhoun, 1961).

accomplished by constructing an 8- by 10-foot grid of 1-foot squares over representative concentrations of burrow and runway systems. Runways and burrows were exposed and their positions transposed to graph paper.

Quarter-acre plots were sampled in order to determine the density of burrows. A 9-meter rope was used as the radius of a circle encompassing an area of 0.25 acre. The center of the circle was located at random. The 0.25 acre area marked off was then systematically examined. A burrow complex was defined as a set of at least three vole holes which was at least 3 feet from the nearest adjacent set of such holes. Each hole in a complex was within 1 foot of another hole.

The numbers of holes and burrow complexes were recorded. The average numbers of holes and complexes per acre and the average number of holes per complex were computed.

The population densities of 38 burrow systems were sampled by placing unbaited Havahart live traps in all runways leading to and/or from each complex of holes. All animals captured were removed for use in the laboratory. Trapping was continued until no animals were captured from an area for 3 days. The number of complexes in an area and the number of animals captured from that area were recorded. The average number of animals per complex was computed from trapping data.

Laboratory Methods

All laboratory experiments were conducted in a room which was maintained at approximately 72°F. Unless otherwise stated, voles were housed in gallon jars containing sawdust and nonabsorbent cotton. The jars were kept on their sides. Holes were punched in the jar lids and replaced with quarter-inch hardware cloth in order to ventilate the jars. The voles were fed air-dried pellets produced by the Experimental Feed Mill, Oregon State University. The component parts of the pellets are listed in Table 2.

Each jar was equipped with a 55 cubic centimeter plastic vial to provide drinking water. The vials were wired to the outsides of the jar lids, so that only the glass drinking tubes extended into the jars through the hardware cloth.

All animals were acclimated to the laboratory situation for at least 5 days (ranging from 5 to 30 days) before being used in any experiment.

The rate of food consumption of 30 adult voles (13 males, 17 females) was measured for a 7-day period in order to estimate food requirements. Animals were weighed and placed in Wahmann wire bottom cages with known quantities of food and an _ad libitum_ water supply. At the end of 7 days the animals and all remaining food, both in the cage and under the cage, were weighed again. The average daily

Table 2. Composition of food pellets used in all laboratory experiments.

Percent	Component	lbs/ton
7	alfalfa	140
35.7	wheat	714
30	barley	600
15	soybean meal	300
5	herring meal	100
3.3	lard (tallow)	60
3	molasses	60
0.5	trace mineralized salt	10
0.8	limestone	16
		2000
	Vitamin A	1,200,000 IU/ton
	Vitamin B	120,000 IU/ton
	bentonite	75 lbs added to mixture as a binding agent

food consumption was computed. Body weights were determined by averaging the initial and final weights of each vole during the experimental period. The number of grams of food consumed per gram of weight per day was computed.

The possibility that the *ad libitum* water requirement could affect habitat selection was explored by measuring the amount of water drunk in the laboratory. The water consumption of 30 adult voles (18 males, 12 females) was measured daily for 10 days, using distilled water. Fifty cubic centimeters of water were added to each animal's water vials each morning. The remaining water was measured 24 hours later and the vials refilled so that each vial again contained 50 cc of water. The average daily water consumption of each vole was computed. Body weight was again computed averaging the initial and final weights of each vole during the experiment. The number of cubic centimeters of water consumed per gram of weight per day was computed.

Experiments were conducted to measure survival time under conditions of reduced water availability. This was accomplished by using increasing concentrations of salt water to reduce the net water available to the animals (Brown, 1964). A point is eventually reached at which the amount of water lost via the kidneys while ridding the body of the excess NaCl exceeds the amount ingested, resulting in a negative water balance. The net effect is the reduction of available water without restricting the amount of water drunk. The length of time a mammal survives under these conditions reflects the degree of its adaptation to low water availability (French, 1956).

Thirty adult voles (14 males, 16 females) were given 0.1 molar NaCl solutions for 5 days, then 0.2 M, 0.3 M, etc. at 5-day intervals until they died. Salt solutions made with reagent NaCl and distilled water were provided ad libitum. The average survival time in days, the average amount of weight loss and the average percent of body weight lost before death were calculated.

The possibility that intraspecific aggressiveness or tolerance affected the spatial arrangement of the voles was explored to ascertain whether this factor influences the density of voles in their preferred habitat. The method of investigation consisted of creating an artificial society in a group of laboratory cages similar to that used by Blair and Howard (1944). Within this society each vole could associate with individuals of the opposite sex, the same sex, both sexes or could remain isolated, because all were kept in the same group of cages.

Four cages of wire screen, each with floor dimensions of 9 by 16 inches, were connected through the sides by means of short (12 cm) wire tunnels. Each vole was permitted access to all cages. Each cage was provided with food, a water bottle, a nest bottle and cotton nesting material.

Each experiment was begun by placing four voles (two males and two females), identifiable by fur clipping, in one of the four interconnected cages. The voles were then free to distribute themselves through the four cages in any of a variety of ways. As there were four cages and four nests, each vole could live in a separate cage.

Each experiment was conducted for 10 days. During each diurnal inactive period, the position of the voles in relation to one another was recorded. The physical appearance of each animal was also examined for evidence of fighting.

In all behavior experiments, voles were chosen which had not associated with one another in the laboratory prior to their combination in the behavior apparatus. The behavior apparatus was washed between tests to reduce the influence of scents from previous tests.

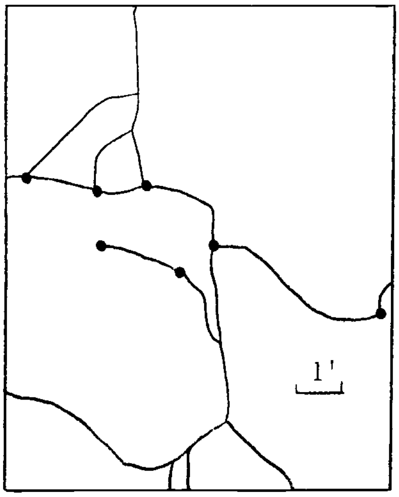
RESULTS

Field Studies

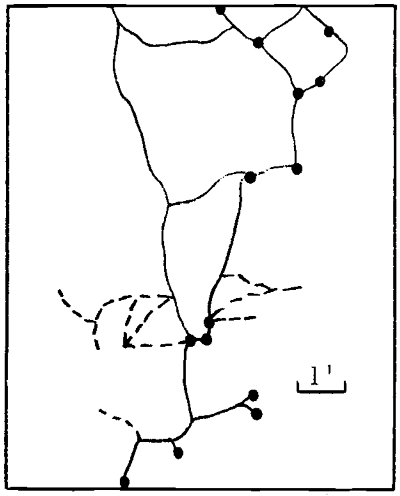
The results of the mapping study, illustrating the runway systems in four different areas, are presented in Figure 3. Each map shows an 8- by 10-foot area of permanent pasture land. The maps are numbered in order, from least dense to most dense, in terms of burrow openings and associated runways. Map 1 (Figure 3) represents a single complex, Map 2 represents two complexes, Map 3 two complexes and Map 4 one large complex.

The runways in a system are of two types. The first is well used, being worn to bare ground and generally extending from one hole to another or from one complex to another as in Maps 1 and 3 (Figure 3). This type of runway commonly contains piles of feces at intersections, and when subjected to trapping, results in the capture of more than one individual. This is especially true if the runway is some distance from the nearest complex of holes.

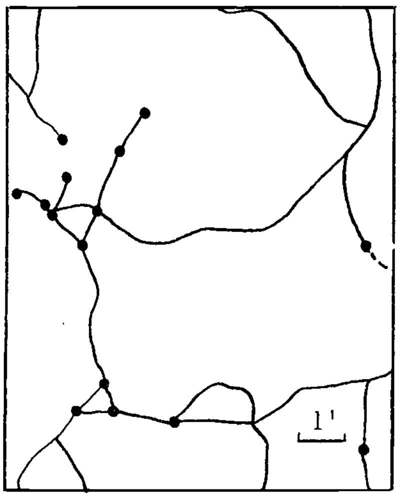
Runways of the second type are less well worn and have matted grass or moss growing in them. These runways usually end abruptly (as in Figure 3, Maps 2 and 4) and commonly contain grass clippings or end in a pile of clippings. These runways are assumed to be used for feeding purposes. They are also more sparsely marked with feces and, when subjected to trapping, result in the capture of one individual.



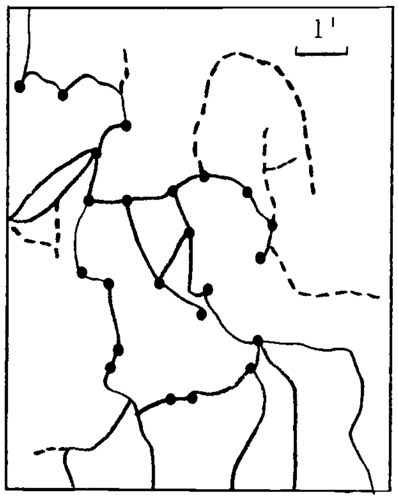
Map 1



Map 2



Map 3



Map 4

Figure 3. Maps of typical permanent pasture land, each representing an area of 8 x 10 feet, and showing the arrangement of burrows (•) and runway systems (⁼⁼⁼). Two types of runways are shown. The first is well worn (solid lines); the second is less well worn and apparently used for feeding (broken lines).

In the following text, one standard deviation is indicated with all average measurements presented.

The average number of vole holes per quarter-acre (N = 10 quarter acres) was 93.25 $\pm$ 27.33 or 373.00 $\pm$ 109.32 holes per acre. These holes were not distributed evenly throughout an acre of ground but were concentrated into complexes. The average distance from one complex to the nearest adjacent complex (measured from peripheral holes) was 8.33 $\pm$ 3.18 feet (N = 23 complexes).

The average number of complexes per quarter-acre sampled was 9.75 $\pm$ 4.40 or 39.00 $\pm$ 17.60 complexes per acre. The largest complex sampled consisted of a set of 47 holes. On the average there were 8.68 $\pm$ 8.53 holes per complex.

Thirty-eight complexes were subjected to trapping intensively in order to determine the average number of animals occupying each complex. All runways linking one complex to another were subjected to trapping. Also, all runways between holes within the complexes were subjected to trapping. A vole moving from complex to complex could then be distinguished from those moving within the complex by the trap in which it was caught. Fifty-five animals were found to inhabit the 38 complexes, or, on the average, 1.45 voles per complex and 6 holes per vole. All complexes trapped had fresh signs of vole activity.

Eighty-five animals were trapped for use in the various laboratory studies. The average weight of 75 of these animals was 29.76 ± 6.74 grams at the time of capture. The average male (N = 37) weighed 33.16 ± 6.39 grams while the average female (N = 38) weighed 26.45 ± 5.31 grams. Differences in mean weights of the sexes were found to be significant at the 1% level using Student's t test.

Trapping success for a 1-year period in terms of males, females and the total number of animals trapped per month is depicted in Figure 4. Traps were set for at least 1 week during each month. The three peaks are probably reasonable indications of periods of high activity levels associated with breeding, since pregnant females were captured in March, June and October. Descended testes in males were observed from March through November. The low level of activity in August may also be associated with a water stress situation (see page 42).

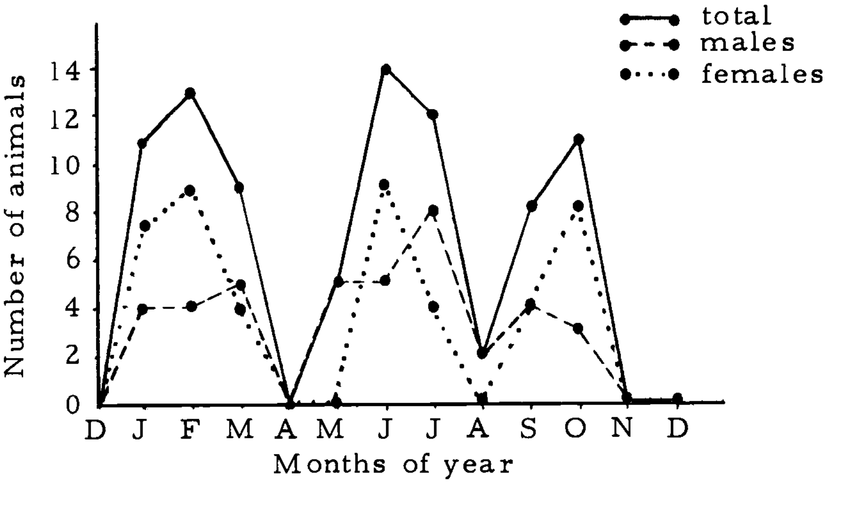


Figure 4. Monthly trapping success of M. canicaudus for a 1-year period distinguishing male, female and total numbers captured.

Trapping success on a daily time scale is illustrated in Figure 5. Based on these results, traps were moved to new complexes whenever 3 days passed without any animals being captured. Apparently, animals used the runways regularly, and most of the voles in an area were trapped within the first days of exposure to traps.

Laboratory Studies

Food Consumption

Thirty voles weighing an average of 29.61 ± 6.71 grams consumed an average of 4.39 ± 0.93 grams of food per day. Thirteen males averaging 32.38 ± 6.21 grams in weight consumed 4.68 ± 1.01 grams of food per day, while 17 females averaging 27.50 ± 6.45 grams in weight consumed an average of 4.17 ± 0.83 grams of food per day. The average consumption of food per gram of weight per day for 30 voles was 0.15 ± 0.03 grams. Males averaged 0.15 ± 0.04 grams of food per gram of weight per day. Females averaged 0.16 ± 0.03 grams of food per gram of weight per day (Table 3). Statistical analysis (Student's *t* test) showed no significant difference (5% level) between male and female food consumption rates.

The food consumption experiment was done over a period of 4 months because of trapping difficulties and restricted laboratory facilities. The average amount of food uptake per month is presented in Table 4. There is a highly significant difference (1% level) between

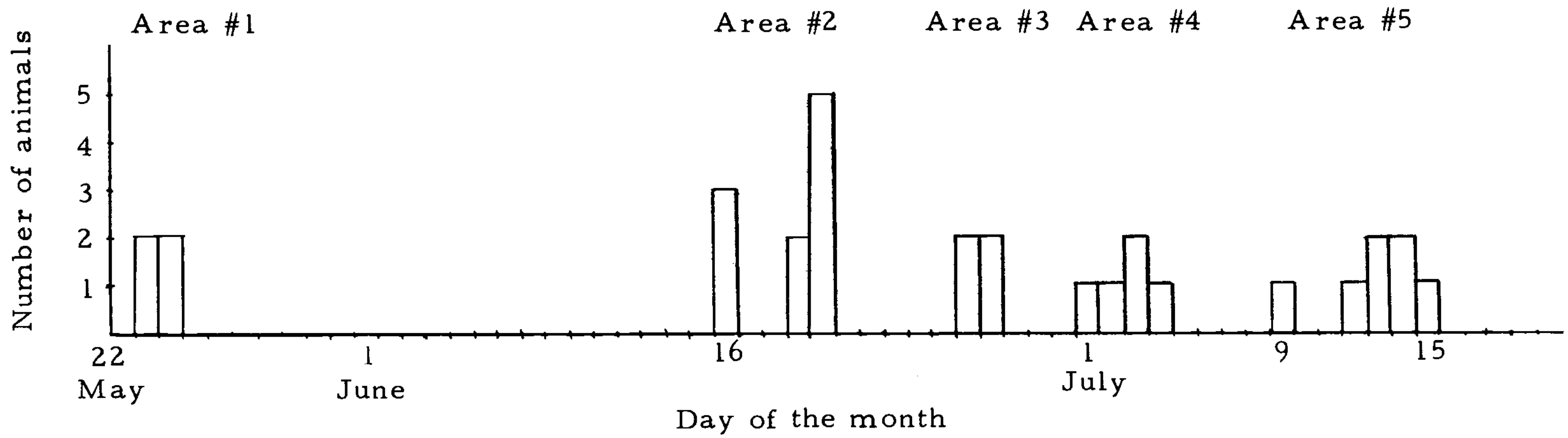


Figure 5. Daily trapping success for M. canicaudus for five different areas of permanent pasture land in the William L. Finley National Wildlife Refuge from May 22, 1970 to July 20, 1970.

Table 3. Summary of food and water uptake experiments with M. canicaudus. Numbers are averages.

Experiment	Consumption per individual				All
	Males		Females		30
	N = 18	N = 13	N = 12	N = 17	
Grams of food/day	-	4.68	-	4.17	4.39
grams of food/gram of wt/day	-	0.15	-	0.16	0.15
cc water/day	12.42	-	10.59	-	11.69
cc water/gram of wt/day	0.39	-	0.43	-	0.41

Table 4. Food consumption rate for M. canicaudus for the months of December through March. Numbers are averages.

	December	January	February	March
grams of food/gram of wt./day	0.13	0.16	0.17	0.17
	(N = 9)	(N = 3)	(N = 12)	(N = 6)

the means for the months of December and February and December and March. Apparently there is a gradual increase in the rate of food consumption in the early part of the year, possibly associated with the increasing activity rate connected with breeding.

Water Consumption

The average daily *ad libitum* water consumption of 30 adult voles weighing an average of 29.31 ± 6.96 grams was 11.69 ± 5.80 cubic centimeters of distilled water per day. Eighteen males averaging 31.68 ± 6.96 grams in weight consumed an average of 12.42 ± 6.58 cc of water per day, while 12 females averaging 25.75 ± 5.46 grams in weight consumed an average of 10.59 ± 4.42 cc of water per day. The average utilization of water per gram of body weight was 0.41 ± 0.22 cc per day. The average utilization of water per gram of body weight for males was 0.39 ± 0.21 cc per gram per day while females utilized an average of 0.43 ± 0.24 cc per gram of body weight per day (Table 3). No significant differences exist between male and female rates of water consumption.

The entire water uptake experiment was done during the month of July. Therefore, a seasonal analysis was not possible.

Water Stress

The results of measuring the length of survival of 30 adult voles on uniformly increasing molarities of salt water indicated that animals succumbed on NaCl solutions ranging in salinity from 0.2 M to 0.5 M (Figure 6). The average time of survival was 14.26 ± 3.70 days with an average weight loss of 6.60 ± 4.60 grams over that period. The percent body weight lost before succumbing for all 30 individuals was 21.17 ± 12.29%. The average rates for males and females are presented in Table 5. Statistical analysis showed no significant difference between male and female responses to the water stress experiment.

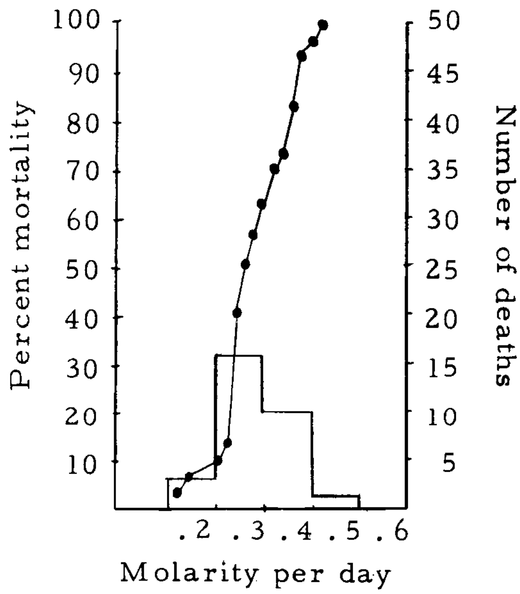


Figure 6. Percent mortality per day of <u>M. canicaudus</u> while drinking increasing concentrations of salt water (graph) and the number of deaths per 5-day period vs. molarity (histogram).

Table 5. Average time of survival, average weight loss and average percent of body weight lost while drinking increasing concentrations of salt water for 30 adult M. canicaudus distinguished by sex.

	Males (N = 14)	Females (N = 16)	All 30
Average survival time (days)	14.14 $\pm$ 3.78	14.37 $\pm$ 3.76	14.26 $\pm$ 3.70
Average weight loss at death (grams)	8.00 $\pm$ 4.75	5.37 $\pm$ 4.22	6.60 $\pm$ 4.60
Percent of body weight lost at death	22.55 $\pm$ 12.39	19.97 $\pm$ 12.48	21.17 $\pm$ 12.29

The data from the water stress experiment were collected during 2 months. One-half of the animals were tested in February and the other half in April. Comparison of the means showed no significant differences between animals tested during the 2 months.

Behavior

The behavior experiments revealed the intraspecific social interactions illustrated in Table 6. Nine different social combinations can occur from four voles living together in each experiment (see columns of social combination scores in Table 6). In the following, the word "pair" indicates the occurrence together of a male and female to the exclusion of the other voles. The voles can be paired simultaneously or either pair can occur while the other two voles are living singly (Table 6, columns I and II). Two combinations are

Table 6. Social groups formed in an experimental society of Microtus canicaudus (two males and two females in each experiment).

			Social combinations										
			I	II	III	IV	V	VI	VII	VIII	IX		
Date experiment started	Experiment number	Total daily records	Double pairs	Single pairs	One female out	One male out	None together	Both males together	Both females together	All four together	Both males together & Both females together	Fighting	Analysis
8/5/70	1	10	0	3	5	1	0	0	0	1	0	1 male killed & partly eaten	1 male dominant
8/18/70	2	10	0	2	0	2	5	1	0	0	0	1 female killed	
8/29/70	3	10	0	3	0	2	3	0	2	0	0		1 male dominant
9/8/70	4	10	0	2	2	0	6	0	0	0	0	1 male killed	1 male dominant
9/19/70	5	10	0	1	0	2	5	0	1	1	0	1 male killed	1 male dominant; 1 litter of 5 (10/13/70)
9/29/70	6	10	0	0	0	1	8	0	1	0	0	1 male bitten; 1 female killed	1 male dominant
10/12/70	7	10	1	4	2	0	3	0	0	0	0		1 male dominant
10/23/70	8	10	0	3	0	0	7	0	0	0	0	1 male killed & partly eaten	1 male dominant
11/4/70	9	10	1	4	0	0	4	0	0	0	1		
2/16/71	10	10	0	0	0	0	9	0	0	1	0	1 male killed	1 male dominant
	Total	100	2	22	9	8	50	1	4	3	1		
	Expected	100	9.4	37.5	9.4	9.4	9.4	9.4	9.4	1.6	4.7		

possible in which three voles nest together to the exclusion of the fourth (Table 6, columns III and IV). In referring to these scores, the excluded animal is referred to as "out" of the aggregation. Other possible combinations are: (column V) no two voles together; (column VI) males together, females living singly; (column VII) females together, males living singly; (column VIII) all four voles together; (column IX) males together in one cage, females together in another.

Whenever a vole was killed early in an experiment, it was generally replaced and the experiment allowed to continue. No marked change in vole behavior accompanied the addition of the new vole. The addition of the new animal was felt to be preferable to the outright end of the experiment due to trapping difficulties. If the death took place late in the 10-day experimental period the remaining three animals were observed.

The probability of occurrence of each social combination on a chance basis is shown at the bottom of Table 6. This was based upon the fact that the four animals can combine 256 different ways (4^4). Each of the nine combinations considered in this study represents a fraction of 256 multiplied by the total daily records (100). As an example, the first social combination, "Double Pairs" (column I, Table 6) represents two possible sets of pairs. In the first, male 1 may pair with female 1 leaving male 2 with female 2. However, the other possibility exists where male 1 pairs with female 2 leaving female 1 with male 2. In either case one pair has a choice of four possible cages in which to live while the second pair has the choice of only three cages in which to live. Therefore the expected probability of "double pairs," under assortment resulting from chance alone, is $((4 \times 3/256) + (4 \times 3/256)) \times 100 = 9.4$.

It is obvious from the daily scores that the distribution of the voles in the four cages was not according to chance. When two adult males and two adult females were placed together in the behavior cage, 8 of the 10 experiments showed that one male dominated the other. This was exemplified by the high frequency with which single males were killed or bitten on the tail or scrotum. This is further suggested by the low frequency of association of both males (Table 6, columns VI and IX). Some aggression toward females was evidenced by the deaths of two females in two separate experiments. However, the exact cause, whether by aggression between females, or between males and females, is unknown. This apparent intraspecific aggression resulted in a high frequency of isolation of all four animals in separate cages. This social combination ("none together") has a frequency equal to the total frequency of all other possible combinations (Table 6, column V). The only other social combination with a frequency higher than that which would be expected to result from chance assortment is that of occurrence of all four animals together (Table 6, column VIII). This seeming contradiction may have been caused by the animals being startled by the approaching observer, since there seems to be little seasonal correlation. In all other social combinations, the observed frequencies were lower than would be expected to result from chance assortment.

The behavior cage used in this study was roughly the same size as a small complex. Therefore, results of this behavior study may further support the premise that each complex has but one vole in residence.

DISCUSSION

As a result of data collected it was concluded that there were approximately 57 ($\pm$ 25) gray-tailed voles occupying each acre of permanent pasture on the William L. Finley National Wildlife Refuge between 1970 and 1971. These animals resided in complexes of burrows with connecting runway systems. Slightly fewer than 1.5 animals occupied each of 39 complexes found on one acre of pasture land. The complexes were located 8 feet apart and consisted of approximately 9 holes each.

Goertz (1959) sampled one strip of permanent grass (8 x 300 feet) in the Willamette Valley and found 284 open holes. This converts to 5,155 holes per acre. If the ratio of 6 holes per vole prevailed at that time and place, a vole density of 858 animals per acre or 14 times the estimate of the present study would have existed.

The population estimate resulting from the present study is probably only true for permanent pasture. On other types of agricultural land in the Willamette Valley, one might expect fewer individuals per acre due to recurrent plowing and field burning, which would result in population limitation.

The population estimate presented here would not be applicable in other years, since this animal is thought to have cyclic population tendencies (Goertz, 1964). Microtus montanus populations at the peak of the 1957-1958 irruption probably reached 2,000 to 3,000 per acre in

November of 1957. Open holes into underground burrow systems numbered 28,000 per acre and averaged 11 holes per vole. However, by January, 1958, there were an estimated 733 voles per acre, and by March, this number had dropped to 80 per acre (Spencer, 1959), a density similar to that estimated for M. canicaudus in the present study.

Conflicts between individuals in the laboratory suggested that intraspecific intolerance may play an important role in the spatial orientation observed in the field. Contrary to Maser and Storm's (1970) statement, M. canicaudus is not a gregarious animal, at least in the cage condition, but apparently prefers to live alone during those times of the year when experiments were run in this study. This apparent lack of tolerance for one another is particularly true between males, as was demonstrated to the author in the field when two males, locked in combat, were easily captured by hand. Similar behavioral work with Peromyscus maniculatus (Blair and Howard, 1944) showed these mice to be more gregarious than M. canicaudus.

Spencer (1959) indicated that a Microtus sp. individual consumed its weight in food per day. Livingston (1953) stated that it had been estimated that one vole (Microtus sp.) could cut up to 30 grams of grass per day. Results of this study indicated that M. canicaudus consumed 15% of its weight per day of a concentrated dry food source.

Cattle eating cubed concentrate rations consumed 17.0 grams of concentrate per kilogram of weight per day (Rogerson, Ledger and Freeman, 1968). Sheep eating grass consumed 18.7 grams per kilogram per day (Langlands, 1968). Food consumption results of the study reported here, when converted to similar units, showed that gray-tailed voles consumed 153 grams of food per kilogram of weight per day; that is, more than 8 times the amount consumed by sheep or cattle per kilogram of weight. White mice (Mus sp.) consumed 209 grams of food per kilogram of weight per day (Chew and Hinegardner, 1957).

A 400-kilogram steer would consume approximately 6,800 grams of food per day. The voles on 1 acre of land would weigh a total of a little more than 1.5 kilograms, and would consume approximately 262 grams of food per day. Therefore, at the population density measured here, all the voles found on 26 acres of land would consume as much as one 400-kilogram steer per day.

Research on Willamette Valley pasture land has been done at Oregon State University at an area called the Hill Pasture, operated by the Department of Animal Science. The types of vegetation found on the Hill Pasture were similar to that found on the study area (Table 1). These types of pastures are classified as native grass mixed with tame grass. The basic overall carrying capacity for the Hill Pasture was established at 2.25 acres per sheep per year (Hedrick, 1959).

One animal unit is defined as 1,000 pounds (453.6 kilograms) live weight of domestic stock. It is also defined as one bull, one cow with calf or five sheep (Krueger, 1971). Therefore, one animal unit would require 11.25 acres per year of permanent pasture similar to that found on the study area. This area (11.25 acres) would have a population of 641 voles, at the population density determined by this study, which would weigh approximately 19.2 kilograms or a little over 4% of one animal unit. These voles would consume 2.9 kilograms of food per day or 37% of the amount of food eaten by one animal unit per day.

However, if one uses Livingston's (1953) estimate of a vole cutting 30 grams of grass per day, the 641 voles found on the acreage required to support one animal unit for 1 year would cut 19.2 kilograms of grass per day. This would be 2.5 times the quantity of food eaten by one animal unit per day.

Livingston (1953) did a seasonal production study of the Hill Pasture. The results of his study are presented in Figure 7. Assuming that voles cut 30 grams of grass per day per individual, then at a population density of 57 voles per acre, the total amount of grass cut per month (30 days) would be 51,300 grams. This figure is well below the lowest production rate measured by Livingston (see Figure 7), and, therefore, it was concluded that at present population levels and during the spring, summer and fall months, food is not likely to be a limiting factor for _M. canicaudus_ in the Willamette Valley.

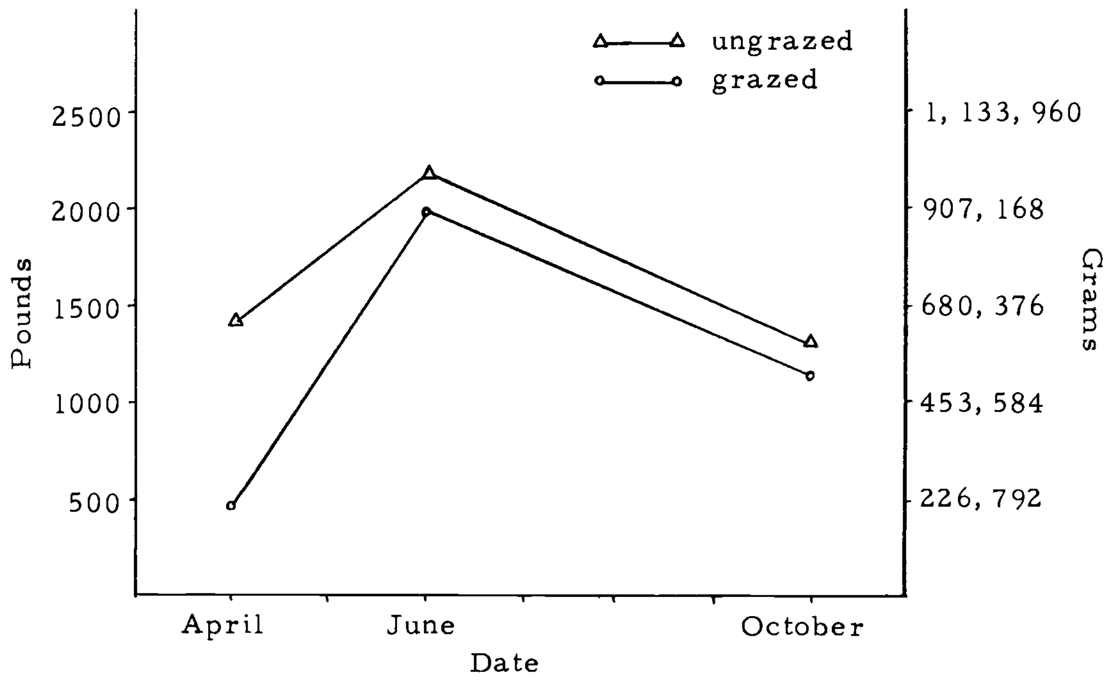


Figure 7. Total production in pounds and grams per month per acre of the Hill Pasture, Oregon State University, Corvallis, Oregon, grazed and ungrazed (from Livingston, 1953).

Figure 8 is a presentation of the possible effect of M. canicaudus on the food resource at various population levels and at three different food consumption rates. At a rate of food consumption equal to 100% of body weight per day (that is, the clipping rate estimated by Livingston), gray-tailed voles could destroy even the most productive food resource at a density of 1700 animals per acre. At a food consumption rate of 50% of body weight per day they are much less likely to do substantial damage to their food resource. If the daily consumption rate is maintained at the level measured in this study (4.4 grams/day), the gray-tailed vole is very unlikely to do permanent damage to its food resource even at a population level of 3000 animals per acre. At present population levels, M. canicaudus, by itself is not a threat to its own food resources, although this animal may be a significant competitor with domestic stock.

In Figure 3, Maps 2 and 4, there is an average of approximately 13 feet of Type II runways. Assuming an availability of food to a depth of 1 inch on either side of these runways, there would be about 2 square feet, or 4.60×10^{-5} acres of food accessible to voles along the length of these runways. Livingston (1953) showed a production rate of about 9.07×10^{5} grams of grass per month per acre on a grazed pasture in June (Figure 7). Therefore, there were 41.72 grams of grass produced per month or 1.4 grams per day along the Type II runways. This is roughly one-fourth of the daily dry food requirement of

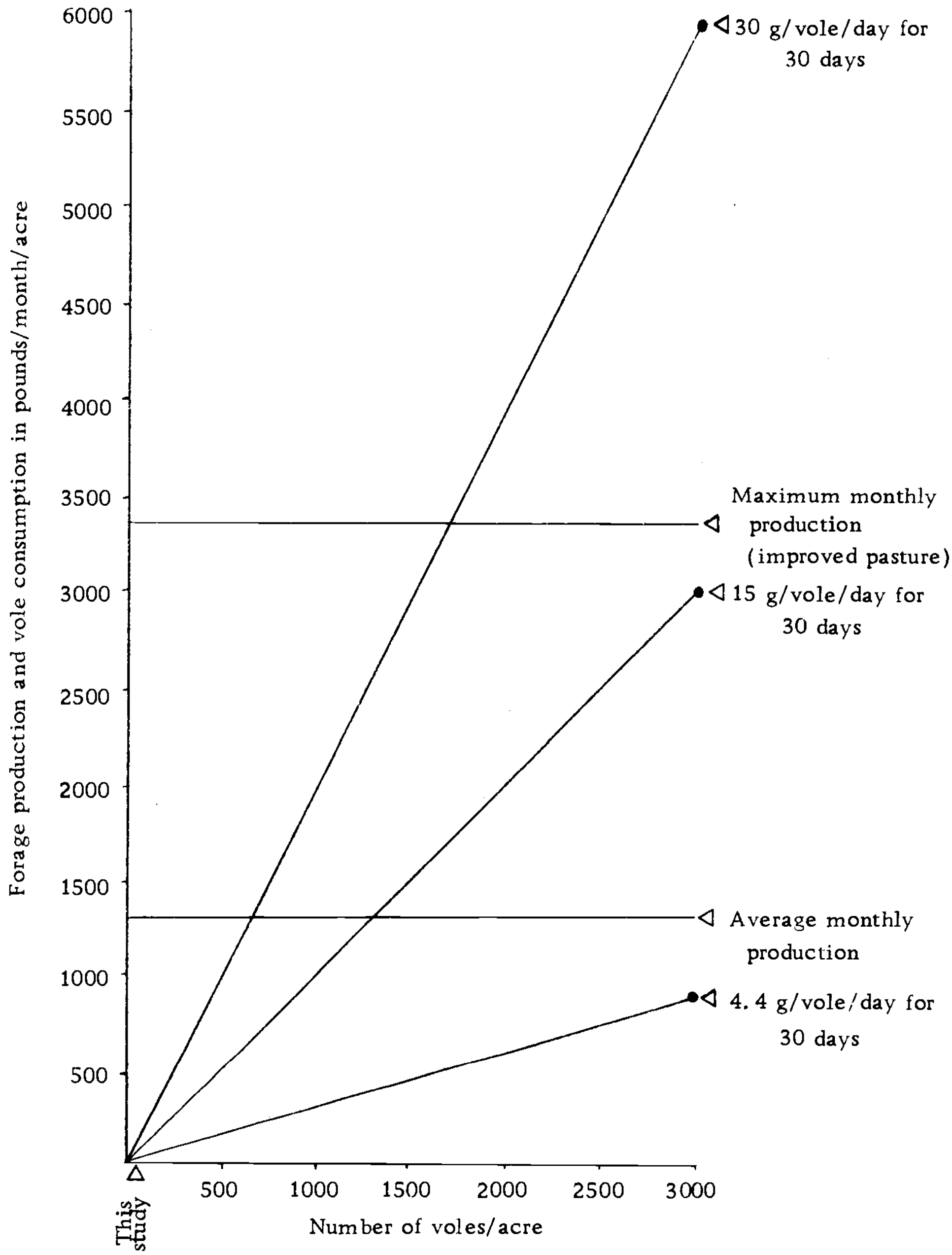


Figure 8. Total production in pounds per acre of the Hill Pasture, Oregon State University, Corvallis, Oregon (Livingston, 1953) with food consumption rate for Microtus canicaudus at various population levels and at various rates of food uptake.

one vole. In months of lower productivity, the discrepancy is magnified. Therefore, additional feeding must take place outside of Type II runways, or voles must slowly extend the Type II runways by consuming standing stock. In this way, Type II runways may eventually become Type I runways.

The gray-tailed vole probably plays an important role in the natural food webs of the Willamette Valley as a primary herbivore. This animal is probably one of the most plentiful and reliable food resources for many of the Valley's predatory reptiles, birds and mammals. Furthermore, the vole makes a contribution to the aeration, percolation and the building of new soil in the Valley through its burrowing. The extent to which the first winter rains penetrate the soil may be influenced by the number of vole holes in an area.

A comparison of *ad libitum* water consumption data from this study with the literature is made difficult by the fact that the food content and activity levels are largely unacknowledged in the reports of many experimenters. Thus comparisons are significant only when the differences in *ad libitum* consumption are marked. The difficulty encountered in making comparisons is underscored by the reported values for the albino mouse which differ by a factor of four (see Table 7).

There does not seem to be any fixed trend relating water consumption to differences in the habitat of the various species listed

Table 7. *Ad libitum* water consumption of different species of rodents.

Species	Weight (g)	Water/ day (cm^3)	Water consumption in % body weight/ day (cc)	Reference
Peromyscus boylii	28.5	3.34	12.4	Brown (1964)
P. leucopus noveboracensis	22.9	2.60	11.3	Odum (1944)
" " "	19.1	1.70	8.9	Dice (1922)
" " "	20.7	5.40	26.0	Chew (1951)
" " "	21.6	2.50	11.5	Lindeborg (1952)
P. leucopus	20.2	3.57	17.9	Brown (1964)
P. leucopus tornillo	29.4	1.90	6.4	Lindeborg (1952)
P. maniculatus	16.3	3.48	20.3	Brown (1964)
P. maniculatus bairdi	18.6	3.00	16.1	Lindeborg (1952)
" " "	13.8	1.70	12.3	Dice (1922)
P. maniculatus blandus	24.0	2.70	11.2	Lindeborg (1952)
P. maniculatus nebrascensis	19.7	1.90	9.6	Lindeborg (1952)
P. maniculatus gracilis	21.5	2.60	12.0	Lindeborg (1952)
P. maniculatus sonoriensis	19.1	2.70	14.1	French (1956)
P. maniculatus nubiterrae	17.3	1.80	10.4	Odum (1944)
P. truei truei	32.4	2.80	8.6	Lindeborg (1952)
P. eremicus eremicus	21.3	2.10	9.8	Lindeborg (1952)
Clethrionomys gapperi maurus	27.9	25.0	89.6	Odum (1944)
Microtus pennsylvanicus p.	28.3	6.0	21.2	Dice (1922)
" " "	34.7	7.2	20.7	Lindeborg (1952)
M. ochrogaster ochrogaster	42.6	15.8	37.0	Chew (1951)
M. canicaudus	29.3	11.7	41.0	This study
M. townsendii	57.3	29.9	52.0	This study
Pitymys pinetorum	18.2	1.8	9.8	Odum (1944)
Mus musculus (albino)	22.4	2.7	12.0	Bing and Mendel (1931)
" " "	35.1	12.0	34.1	Chew and Hinegardner (1957)
White mice (8 strains)	24-34	4.3-10.0	17.9-29.4	Silverstein (1961)
Dipodomys panamintinus	79.0	16.0	20.2	Nichter (1957)
D. merriami	33.9	-	15.6	MacMillan and Hudson (cited by Hudson, 1962)

(Continued on next page)

Table 7. (Continued)

Species	Weight (g)	Water/ day (cm^3)	Water consumption in % body weight/day (cc)	Reference
Dipodomys morroensis	68.0	14.8	21.7	Nichter (1957)
D. ordii	44.0	1.2	2.7	Lindeborg (cited by Chew, 1965)
D. ordii columbianus	44.0	6.0	13.6	Howell and Gersh (1935)
Citellus leucurus	85.0	10.2	12.0	Bartholomew and Hudson (1959)
" "	92.5	13.4	14.4	Hudson (1962)
Rattus norvegicus	394.0	26.8	6.8	Chitty (1954)
R. norvegicus (albino)	288.0	34.8	12.0	Dicker and Nunn (1957)
Neotoma pennsylvanica	200.0	113.0	56.5	Patterson (1933)
N. lepida (desert)	110.0	36.6	33.2	Lee (1963)
" " (coastal)	139.0	18.1	13.0	Lee (1963)
N. fuscipes	187.0	45.7	24.4	Lee (1963)

in Table 7. For example, *Dipodomys merriami*, an animal of extremely arid environments, has a percent body weight consumption five times greater than *Dipodomys ordii*, an animal also found in arid regions. Furthermore, *D. merriami* consumed proportionately more than *Neotoma lepida*, a species also found in arid environments. *Microtus* sp., *Neotoma* sp. and *Peromyscus* sp., however, show consumptions that correlate somewhat with their habitats (mesic, mesic and xeric, respectively). The high water requirement shown by the red-backed mouse (*Clethrionomys gapperi maurus*) in captivity is possibly a limiting factor in its habitat selection; it occurs only in the wettest microhabitats (Odum, 1944). Lindeborg (1952) found striking differences in daily water consumption between genera of mice inhabiting different geographic areas, although he concluded that the amounts of water consumed voluntarily in captivity are not very reliable for the estimation of water needs in nature. He further concluded that the more logical and effective basis for comparing species was in terms of their ability to maintain weight and survive on reduced rations of water.

Apparently the *ad libitum* water consumption rate of *M. canicaudus* measured in this study agrees with figures reported for other *Microtus* species. The gray-tailed vole has a relatively high rate of *ad libitum* water consumption in comparison with other members of the genus, and has one of the highest rates of water consumption of any species reported. The high water requirement may be a limiting factor in habitat selection and distribution of *M. canicaudus*.

Salt metabolism has been studied in several rodents: *Perognathus* (Schmidt-Nielsen, Schmidt-Nielsen and Schneiderman, 1948), *Dipodomys* (Schmidt-Nielsen *et al.*, 1948; Schmidt-Nielsen and Schmidt-Nielsen, 1950; Nichols as cited by Chew, 1965), *Gerbillus* (Burns, 1956), antelope ground squirrel (Bartholomew and Hudson, 1959), and *Peromyscus* (Brown, 1964). Some literature on kidney function in the white rat offers an additional comparative basis. Richter and Moiser (1954) reported that white rats maintain their weight when drinking the equivalent of 0.29-0.34 molar NaCl solutions. This agrees with Adolph's (1943) observation that white rats can maintain themselves on water half as saline as sea water. The only mammals known to be capable of effectively using sea water are the kangaroo rat *Dipodomys merriami* (Schmidt-Nielsen and Schmidt-Nielsen, 1950), which maintained its weight on the equivalent of 0.545 and 0.585 molar NaCl, the Mongolian gerbil *Meriones unguiculatus*, which maintained normal body weight on 0.8 molar NaCl and derived some benefit from 1.0 molar NaCl (Winkelmann and Getz, 1962), and the antelope ground squirrel *Citellus leucurus* which maintained its weight on 0.8 molar NaCl (Bartholomew and Hudson, 1959). Bartholomew and Hudson (1959) concluded that the antelope ground squirrel could use salt solutions almost three times as concentrated as those which can be handled by the white rat and that the efficiency of its excretory system may be greater than that of the kangaroo rat. Brown (1964) found that *Peromyscus* sp. succumbed on NaCl solutions ranging in salinity from 0.3 to 0.5 molar NaCl with an average time of survival of 17.9 to 19.6 days when given increasing concentrations of saline solutions.

The results of this study indicated that *M. canicaudus* is not particularly adapted to a water stress situation. This vole can maintain itself on salt solutions roughly as well as can the white rat, but is somewhat less able to handle salt solutions than are *Peromyscus* species. However, *M. canicaudus* withstood approximately the same amount of weight loss before death as did both *Peromyscus* sp. [20.26% weight loss (Brown, 1964)] and *Citellus* sp. [20-25% weight loss (Bartholomew and Hudson, 1959)]. Other species' levels of tolerance are presented in Table 8.

Lindeborg (1952) compared the ability of *Perognathus* sp., *Peromyscus* sp. and *Microtus* sp. to survive on a deficient water supply. *Microtus* showed the least ability to survive. *Peromyscus* occupied a position intermediate between *Perognathus* and *Microtus* in its ability to survive. Lindeborg (1952) found a correlation between ability to survive on a reduced water supply and occurrence in arid or more humid conditions. He further concluded that *Microtus* would find extended dry periods critical to survival.

Table 8. Some tolerable weight losses for rodents due to dehydration.

Species	Percent weight lost	Reference
Peromyscus leucopus	32-52	Chew, 1951
Microtus pennsylvanicus	32	Hall, 1922
Mus musculus (albino)	35-40	Cullingham, 1960
Microtus oeconomus and *M. arvalis*	27-35	Hermann as cited by Chew, 1965
Citellus leucurus	44.6	Hudson, 1962
Neotoma albigula	30	Schmidt-Nielsen *et al.*, 1948
Rattus norvegicus (albino)	40-50	Barker and Adolph, 1953
Microtus canicaudus	21.2	This study

The results of this study would tend to reinforce Lindeborg's (1952) conclusions. Apparently M. canicaudus has not acquired physiological adaptations to xeric habitats, and is therefore confined to more mesic habitats as are most other members of the genus. However, the considerable individual variation in the tolerance of high salt concentrations (Figure 5) may indicate that under the proper selective pressure, the gray-tailed vole could possibly adapt more quickly in this respect to drying habitats such as saline areas and deserts than if there was less individual variation (Fisler, 1962a).

From field observations, it is obvious that many voles do not have surface water available for drinking during much of the summer and must survive without it (see Figure 2). Microtus californicus showed a highly significant selection of traps baited with a thimble of water in preference to traps that were unbaited. Water-baited traps were entered as frequently as those baited with rolled oats (Fisler, 1962b). The fact that maximum activity of this rodent (M. californicus) during the summer time occurs during the 4 hours after sunrise may be related to the availability of dew at that time of day (Pearson, 1960). Dew is often proposed as a source of drinking water, but its use is rarely observed (Chew, 1965).

By force of circumstances, free water in their food is the only dependable external source of water for many mammals (Chew, 1965). Because of the lack of succulent appearance of some foods, the quantity of water available may be underestimated. As shown by Schmidt-Nielsen and Schmidt-Nielsen (1951), the water content of "air-dried" barley at 25°C varies from 3.5% at 10% relative humidity to 18% at 76% relative humidity. These relatively small amounts, plus metabolic water, are sufficient for some mammals. The food preferences of larger desert rodents clearly vary with the seasonal succulence of different plants (Vorhies and Taylor as cited by Chew, 1965). In captivity, _Microtus ochrogaster_ survived, given nothing but fresh green grass (Dice, 1922). Wild rabbits (_Oryctolagus cuniculus_), lacking access to drinking water gained weight through the spring, when the pastures were still succulent (68-77% water in grasses), but lost weight when the pastures dried up in the summer (to as little as 7-10% water in grasses) (Hayward as cited by Chew, 1965).

During periods of water stress, _M. canicaudus_ must depend upon dew and its food to get an adequate water intake. In the Willamette Valley, dew may be the more important source of water, since, during the summer when rain is rare, dew is an almost inevitable nightly occurrence, although actual measurements are not available (Bates, 1971). This is because conditions necessary for dew production are commonly met during the summer. Clear night skies allow radiation absorbed by the ground during the day to be reradiated at night in the form of long-wave heat radiation. The drier the atmosphere, the greater the amount of outgoing heat radiation. As leaves and other surfaces lose heat through the radiation, they are cooled and ultimately may reach the dewpoint of the air (Went, 1955). Went (1955) calculated that for a whole year of 365 cloudless nights, the equivalent of 15 inches of rain at the rate of 1 millimeter of dew per night may be deposited. Actual measurements in Ohio indicated that an average equivalent of 9.1 inches of rain was deposited throughout the year in the form of dew or 20% of the total water supply (Went, 1955). Actual measurements for the Willamette Valley are not available (Bates, 1971).

During particularly stressful periods, a weight loss due to dehydration may be evident in the gray-tailed vole. However, the behavioral characteristics of this animal may well be the key to its survival during these periods of water stress. The indication that each individual lives a relatively solitary life in a complex of holes some 8 feet from the nearest neighbor may guarantee an adequate supply of succulent plants and dew for each individual. Furthermore, microhabitat selection and distribution may be limited by the availability of water during the driest period of the year, since it is doubtful that food would be limiting (see page 35). Periods of high and low activity levels (Figure 4) may also be related to water availability, particularly the period of low activity in August.

NOTES ON MICROTUS TOWNSENDII

This study of *M. canicaudus* had its origins in a comparative study of *M. townsendii* and *M. canicaudus*. Due to the author's inability to find and capture *M. townsendii*, it was decided to limit the study to *M. canicaudus*. However, because very little work has been done on the life history of Townsend's vole, it was decided that what sparse data were collected during this study should be included in this dissertation.

Eleven Townsend's voles were captured. Their average weight was 59.55 ± 9.64 grams. The males (N = 7) averaged 64.00 ± 6.81 grams, while the females (N = 4) averaged 51.75 ± 4.95 grams. The difference in weight between males and females was found to be significant at the 5% level, using Student's *t* test. In addition to captured wild animals, a litter of five young was obtained from a captive pair of voles on 28 August 1970. At 63 days of age, the three surviving young weighed an average of 53 grams (one male at 61 grams and two females at 43 and 55 grams).

Water uptake experiments were conducted on 13 Townsend's voles. The average daily consumption was 30.01 ± 11.07 cubic centimeters per day. Males (N = 7) averaged 20.92 ± 13.43 cubic centimeters per day, while females (N = 6) averaged 28.95 ± 8.67 cubic centimeters per day. Water consumption per gram of body weight was 0.53 ± 0.18 cubic centimeters per gram of body weight per day. Males consumed 0.48 ± 0.18 cubic centimeters per gram of body weight per day while females consumed 0.59 ± 0.17 cubic centimeters per gram of body weight per day. No significant difference between male and female rates of water consumption was found.

The rate of food consumption was determined for four individuals. The average rate of intake was 6.57 ± 1.69 grams per day. Food intake per gram of body weight per day averaged 0.13 ± 0.02 grams.

Only one behavioral experiment was conducted with Townsend's vole. The data from this experiment are presented in Table 9. The most common social combination recorded was where all four individuals nested together indicating a possible high level of gregariousness and all other observations showed "togetherness," also. The physical condition of one male indicated one male's dominance over the other.

Field data indicated that *M. townsendii* may be dominant over *M. canicaudus*. In two areas on Finley Wildlife Refuge where Townsend's voles were successfully captured, *M. canicaudus* were trapped only after *M. townsendii* had been trapped and removed.

Townsend's vole is a larger animal than the gray-tailed vole and may be dominant over *M. canicaudus* where their habitats overlap. *M. townsendii* is probably a more gregarious animal than *M. canicaudus* although some intraspecific aggression was evident.

Table 9. Social groups formed in an experimental society of <u>Microtus townsendii</u>. Two pairs of voles were used in the experiment.

			Social combinations										
Date	Experiment Number	Total daily records	Double pairs	Single pairs	One female out	One male out	None together	Both males together	Both females together	All four together	Both males together & both females together	Fighting	Analysis
11/27/70	1	10	1	0	3	0	0	0	0	6	0	1 male in poor shape	1 male dominant
Total		10	1	0	3	0	0	0	0	6	0		
Expected		10	.94	3.7	.94	.94	.94	.94	.94	.16	.47		

Townsend's vole apparently has an even greater daily water uptake requirement than the gray-tailed vole and therefore is probably even more limited in habitat selection by this factor than is _M. canicaudus_.

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