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AN ANALYSIS OF SOUND COMMUNICATION IN THE WATER VOLE,
MICROTUS RICHARDSONI (RODENTIA: MICROTINAE)

by

Dane R. Tang

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Biology

Approved:

Major Professor

Committee Member

Committee Member

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1975

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ABSTRACT

An Analysis of Sound Communication in the Water Vole,

Microtus richardsoni (Rodentia: Microtinae)

by

Dane R. Tang, Master of Science

Utah State University, 1975

Major Professor: Dr. Emily C. Oaks
Department: Biology

Adult members of the species Microtus richardsoni were used to study the importance of acoustic communication in these voles. Tests were run with single individuals and nonbreeding pairs of voles to obtain recordings and sonographs of sounds emitted during exploration of a new cage, agonistic encounters, encounters with a potential predator and in response to miscellaneous aversive stimuli. Of the four groups of tests conducted, sounds were used by M. richardsoni during the last three. The results of this study showed that the water vole emitted ten different call types or sounds. These sounds were separated by similarity into Group I, Group II, tooth-chatter and miscellaneous sound types. Group I calls included the squeal, squawk, grind and complex. These calls were similar in intensity and in having harmonics extending into the ultrasonic range. The squeal consisted of a fundamental frequency plus several distinct, harmonically-related overtones. The squawk resembled the squeal, but the harmonics in the higher frequencies of the former call were obscured by noise. The complex was found to be a combination of two or all three of the other calls. The Group II call types emitted by the water vole were

the voiced and voiceless whimpers. These two calls were similar in that each was emitted at low intensity and neither call had harmonics extending into the ultrasonic range. The voiceless whimper was different from the voiced whimper in that its harmonics were obscured by noise. The squawk, grind, complex, voiced whimper and voiceless whimper are inferred to be modifications of the squeal. The primary function of these six call types is postulated to indicate the degree of submissiveness of the vocalizing vole. Modification of the calls is probably related to the motivational state of the animal emitting the call. A secondary effect of the calls might be to inhibit further aggression by the opponent. A seventh sound emitted by the water vole was the tooth-chatter. This sound, also used by many other rodents, was used to communicate threat. The miscellaneous sounds emitted by these voles included the ultrasonic chirp, the peep and the "whooping" call. These calls were not emitted frequently enough to postulate their function. This study showed that sound is used mainly by Microtus richardsoni during agonistic situations and may be adaptive in inhibiting aggression. The use of the physical characteristics of sounds in determining taxonomic relationships is postulated.

(53 pages)

INTRODUCTION

That certain rodents use sound as a means of communication is well known. Some of the rodents, such as the Uinta ground squirrel (Balph and Balph, 1966), the yellow-bellied marmot (Waring, 1966), and the prairie dog (Waring, 1970) are conspicuously vocal. The calls emitted by these animals communicate alarm to conspecifics, and other species may even respond to these alarm calls. The calls of the ground squirrel are also used in agonistic encounters with conspecifics and serve to maintain the social organization of these mammals (Balph and Balph, 1966). The prairie dog also uses calls for group cohesion (Waring, 1970). These rodents are all members of the family Sciuridae and vocalize in the sonic range.

Common laboratory mice and rats (muroids), on the other hand, have been found to vocalize mainly in the ultrasonic range (Anderson, 1954; Noirot, 1966, 1968; Sewell, 1970). Sales (1972) conducted a study of aggressive behavior in adults of rats and fourteen other small mammals (muroids and a shrew) in which she found that ultrasound served to inhibit aggression. She suggested that the production of ultrasound during aggressive encounters may play a part in maintaining the social structure of a certain species of myomorph rodents. Nonsocial mammals tested in her study, such as Microtus agrestis, Lagurus lagurus and Mus musculus, were found not to use ultrasound as adults. She, therefore, suggested that ultrasound may not be important for communication within a solitary species. Brooks and Banks (1973) found that

the collared lemming (Dicrostonyx groenlandicus), a solitary species, did use ultrasound, but only in mating situations or in eliciting maternal retrieval of young. In agonistic encounters among adult lemmings, only audible sounds were emitted. Brooks and Banks suggested that in mating situations ultrasound inhibits aggression in the female, thus enabling the male to mount. They suggested that the audible sounds, on the other hand, served to communicate the motivational state of the animal. Thus, audible sounds and ultrasounds served two different purposes in the collared lemming. The collared lemming did not emit ultrasounds during agonistic encounters to reduce aggression. Sounds with such a function were used only when these animals came into contact for mating.

The purpose of this present study is to record and catalog the sounds, both audible and ultrasonic, produced by adult members of another solitary murid species, Microtus richardsoni, and to explore the role which these sounds play in the communication system of these mammals.

MATERIALS AND METHODS

Nine males and twelve females, all adults, were used in this study. These were caught alive along the Logan River and its tributaries northeast of Logan, Utah (northeastern Cache County), and maintained individually in small plastic cages but not in visual isolation. The animals were provided with food and water ad libitum, and nest material and cage litter were replaced periodically.

Single individuals and nonbreeding pairs of voles were observed at different times. The observations took place while the animals were in recording arenas which consisted of two glass terraria (74 x 39 x 40 cm and 69 x 25 x 42 cm) covered with hardware cloth through which a microphone was inserted. Tape recordings were made during the time the animals were in the terraria. After each test, the glass walls of the arena were wiped with a damp cloth and the sawdust covering the floor changed.

Equipment

Sounds were recorded at 15 ips on a Midwestern Instruments/Telex Alpha-434 instrumentation tape recorder, with a flat (± 3 dB) frequency response of 100 Hz to 60 kHz at this speed. The microphone used was a Bruel and Kjaer type 4136- $\frac{1}{4}$ microphone, which was attached to a Bruel and Kjaer type 2618 preamplifier. Together, the microphone and preamplifier have a flat (± 0.5 dB) response from 2 Hz to 70 kHz.

The sounds were analyzed by using a Kay Elemetrics Co. Sonagraph

Model 6061-B. The sonagraph runs at either of two speeds over a total frequency range of 8 Hz to 16 kHz. The tape recorder was played back at $\frac{1}{4}$ -speed to detect sounds in the ultrasonic range to 64 kHz. Most of the sonagrams were produced at the lower sonagraph speed with a nominal frequency range of 8 Hz to 8000 Hz. Coupled with the reduced speed of the recorder, calls of up to 32 kHz could be sonographed. The higher speed of the sonagraph was used to reproduce and portray sounds containing frequencies higher than 32 kHz. Since the major concern of analysis in this study was frequencies of sounds produced, the narrow filter band width was used. The FL-1 setting was used to produce all sonagrams, since it had a flatter response than the H-S (human speech) setting. The automatic gain control, which serves to compress the emphasized frequencies, was set at the minimum.

Over 800 calls were sonographed. Only those calls recorded which could be correlated with a specific behavioral component were sonographed. The physical parameters considered for each call were: duration (msec), fundamental frequency (Hz), maximum frequency (Hz), harmonic frequencies (Hz) and frequency bands emphasized (Hz). The frequency measurements were made to the nearest 240 Hz on sonagrams made at low sonagraph speeds, and to 480 Hz on those made at high sonagraph speeds. The durations of the calls are rough measurements, since the narrow analyzing filter band was used.

Observations

Each observation lasted 10 minutes and no animal was tested more than twice a day nor was subjected to tests less than six hours apart.

The observations tested were as follows:

1. Exploring: The purpose of this test was to find out if M. richardsoni used sound concomitant with exploration. Each individual was transferred from its cage to a clean recording arena (74 x 39 x 40 cm) via a Sherman live trap and allowed to explore undisturbed for 3 minutes. Then an obstacle was placed within the area each minute after, up to 10 minutes, a total of 7 obstacles. The obstacles were small glass jars (approximately 10 cm tall and 5 cm in diameter) and were used to provide a more complex environment for the animal. Ten tests were recorded, using ten individuals.
2. Paired encounters: The purpose of this test was to record sounds associated with agonistic and sexual behavior. A partition was placed in the center of the smaller arena (69 x 25 x 42 cm) and an individual introduced into each half of the arena simultaneously. After a 2- to 3-minute calming-down period, the partition was removed, allowing the two individuals to encounter each other. Pairs tested were as follows:
 - a. Male-male: 6 males used, 10 encounters observed.
 - b. Female-female: 9 females used, 10 encounters observed.
All females were anestrous.
 - c. Male-anestrous female: 6 males and 9 females used, 25 encounters observed.
 - d. Male-estrous female: 3 males and 2 females used, 4 encounters observed.

During the male-male, female-female, and male-anestrous female encounters, a slice of apple was introduced after two minutes of recording to facilitate interaction.

3. Response to a potential predator: The purpose of this observation was to record any calls emitted by the voles that may serve as alarm calls. For this test, two preliminary observations were made by introducing a predator (a cat) and a vole into a very large area (1.52 x 2.44 m). No recording was done, but the behavior of the vole was observed and calls emitted at the time noted. Then the test was repeated in one of the recording arenas (74 x 39 x 40 cm) with one of two other predators, a bull snake (Pituophis melanoleucus) and a white rat. Two observations were made with the bull snake and ten with the white rat. The purpose of the preliminary tests was to determine whether the closeness of a predator, as in the recording arena, might inhibit vocalization of the vole. The predator and the vole were introduced into the recording arena in the same manner as that used in the paired encounters.
4. Response to miscellaneous stimuli: An individual was placed into the smaller arena and allowed 2 to 3 minutes to calm down. The vole's response to three different stimuli was recorded.
 - a. Response to approach of my hand.
 - b. Response to being poked with a foreign object (teasing needle).
 - c. Response to my pinching of its tail and its hind foot with my hand.

During each test, I recorded the behavior of the animals in the arena

as it corresponded to the footage count on the tape recorder. Specific behavioral components I looked for were:

1. Self-grooming: Either animal licking or cleaning itself.
2. Allo-grooming: One animal making oral or nasal contact with any part of the other animal's body except for the nose or anal region.
3. Anal-sniff: One animal sniffing the other's anal region.
4. Naso-sniff: Each animal coming into contact with the nose or vibrissae of the other.
5. Boxing: One or both animals rearing on hindlegs and lashing out at the other as though boxing. The head is raised and the neck bared to the other animal.
6. Huddling: Both animals' bodies in close contact. Usually one is on top of the other with its body at right angles to the other.
7. Shiver: Either animal hunched up and appearing to shake as though cold.
8. Approach: One or both animals moving toward the other.
9. Mount: One animal mounting the other from the rear.
10. Avoid: One or both animals moving away from the other.

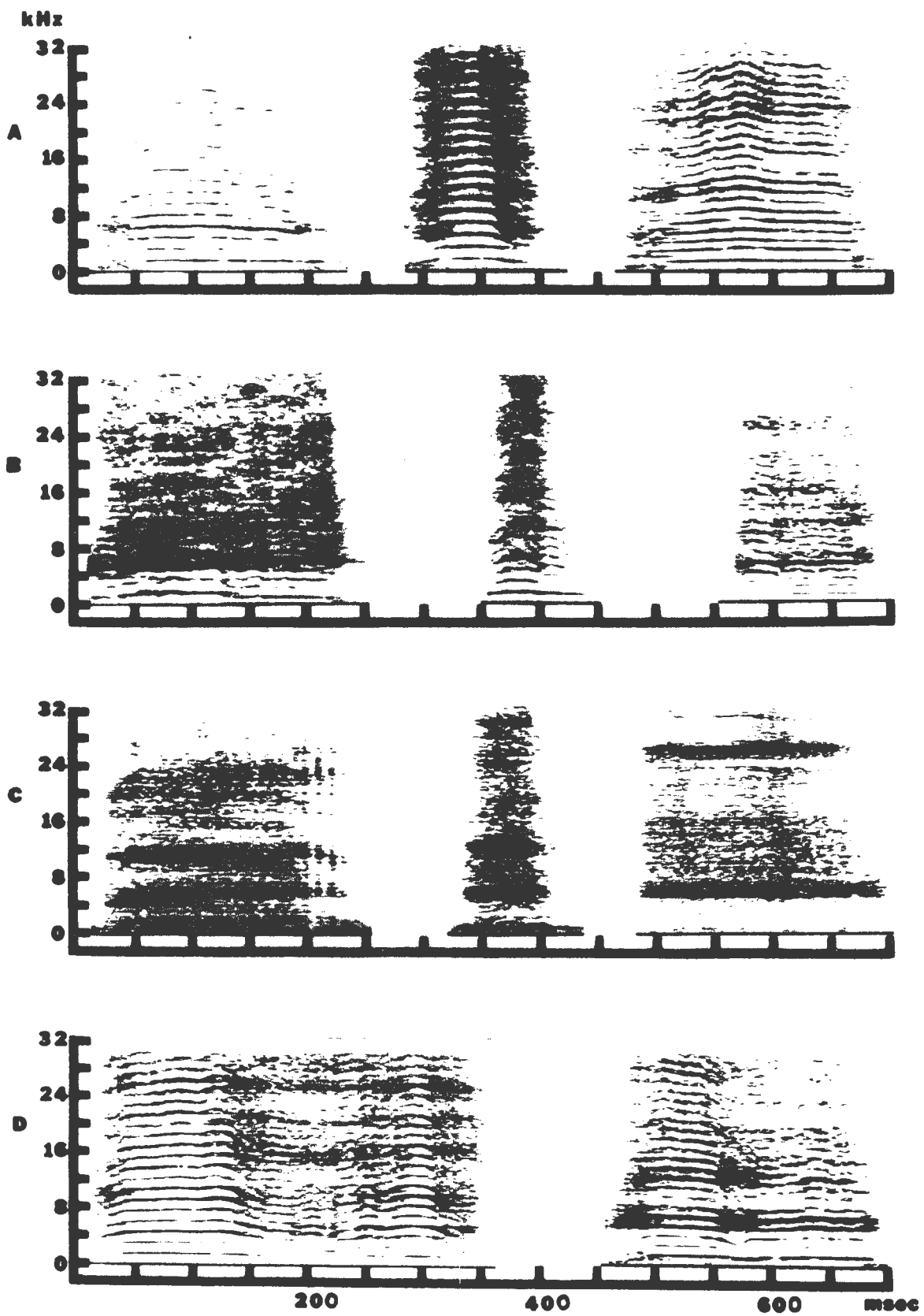
RESULTS

Physical Properties of Calls

The calls made by M. richardsoni showed variation within as well as among individuals. Although most calls could be categorized easily, some seemed to be intergradations of two calls. An effort was made to use the categories already defined by previous investigators for ease in comparing vocalizations of related species. Calls previously undescribed were placed into new categories. Each type of call has a characteristic frequency pattern and duration and can be recognized audibly at $\frac{1}{4}$ -speed as well as sonographically.

SQUEAL: This call can be recognized audibly at $\frac{1}{4}$ -speed as a sound of pure tonal quality, having little noise in it. Arvola, Ilmen and Koponen (1962) described such a sound with no noise as being "voiced." Sonographically, the squeal is characterized by a distinct fundamental frequency with several harmonically-related overtones extending into the ultrasonic range (Figure 1-A). The mean fundamental frequency is 1490 ± 150 Hz. Commonly, there are one or more frequency bands emphasized more than the others. For the squeal, the most commonly emphasized band occurs at 5760 ± 900 Hz, with other emphasized bands occurring occasionally above or below this frequency. The squeal usually occurs as an isolated call but may sometimes be emitted several times in a row, but there is no fixed call-to-call interval. The frequency rises and falls within a call one or more times. The mean duration was 172 ± 53 msec and was generally longer than that of either of the next two calls described.

Figure 1. Representative sonagrams, as emitted by Microtus richardsoni, of the (A) squeal, (B) squawk, (C) grind, (D) complex. Record speed: 15 ips. Reproduce speed: 3-3-3/4 ips. Sonagraph speed: 80 to 8000 Hz.



SQUAWK: The squawk differs from the squeal in that it is a more harsh-sounding call, having some noise or voiceless qualities associated with it. Sonographically, the squawk consists of a fundamental frequency plus several harmonically-related overtones. The harmonics are distinct at the lower frequencies, but become indistinct at the higher audible frequencies as well as in the ultrasonic range (Figure 1-B). Using the student's t-test for comparison of two means, I found that the fundamental frequency (1230 ± 280 Hz) is significantly lower (.01 level) than that found in the squeal (Table 1). There is also an emphasized band at 5870 ± 910 Hz. The duration of this call is 153 ± 61 msec. Usually, the fundamental frequency and the emphasized frequency rise and fall several times within a call. The squawk is used almost three times as often as the squeal (Table 1) but, like the squeal, it is usually emitted as an isolated call.

GRIND: As the name suggests, this call, when played back at slow speeds, is a grinding sound. Arvola, Ilmen and Koponen (1962) described this sound as being voiceless. When sonographed, the grind appears as a solid band of noise extending from the baseline into the ultrasonic range (Figure 1-C). There is no distinct harmonic structure as in the squeal or squawk; however, there is a wide emphasized band occurring usually at 5980 ± 650 Hz to 6330 ± 1110 Hz (Table 1). Occasionally, there are also other bands emphasized above or below this band, such as the bands at about 12 kHz and 24 kHz in Figure 1-C. The emphasized band is usually constant in frequency within a call. The mean duration is 140 ± 70 msec. The grind is given as an isolated

Table 1. Physical properties of calls emitted by Microtus richardsoni

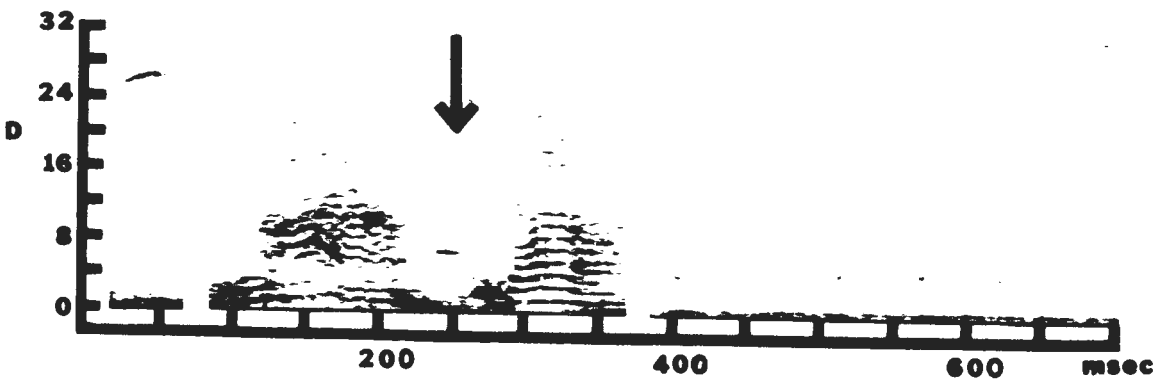
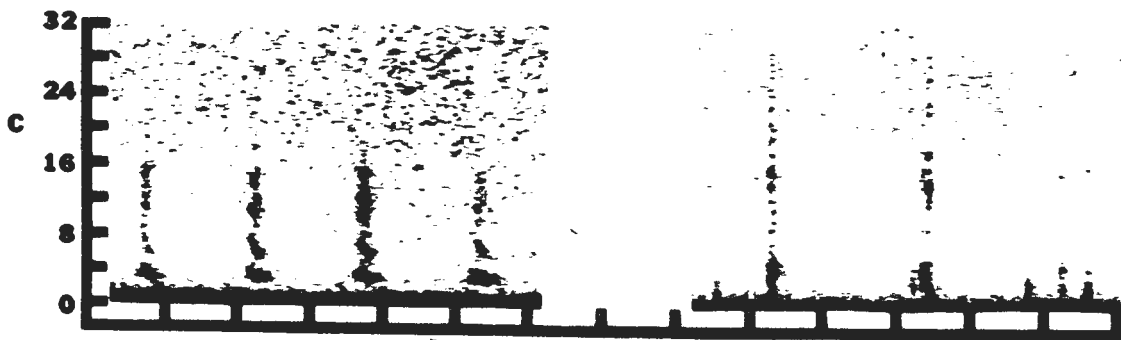
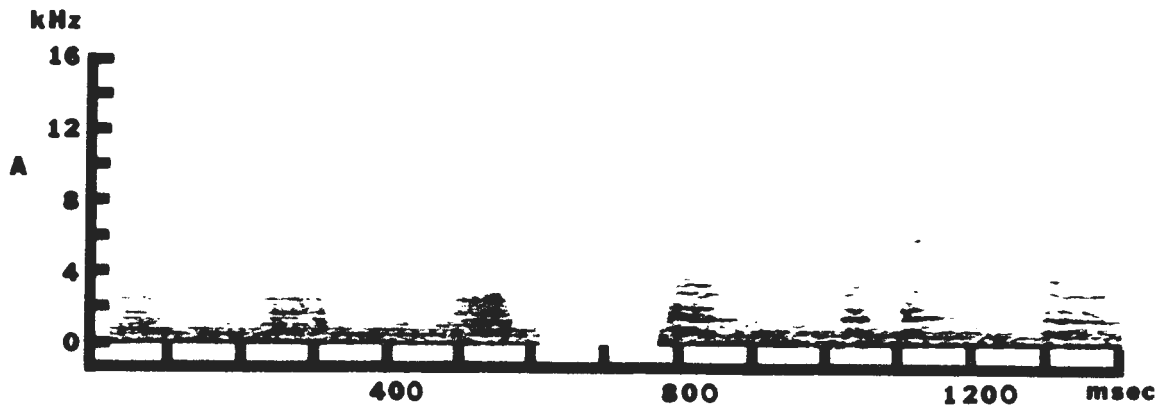
Call type	N	Duration (msec)		Maximum frequency (Hz)			Fundamental frequency (Hz)			Emphasized frequency (Hz)		
		\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD	Range	\bar{x}	SD
Squeal	57	172 ± 53		76-280			1490 ± 150		960-1760	5760 ± 900		4320-7200
Squawk	155	153 ± 61		48-320			1230 ± 280		640-1920	5870 ± 910		1600-9600
Grind	248	140 ± 71		38-364						4980 ± 650		2560-7360
										to		to
										6330 ± 1110		4160-14400
Complex	99	236 ± 77		82-460						5710 ± 590		3840-7040
Voiced whimper	143	63 ± 37		16-194			1570 ± 270		800-3200			
Voiceless whimper	141	72 ± 37		8-230	4900 ± 2590		1280-13600					

call or sometimes in a series, but with no consistent call-to-call interval or number of calls per series. This call is the one that was most often emitted by the test animals.

COMPLEX: As mentioned earlier, the calls of M. richardsoni show variation within and among individuals. Many calls seemed to be intergradations of two calls. The complex is such a call. It is a combination of two or all three of the previously-described calls (Figure 1-D). The complex is of longer duration (236 ± 77 msec) than any of the uncombined calls alone (Table 1). There is usually a band of emphasized frequency at 5710 ± 590 Hz with other such bands occurring occasionally above or below it.

VOICED WHIMPER: This call is emitted at such a low intensity and short duration by the vole that it may not be heard unless the listener is close to the animal. Played back at normal speed, the call sounds like a click, but at a slower speed, this call sounds like a whimper. As the name of this call implies, the voiced whimper is a pure sound not mixed with any noise. On the sonagram, the whimper has a harmonic structure of two to four (usually two) narrow frequency bands (Figure 2-B). The overtones of this call never reach the ultrasonic frequency range. The mean fundamental frequency is 1570 ± 270 Hz and lasts almost two times as long as any of its harmonics. Characteristically, the duration of this call (63 ± 37 msec) is shorter than that of any of the previously described calls (Table 1). The voiced whimper occurs either as an isolated call or in a series.

Figure 2. Representative sonagrams, as emitted by Microtus richardsoni, of the (A) voiceless whimper, (B) voiced whimper, (C) two series of tooth-chatter, (D) ultrasonic chirp (far left), peep (arrow) and "whooping" call (far right). Record speed: 15 ips. Reproduce speed for (A): $7\frac{1}{2}$ ips. Reproduce speed for (B) (C) (D): $3\frac{3}{4}$ ips. Sonagraph speed: 80 to 8000 Hz.



VOICELESS WHIMPER: This call, like the voiced whimper, is of low intensity, short duration (72 ± 37 msec) and does not appear to reach the ultrasonic range (Figure 2-B). The maximum frequency is 4900 ± 2590 Hz. Unlike the voiced whimper, this call does not have distinct narrow frequency bands unmixed with noise. Sonographically, the voiceless whimper appears either as a solid band or sometimes as two to four harmonically-related frequency bands with noise or voiceless components intermingled, obscuring the bands. The voiceless whimper may be emitted as an isolated call or in a series.

TOOTH-CHATTER: The tooth-chatter is a sound not emitted from the glottis and thus is not really a call, but is caused by pulling the upper and lower incisors across each other to produce a clicking sound. Of those tooth-chatters sonographed, all show a wide range of variation in duration of tooth clicks and duration of intervals between tooth clicks within and among individual voles (Table 2). Besides varying from one series of tooth-chattering to another, the duration of clicks and intervals also varies within series. The frequencies of a tooth click, on the other hand, remain constant within a series but vary from one series to another (Figure 2-C).

MISCELLANEOUS SOUNDS: Besides the seven calls just described, the voles also emitted several miscellaneous calls, but not often enough to make valid statistical analysis. Also, these calls cannot be correlated with a specific behavior, but do deserve some mention. The "ultrasonic chirp" is a call produced as a discrete unit sound in the ultrasonic range (Figure 2-D). Nine chirps were recorded and analyzed. It is a call of short duration (8 to 26 msec) and usually

Table 2. Comparison of physical properties of individual tooth-chatters

Test	Duration of		Beginning frequency (Hz)	Emphasized frequency (Hz)	Maximum frequency (Hz)
	Click (msec)	Interval (msec)			
Response to pain	5 to 11	38 to 47	baseline	1,120 to 1,600	23,680
Response to pain	6 to 12	45 to 57	3,200	5,760 to 11,840	20,800
Response to pain	5	38	7,040	7,040	1,600
Response to pain	3 to 5	33 to 36	4,800 to 7,040	12,800 to 14,400	14,400
Response to pain	5 to 6	9 to 92	baseline	1,920 to 5,448	28,800
Response to pain	6 to 8	23 to 126	baseline	1,920 to 5,760	27,840
Response to pain	12 to 18	42 to 45	1,600	1,600	14,400
Response to pain	6 to 14	48 to 53	1,600	1,600	3,200
Response to pain	5 to 15	42 to 45	1,600	1,600	11,200
Response to pain	5	39 to 41	baseline	none	24,000
Response to pain	5 to 8	51 to 53	1,600	1,600	17,920
Paired encounter	6 to 9	30	11,520	17,280 to 24,960	ultrasonic
Paired encounter	6	28	13,760	13,760 to 17,280	ultrasonic
Paired encounter	11 to 14	27 to 28	baseline	none	ultrasonic
Paired encounter	9 to 12	26 to 57	baseline	12,160 to 16,320	ultrasonic
Paired encounter	5 to 12	28 to 30	baseline	15,040	21,440
Paired encounter	11 to 20	46	12,800	none	ultrasonic

has a characteristic inverted "u" shape (rising and falling). The beginning frequencies of the ultrasonic chirps sonographed range from 17,280 to 32,160 Hz. Some calls peaked at frequencies ranging from 21,440 to 25,280 Hz and ended at frequencies lower than the maximum, but other calls reached a maximum frequency (19,890 to 32,280 Hz) and trailed off at this frequency. The ultrasonic chirps emitted during this study were always isolated calls and were emitted during the paired encounters tests.

The "peep" was another isolated call emitted by the test animals. Seven peeps were recorded and analyzed. Although a specific function could not be related to the peep, it was emitted during the paired encounters only. This call resembles the voiced whimper in that it is of short duration (8 to 38 msec) and low intensity (Figure 2-D). The peep differs from the voiced whimper in that there are no harmonics associated with the fundamental, which ranges from 3000 Hz in one call to 18,560 Hz in another. The fundamental frequency of the "peep" is also higher than that in the voiced whimper (Table 1). The peep differs from the ultrasonic chirp in that the fundamental frequency does not rise and fall as it does in the latter call.

An interesting call emitted three times by the same male vole during three different paired encounters was a "whooping" call. It consists of a series of low-intensity pulses (Figure 2-D). Of the three series emitted two were emitted at 4800 Hz and one at 1600 Hz. Among series, the duration of the intervals between pulses ranges from 33 to 46 msec, while the duration of each pulse ranges from 5 to 12 msec. The pulses within a series vary 1 to 3 msec in duration, but the duration of the intervals between pulses is constant.

Analysis of the Behavioral Role of Calls

EXPLORING: The purpose of this test was to find out if the water vole used sounds while exploring, perhaps aiding in echolocation. Obstacles were placed into the arena to find out if more sounds would be produced when the environment became more complex.

When placed into unfamiliar surroundings, each animal sniffed around the edge of the arena. Sometimes it stood up on two feet and jumped up along the glass walls, perhaps trying to get out. After the obstacles were introduced, the animals would sometimes stand on their hindlegs and walk around sniffing the air. Sometimes the animals would climb onto the obstacles and try to jump out of the arena. No sounds, except some scratching on the glass and tapping of claws on the obstacles, were recorded.

PAIRED ENCOUNTERS: For this series of tests, an attempt was made to designate which individual was dominant and which was subordinate, according to procedures reported by Getz (1962). In most cases, dominance was clear-cut, but in cases where there was co-dominance, the encounters were not used in the analysis.

Behavior in the male-male, male-anestrous female and female-female encounters did not differ noticeably. Amount of vocalization and interaction varied among encounters, yet all were similar in that each animal showed aggressive behavior toward each other. Avoidance, boxing and approach, respectively, were the types of behavior most often observed during the encounters. Vocalizations often accompanied these three types of behavior. During boxing behavior, the animal doing the boxing also vocalized. Sometimes, both animals boxed and

vocalized. During avoidance behavior, the vocalizing animal ran to the opposite end of the arena. Occasionally, if the opposing animal was stationary, its body would jerk when the call was given. During approaching behavior, either the approaching animal or the one being approached would vocalize.

When introduced, the slice of apple provided a source for interaction. Usually one animal would discover the morsel first and immediately begin nibbling on it. When the other animal discovered the apple, it would do one of three things: (1) nudge up close to the animal that was eating, as though begging for some of the food; (2) begin nibbling on the apple also, the two sharing the food; (3) take the apple away completely from the other animal. In the last case, the apple was fought over intensely and possession of it changed several times during the testing period. The following is an analysis of the vocalizations that took place during the paired encounters and of the significance of these vocalizations.

Tables 3 and 4 show the physical properties of calls emitted by males in encounters with other males and with anestrus females, and the calls emitted by anestrus females in encounters with other females and with males, respectively. Calls emitted by individuals paired with members of their own sex did not differ significantly (.01 level) from calls emitted while paired with the opposite sex, except in two situations. The two exceptions are the duration of the complex emitted by males and duration of the voiceless whimper emitted by females. In the former case, the sample size may have been too small to make a valid comparison. Because of the difference in duration of

Table 3. Physical properties of calls emitted by males

Call type	Paired with males								Paired with anestrus females									
	N	Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)		N	Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Squeal	12	177 ± 52				1530 ± 120		5530 ± 1020		15	156 ± 60				1480 ± 140		5150 ± 1190	
Squawk	25	145 ± 47				1280 ± 200		6000 ± 1490		36	125 ± 60				1480 ± 880		5860 ± 920	
Grind	25	101 ± 35						5230 ± 660 to 6460 ± 1030		31	121 ± 63						4830 ± 760 to 6290 ± 1580	
Complex	12	234 ± 54*						5710 ± 780		13	170 ± 55*						5410 ± 680	
Voiced whimper	18	65 ± 38				1570 ± 180				15	45 ± 21				1370 ± 260			
Voiceless whimper	12	66 ± 54		3670 ± 1600						13	77 ± 29		4850 ± 2400					

*Denotes a significant difference in this property between encounters with males and encounters with anestrus females at the .01 level, using the student's t-test for comparison of two means.

Table 4. Physical properties of calls emitted by anestrous females

Call type	Paired with females								Paired with males									
	N	Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)		N	Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Squeal	13	191 ± 44				1420 ± 210		6260 ± 620		8	168 ± 44				1560 ± 740		5890 ± 960	
Squawk	37	160 ± 65				1130 ± 300		5690 ± 700		40	160 ± 55				1190 ± 270		5980 ± 770	
Grind	84	154 ± 79						4940 ± 720 to 6270 ± 1110		61	137 ± 58						5030 ± 640 to 6480 ± 1270	
Complex	47	236 ± 68						5790 ± 590		15	265 ± 87						5740 ± 490	
Voiced whimper	77	66 ± 35				1580 ± 200				11	75 ± 59				1580 ± 300			
Voiceless whimper	66	81 ± 30*		5240 ± 2740						29	54 ± 25*		5530 ± 2910					

*Denotes a significant difference in this property between encounters with other females and encounters with males at the .01 level, using the student's t-test for comparison of two means.

the voiceless whimper emitted by females, this call was omitted from the comparison of the physical properties of calls emitted by males and females. For all of the other calls, the physical properties of these calls given by the voles did not differ significantly whether the voles were confined with the same sex or the opposite sex. Because of this similarity, the calls of males and females were lumped in the analysis of the physical properties of the calls emitted by males and females.

Table 5 provides a summary of these physical properties. The duration of all the calls emitted by females was greater than that of those calls emitted by males. The difference is significant at the .05 level for the squawk, grind and complex. At the .01 level, only the grind lasted significantly longer in the females than in the males. Of all the frequencies contained in the different calls, only the fundamental frequency of the squawk differed significantly between sexes. In the males, the frequency was higher at the .01 level of significance.

The following set of analyses was done using two groups of similar call types rather than comparing all six categories because not enough calls of each category were recorded to make valid comparisons. Group I includes the squeal, squawk, grind and complex which are similar in that they are emitted with a greater intensity than the voiced whimper and the voiceless whimper. The voiced and voiceless whimper are included in Group II. Also, Group I calls have overtones extending into the ultrasonic range.

Tables 6 and 7 summarize the number of calls emitted by voles in different behavioral contexts, paired with members of the opposite

Table 5. Comparison of physical properties of calls emitted by males and females

Call types	Males								Females							
	Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)		Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Squeal	165 ± 57				1510 ± 130				182 ± 45				1470 ± 180			
Squawk	140 ± 59**				1330 ± 250*		5520 ± 940		162 ± 60**				1180 ± 190*		6050 ± 720	
Grind	115 ± 59*						5030 ± 680 to 6340 ± 1230		147 ± 71*				4970 ± 690 to 6320 ± 1140			
Complex	205 ± 65**						5550 ± 680		243 ± 73**				5770 ± 560			
Voiced whimper	55 ± 32				1490 ± 250				67 ± 38				1590 ± 270			

*Denotes a significant difference of the corresponding physical property in males and females at the .01 level.
 **Denotes a significant difference of the corresponding physical property in males and females at the .05 level.

Table 6. Frequency of acts observed during male-anestrous female encounters and accompanying vocalizations emitted by the females

Behavior	Number of observed acts	Number of calls emitted	Call types	
			Group I Squeal Squawk Grind Complex	Group II Voiced or voiceless whimper
Self-groom	83	0	-	-
Allo-groom	74	5	3	2
Anal-sniff	53	6	4	2
Naso-sniff	41	4	4	0
Boxing	115	31	22**	9
Huddling	53	6	5	1
Shiver	76	0	-	-
Approach (submissive)	47	18	15***	3
Approach (aggressive)	115	8	7*	1
Avoid	425	215	215****	0
Fighting over apple	129	21	9	12
Totals	1211	314		

*Denotes a group of call types emitted significantly more ($P < .05$).

**Denotes a group of call types emitted significantly more ($P < .01$).

***Denotes a group of call types emitted significantly more ($P < .005$).

****Denotes a group of call types emitted significantly more ($P < .001$).

Table 7. Frequency of acts observed during male-anestrous female encounters and accompanying vocalizations emitted by the males

Behavior	Number of observed acts	Number of calls emitted	Call types	
			Group I Squeal Squawk Grind Complex	Group II Voiced or voiceless whimper
Self-groom	83	0	-	-
Allo-groom	74	5	1	4
Anal-sniff	53	3	3	0
Naso-sniff	41	9	9*	0
Boxing	115	40	38*	2
Huddling	53	0	-	-
Shiver	76	10	7	3
Approach (submissive)	47	22	20*	2
Approach (aggressive)	115	5	5	0
Avoid	425	259	256*	3
Fighting over apple	129	43	11	32**
Totals	1211	396		

* Denotes a group of calls emitted significantly more ($P < .001$).

**Denotes a group of calls emitted significantly more ($P < .005$).

sex. Females generally tended to vocalize more than the males. Also, in most encounters, females were found to be subordinate. Most of the vocalizing occurred during avoidance behavior. During submissive approach in both males and females, the calls were usually emitted by the approaching animal. During aggressive approach, the calls were emitted by the animal that was standing still. Looking at the specific behavioral components, approach, avoidance, and boxing, one sees a correlation with the Group I vocalizations. The significance of the correlation is obvious for the calls emitted by females. For the males' calls, a chi-square test was used to test for significant difference. During boxing behavior and aggressive approach, the males used the calls in Group I significantly more than the calls in Group II ($P < .05$). During submissive approach, the difference was significant with $P < .005$. For avoidance behavior, all calls emitted were from Group I. The only behavioral component with which the less intense voiced and voiceless whimper correlated was the fight over the slice of apple. These calls were emitted while both animals were close together (vibrissae touching). Usually one individual was eating the apple and the other had its nose edged beneath the other's head. Sometimes when the apple was stolen from one vole by the other, a voiced or voiceless whimper was recorded. The correlation of the whimper with fighting over the apple is apparent when the females emitted the calls, but there was no significant difference between the calls emitted by the males.

Table 8 summarizes the calls emitted by males paired with other males. Although males did not vocalize as much as females, there is

Table 8. Frequency of acts and accompanying vocalizations during male-male encounters

Behavior	Dominant males				Subordinate males		
	Number of observed acts	Number of calls emitted	Call types		Number of calls emitted	Call types	
			Group I Squeal Squawk Grind Complex	Group II Voiced or voiceless whimper		Group I Squeal Squawk Grind Complex	Group II Voiced or voiceless whimper
Self-groom	25	0	-	-	0	-	-
Allo-groom	7	0	-	-	3	1	2
Anal-sniff	6	1	0	1	1	1	0
Naso-sniff	6	1	1	0	1	1	0
Boxing	13	1	1	0	16	14*	2
Huddling	0	-	-	-	-	-	-
Shiver	33	0	-	-	0	-	-
Approach (submissive)	31	9	7*	2	1	1	0
Approach (aggressive)	16	0	-	-	6	2	4
Avoid	117	9	9*	0	74	73*	1
Fighting over apple	48	3	0	3	12	2	10*
Totals	302	23			114**		

* Denotes a group of call types emitted significantly more than the other ($P < .001$).

**Denotes that the subordinate males emitted more calls than the dominant males ($P < .001$).

a correlation between the dominance of the individual and how much it vocalized. Subordinate males vocalized more than dominant males. Most of the calls emitted by the dominant male were emitted during submissive approach. These calls were mostly from Group I. The subordinate male also emitted Group I calls significantly more than Group II calls during boxing and avoidance behavior. Calls of the latter group were emitted more often while the voles were fighting over the apple.

The calls emitted by females paired with other females are summarized in Table 9. Again, the subordinate individual vocalized more than the dominant one. During boxing and avoidance behavior, both dominant and subordinate females emitted Group I calls more often than Group II calls, although both types were used. While fighting over the apple, the subordinate female emitted Group II calls more often than Group I calls. For the dominant female this difference is also significant ($P < .01$).

Only four male-estrous female encounters were observed because not many females came into estrous in captivity. Those two that did become estrous were used as much as possible, allowing for six hours between tests, to obtain enough recordings for analysis. Of all encounters observed, males did all of the vocalizing and were the subordinate individuals. In three encounters, the female groomed the male or attempted to do so. The behavior of the male was one of hostility toward the female. The female would approach to groom, but the male avoided her. The behavior of the female was amiable rather than hostile. The female was the one to approach the male and

Table 9. Frequency of acts and accompanying vocalizations during female-female encounters

Behavior	Dominant females				Subordinate females		
	Number of observed acts	Number of calls emitted	Call types		Number of calls emitted	Call types	
			Group I Squeal Squawk Grind Complex	Group II Voiced or voiceless whimper		Group I Squeal Squawk Grind Complex	Group II Voiced or voiceless whimper
Self-groom	44	0	-	-	0	-	-
Allo-groom	40	4	3	1	11	5	6
Anal-sniff	20	5	3	2	6	1	5
Naso-sniff	21	3	3	1	12	9	3
Boxing	59	56	53**	3	46	42**	4
Huddling	18	0	-	-	9	4	5
Shiver	0	0	-	-	0	-	-
Approach (submissive)	44	11	10**	1	18	12	6
Approach (aggressive)	42	5	3	2	22	14	8
Avoid	275	93	92**	1	167	161**	6
Fighting over apple	80	23	6	17*	86	17	69**
Totals	648	203			384**		

*Denotes a group of call types emitted more than the other ($P < .01$).

**Denotes a group of call types emitted more than the other ($P < .001$).

***Denotes that the subordinate females emitted more calls than the dominant females ($P < .001$).

the one to allogroom. Only in one encounter did a female display a posture not typically seen in anestrous females. This female flattened her ano-genital region against the floor of the arena in front of the male. The female's ano-genital region was exposed to the male. This posture elicited no response from the male. None of the males attempted to mount the females but tended to avoid them. Table 10 is a summary of the physical properties of the calls emitted by males paired with estrous females. The duration of the squawk was longer than that given by males paired with anestrous females or with other males at the .01 level of significance. Other properties did not differ significantly. The majority of calls emitted during this test were recorded during avoidance behavior. No voiced or voiceless whimpers were emitted; these were recorded in almost all other encounters, however.

RESPONSE TO PREDATORS: The preliminary tests showed that a vole, when a predator is nearby, will run for cover. The cage in which the preliminary test took place was covered with sawdust and alfalfa. As soon as a cat was introduced, the vole would scramble under the alfalfa. No audible sounds were emitted.

In the small arena, the voles did not emit many calls. During the tests with the rat, the voles would explore the arena and upon seeing the rat would jump up, turn and run to the other end of the arena. Only one or two calls were emitted by any of the voles. The calls were usually squeals, squawks, grinds or complexes. The rat vocalized also, emitting a continuous ultrasonic note. There appeared to be no effect of this call on the vole.

Table 10. Physical properties of calls emitted by males paired with estrous females

Call type	N	Duration (msec)		Maximum frequency (Hz)		Fundamental frequency (Hz)		Emphasized frequency (Hz)	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Squeal	3	189	± 82			1600	± 00	4800	± 00
Squawk	6	221	± 36*			1360	± 320	5810	± 590
Grind	11	142	± 30					5000	± 330 to 6510 ± 1280
Complex		none emitted							
Voiced whimper		none emitted							
Voiceless whimper		none emitted							

*Denotes a significant difference from males paired with anestrus females or other males at .01 level.

For the tests with the bull snake, only two voles were used because the snake was very aggressive and captured the animals several times during the testing. No animals were lost, but the snake had to be forced several times to release a vole which would have been strangled to death. When a bull snake was introduced into the arena, the voles did not even try to find cover. It appeared as though the vole did not even notice the snake. When captured by the snake, the voles did not emit any sounds.

RESPONSE TO MISCELLANEOUS STIMULI: The test animals always ran for cover when my hand approached to catch and transfer them to the testing arena. During the test for the response to miscellaneous stimuli, the voles had no cover. As my hand approached them in the testing arena, they responded with tooth-chatter while facing my hand until I removed it. A few audible calls were also emitted during the testing. These were all Group I calls and did not differ from those emitted during the paired encounters. There was one individual which emitted a Group I call whenever I walked near its cage. None of the other test animals did this. Again, they usually found cover whenever I approached their cage, such as during feedings.

The response to being poked with a foreign object and being pinched was the same. No calls were emitted. Often, an animal would try to bite me or the foreign object. At one time, I drew blood poking one animal, and still it did not vocalize. Most of the animals would just try to escape by running away.

DISCUSSION

This study found that Microtus richardsoni, the North American water vole, emits seven major types of sounds. Four of these, the squeal, squawk, grind and complex, are similar in physical properties and are classified as Group I calls. Group II calls include the voiced and voiceless whimpers which also have similar physical properties. Finally there is the tooth-chatter, a sound different from the other sound types in that it is not produced from the glottis. Also, a variety of miscellaneous peeps and ultrasounds were emitted, making a total of ten calls emitted by these voles. All these sounds exhibited individual variation in physical properties.

There have been only three other detailed studies on the vocalizations of adult members of the Subfamily Microtinae. Brooks and Banks (1973) did an extensive study on the calls emitted by adult collared lemmings (Dicrostonyx groenlandicus). Arvola, Ilmen and Koponen (1962) studied the calls emitted during aggressive behavior in adult Norwegian lemmings (Lemmus lemmus). Johst (1973) recorded and analyzed some vocalizations of the Old World water vole (Arvicola terrestris) in agonistic encounters. This particular microtine is the species considered to be most closely related to M. richardsoni by Hooper and Hart (1962). Many of the calls found in the present study were similar to those found in the three previous studies. Other workers on microtine behavior have reported hearing vocalizations from M. pennsylvanicus (Bailey, 1924; Getz, 1962), M. californicus

(Hatfield, 1935), M. agrestis (Clarke, 1956), M. ochrogaster (Getz, 1962) and Lemmus sp. (Clough, 1965). The calls in these were not recorded, but were similar to the audible squeal, squawk, grind or complex.

The squeal and squawk emitted by M. richardsoni are similar to the voiced cry described in the Norwegian lemming. The voiced cry of this lemming was usually followed by voiceless snarling, a sound very similar to the grind. The voiced cry had a fundamental frequency ranging from 1 to 8 kHz with several harmonically-related overtones. The voiceless snarling, on the other hand, showed no distinct frequency bands, but had an intensive sound area which fell between 2.5 and 9.0 kHz. Both the voiced cry and the voiceless snarling were emitted during aggressive encounters by the inferior or subordinate animal, usually while the vocalizing animal was displaying threat movements against an enemy. Arvola, Ilmen and Koponen (1962) suggested that the function of the voiced cry and voiceless snarling was to inhibit attack by the opponent.

Brooks and Banks (1973) combined the squeal, squawk, grind and complex into one category: the squeal-squawk-grind complex. They suggested that this complex in the collared lemming is an intergradation of several call types. The physical properties of these several call types making up the squeal-squawk-grind complex are similar to those of the corresponding call types of the Group I calls emitted by the water vole. I separated the Group I calls into different categories because their physical properties were distinct enough to warrant doing so. Brooks and Banks suggested that the intergradation of several call types and the gradual variation in

properties of the complex emitted by the collared lemming may reflect a variety of internal physiological states related to fear response.

The Old World water vole (Arvicola terrestris) utters a "thrust" call in agonistic situations which is a short call with a clear harmonic structure (Johst, 1973). The average duration of this call is 11 msec and the fundamental frequencies range from 2.4 to 4.4 kHz. The structure of the call emitted by A. terrestris appears to be similar to the squeal emitted by M. richardsoni, the North American water vole. The range of the fundamental frequency of the squeal, however, is lower in M. richardsoni, ranging from .96 to 1.76 kHz. The function of the call emitted by A. terrestris was demonstrated to be one of inhibition of closer approach by conspecifics. An increase in the intensity of the call causes a significant increase in the inhibition effect on the receiver of the signal. No call similar to the voiceless snarling found in L. lemmus or the grind found in D. groenlandicus and M. richardsoni was recorded for A. terrestris in this study. Johst also recorded and sonagraphed some calls of Microtis agrestis in agonistic encounters in his study. The calls emitted by M. agrestis resemble the squeal and squawk emitted by M. richardsoni. The fundamental frequencies found in the calls of the former (.75 to 1.8 kHz) approximate that found in the latter Microtus. The calls of M. agrestis also served to inhibit approach of A. terrestris. Thus, although there are species-specific differences in the calls emitted by the two species used in Johst's study, there appears to be no species-specific effects of the calls.

In the North American water vole, as in the collared lemming, Norwegian lemming and Old World water vole, the squeal, squawk, grind

and complex were emitted during agonistic encounters. These four calls were emitted mostly during approaching, avoidance and boxing behavior. The function of these four calls may be the same as that in the Norwegian lemming and Old World water vole, to inhibit aggression or attack by the opponent.

It was difficult to assess if each of these calls conveyed a specific meaning to the receiver. One reason for this is that the physical properties of one call grade into the physical properties of the other calls. I could not tell the difference among these graded calls without sonographing them. It was not feasible to sonograph all the calls emitted during the testing; it would have been too time-consuming. Because of this, whether one call was used more often than another during specific behavioral actions observed within recording sessions cannot be assessed. Also, whether an animal responded specifically to one of the Group I calls or not is not known. The North American water vole did emit several high intensity calls, which all sounded acoustically similar to me, with consistency during highly aggressive encounters, but if the animals could distinguish a specific call type from another and respond accordingly is not known.

Intergradation of calls is not limited to microtine vocalizations. Investigators of primate vocalizations have reported that many calls grade one into another (Rowell and Hinde, 1962; Itani, 1963; Marler and Hamilton, 1966). Marler and Hamilton (1966) suggest that this lack of structuring in primate calls is compensated by the temporal patterning of the calls. The number of calls emitted in a series may communicate a specific signal. Even then, the meaning of a signal

may vary among primate troops and even among individuals. Thus, the response to a signal must be learned by members of a troop in order for its communication system to be effective (Kummer, 1971). However, a microtine has a short life span, and a communication system in which meanings and responses are specific would probably be more adaptive than a system in which meaning and responses are learned. A stylized signal is more effective or free of error than a signal which varies according to the communicator and recipient of the message (Smith, 1969). Therefore, the graded calls of the squeal, squawk, grind and complex may not necessarily communicate specific meanings due to the fact that one call grades into the other, thereby making it difficult to distinguish where one call ends and another begins.

My thesis is that these four calls of high intensity and having harmonics extending into the ultrasonic range serve to inhibit aggression by the opposing animal. The graded differences in these calls may give a clue to the motivational state of the vocalizing animal. Brooks and Banks (1973) suggest that the loudest and shrillest call (squeal) is emitted by a highly frightened animal, whereas an animal less motivated by fear emits the quieter call (grind). Although the degree of fear shown by the vocalizing animals was not determined in my study, the calls of the North American water vole may also be related to the same motivational states shown for the collared lemming. A clue to how each of the calls in Group I reflect different levels of motivation may be seen in the mechanism by which audible cries are produced. Audible cries are produced by vibrating vocal cords, activated by the respiratory air flow, controlled by muscle

action and modified by vocal tract resonances (Roberts, 1975). Both the buccal and nasal cavity resonances contribute to the harmonic pattern of the cries. The vibrating of the vocal cords is controlled by the crico-thyroid muscle which is innervated by the superior laryngeal nerve of a rat. In his study, Roberts (1975) sectioned the superior laryngeal nerve of a rat. This operation resulted in the changing of audible cries from squeals to weak "scratchy" cries. Negus (1949) stated that pure voiced tones are produced by a sharp-edged margin of the vocal cords. The tautness of the vocal cords is determined by the tension of the crico-thyroid muscle which is innervated by the superior laryngeal nerve. A highly submissive animal may increase the tension of the crico-thyroid muscle producing a voiced or pure sound, whereas a less highly submissive animal may decrease tension on this muscle and produce a "scratchy" (voiceless) cry. Other physiological factors may also enter into sound production besides tension of the laryngeal muscles. The frequency of a sound produced may be increased by increasing the pressure of the escaping air current if the elasticity of the vocal cords remains constant (Negus, 1949). The higher frequencies of the fundamental and harmonics of the squeal in relation to the frequencies of the squawk may reflect this difference in pressure passing through the glottis. A submissive animal might build up internal pressure and as this high pressure is released, a characteristically high-pitched call is emitted. The individual call types of squeal, squawk, grind and complex, therefore, might indicate the internal motivational state of the water vole as it relates to the submissive response.

The voiced whimper emitted by the water vole is similar to the short voiced cry emitted by the Norwegian lemming as described by Arvola, Ilmen and Koponen (1962). The short voiced cry was usually emitted in a series and the fundamental occurred between 1.8 to 3.1 kHz, with an overtone occurring between 3.5 to 4.2 kHz. This call was nonaggressive and was emitted by lemming males during mating. No call similar to the voiced whimper was mentioned for the collared lemming by Brooks and Banks (1973) or the Old World water vole by Johst (1973).

The function of the voiced whimper in the North American water vole is not clear because it did not elicit a specific response. In the Norwegian lemming, this call was associated with mating, but if it elicited a specific response, it was not mentioned. Considering that it was emitted mostly during the time one of the test animals in the present study had the apple, the call appears to serve as a begging signal given by the animal not eating. The structure of voiced whimper is similar to the squeal and is, in Rattus, actually the squeal emitted with the mouth closed (Roberts, 1975). By closing the mouth, the animal suppresses the higher harmonics of the squeal in addition to decreasing the intensity of the call. Thus, the function of the voiced whimper appears to be the same as that of the squeal: to inhibit aggression, enabling the submissive animal to get some food or to inhibit the animal without the food from taking it. The low intensity and suppressed harmonics may be a result of the closeness of the animals to each other. Loud calls may render the animals conspicuous to potential predators and be disadvantageous, whereas low intensity calls may communicate the same message effectively.

The voiceless whimper is a call which shows the modification of both the tautness of the vocal cords and the size of the resonance cavities. Like the grind, the voiceless whimper is emitted with the crico-thyroid muscle not fully contracted (Roberts, 1975). Thus, the clear harmonic structure is not seen and the call is mixed with noise. Like the voiced whimper, the voiceless whimper is emitted with the mouth closed, and the frequencies of the call do not extend into the ultrasonic range (Roberts, 1975). The voiceless whimper was usually emitted by the North American water vole during interaction of the test animals over the slice of apple. Therefore, the function of this call might be the same as that in the voiced whimper. The former may be a variation of the latter call. The presence of noise mixed with the harmonics of the voiceless whimper may indicate an animal not as submissive as an animal emitting the voiced whimper. The voiceless whimper was not mentioned in any of the other studies on microtine vocalizations.

The tooth-chatter is a type of sound produced by a variety of sciurids (Balph and Balph, 1966; Waring, 1966, 1970) and microtines (Bailey, 1942; Hatfield, 1935; Clarke, 1956; Getz, 1962; Arvola, Ilmen and Koponen, 1962; Brooks and Banks, 1973). In all of these studies, the tooth-chatter was emitted during aggressive encounters and in each situation was associated with threat posture. In M. richardsoni, the tooth-chatter also appears to communicate threat. The sound was produced during paired encounters, but most of the recordings were not loud enough to produce satisfactory sonographs. The tooth-chatter was heard mostly during the tests of response to various stimuli. The sound was produced in response to the approach of my hand or the teasing needle.

Of the miscellaneous calls produced by the North American water vole, the peep was reported for only one other species, the collared lemming. This call was not emitted very frequently by the lemmings, and the physical properties of this call varied significantly according to the behavioral context in which the sound was emitted (Brooks and Banks, 1973). The peeps emitted by the collared lemming usually accompanied agonistic behavior. Brooks and Banks suggested that this call was a form of low-intensity squeals or squawks. If this is true, the peep of the collared lemming may be similar to the voiced whimper of the North American water vole, although the former is seen to lack harmonics. A function for the peep as it is emitted by M. richardsoni is not known, but this call was emitted during agonistic encounters.

Ultrasounds were not emitted frequently by the North American water vole, and the function of these sounds is not known, but they have been recorded and studied extensively in other species of rodents. Most of the studies have been on production of ultrasounds in neonatal muroid rodents. The ultrasonic sounds were found to elicit maternal retrieval of young pups of Peromyscus maniculatus (Hart and King, 1966), albino rats (Noirot, 1968), albino mice (Noirot, 1966; Noirot and Pye, 1969; Okon, 1970a), M. pennsylvanicus, M. montanus, M. californicus, M. longicaudus and M. ochrogaster (M. A. Colvin, 1973) and D. groenlandicus (Brooks and Banks, 1973) exposed to cold. On the other hand, the ultrasounds produced by neonates in response to tactile stimulus have been found to inhibit maternal aggression (Okon, 1970b; Noirot, 1974).

Adult rodents of some muroid species have been found to produce ultrasounds (Anderson, 1954; Sewell, 1970; Sales, 1972). In these studies, ultrasounds appear to inhibit aggression during agonistic encounters in muroid rodents. Sales (1972) suggested that social species emit ultrasounds to establish and maintain dominance relationships. Perhaps ultrasounds are used only for intraspecific communication, especially in social species. Microtines are generally asocial animals (Ognev, 1964) and do not establish social hierarchies. If ultrasounds are used specifically to establish dominance relationships, then ultrasonic communication may not be useful in these rodents. Microtus richardsoni is a solitary mammal (Hooven, 1973), and the adults do not emit ultrasounds frequently. The function of the few ultrasounds emitted by the vole is not known, although these sounds were recorded during agonistic encounters.

The repertoire of sounds produced by microtines does not appear to be great. In general, sounds produced by microtines appear to function mainly to inhibit aggression or to elicit maternal retrieval of young. The audible sounds are probably generalized calls emitted by a submissive individual. The intensity, frequency and amount of noise associated with a call may communicate the degree to which the animal is submissive. Inhibition of approach, attack or any act of aggression by the receiver are probably secondary effects of the audible cries. The dominant animal may perceive the submissiveness of the other rodent, decide not to attack, and thereby save energy. Clough (1965) suggests that the mass migrations of lemmings in Europe may be in response to increase of vocalization due to crowding in a

year of high population density. Thus, acoustic communication could be adaptive for both dominant and subordinate individuals.

Ultrasounds appear to have more specific communicative functions than audible cries for young and social species of rodents. Such calls have been found to elicit maternal retrieval of young and to maintain social structure in social species of rodents. During paired encounters conducted with rats, production of ultrasound was found to be associated with a decrease in aggressive activity (Sales, 1972). Thus, inhibition of aggression appears to be a primary function of adult production of ultrasound, at least in this species. In species in which individuals come into contact often, ultrasound might have such communicative value. However, adults of certain solitary species of rodents have been found to produce ultrasound during mating (Brooks and Banks, 1973); communication should be useful at these times. Even asocial animals may come into contact with each other occasionally. Perhaps no ultrasounds were heard from M. richardsoni during male-estrous female encounters due to the short observation time.

Of the solitary species of microtines studied, all emitted audible calls with similar structural properties. The fundamental frequencies of the calls vary from species to species. Microtus richardsoni emitted one call, the voiceless whimper, that was not recorded in any of the previous studies. Some audible calls differing between microtine species have been found not to elicit species-specific responses (Johst, 1973). Perhaps these rodents are responding as a single-species system. Thus, audible calls may be important in inter-specific encounters. For example, M. pennsylvanicus and M. montanus

have been found to occupy adjacent habitats (Koplin and Hoffman, 1968). Murie (1971) found that M. pennsylvanicus was dominant over M. montanus and was excluding the latter vole from the more mesic habitat that the former vole occupied. So, members of these two species probably come into contact in the field and possibly communicate by vocalizing audibly. D. V. Colvin (1973) observed an encounter between M. montanus and M. longicaudus in which the two animals were fighting and vocalizing loudly. The audible calls may not communicate specific information, but a cry indicating submissiveness may still be useful in inhibiting further aggression.

Many diurnal, sciurid rodents emit alarm calls to warn conspecifics of an approaching predator (Balph and Balph, 1966; Waring, 1966, 1970; Dunford, 1970). None of the previously mentioned studies on microtine vocalizations found any alarm calls used by these animals. Being solitary and cryptic rodents, most microtines may not emit alarm calls. However, there is a gregarious Eurasian vole, Microtus brandtii, that emits a "sharp squeaking whistle" (Ognev, 1964). These voles live in large colonies and are quite noisy, often emitting choruses of squeaks, with a role in communicating alarm (Tembrock, 1968). M. richardsoni does not do this calling. The hamster has been found to secrete an alarm pheromone which is released with the urine (Sherman, 1974). The voles used in the present study urinated frequently when handled and may also have released some sort of alarm pheromone at the time.

Bats and shrews use ultrasounds for echolocation (Griffin, 1958; Gould, Negus and Novick, 1964). Apodemus sylvaticus was found to use

ultrasound upon emerging from the nest after the cage had been disturbed (Sewell, 1968). Also she found that these animals produced ultrasounds after being introduced into a new cage. Thus, that rodents may use these sounds for echolocation while exploring unfamiliar places is also possible. Rosenzweig, Riley and Kreck (1955) studied exploratory behavior in blinded rats and found that although these animals did not emit ultrasounds during exploring, they did produce other sounds such as tapping against the walls of the maze used in the experiment. They suggested that perhaps the animals were using these nonvocal sounds to echolocate. None of the microtines was found to produce ultrasounds while exploring, nor did any incidental sounds appear to be used for echolocation.

It is well known that mammals have well-developed olfactory neural centers. Thus, acoustic information may be enhanced by olfactory cues. Many microtines have been found to possess enlarged, modified sebaceous glands. Arvicola terrestris and M. richardsoni both have especially well-developed and structurally-specialized flank glands (Quay, 1963). In A. terrestris, these flank glands have been found to increase in weight and amount of secretory tissue in males during the mating season (Stoddart, 1972). Secretion of the same scent glands has also been observed in M. richardsoni during some of the paired encounter tests conducted in the present study. Jannett and Jannett (1974) observed M. richardsoni using the flank glands in agonistic encounters to mark the floor of the test arena. They called this behavior drum-marking and described it as the animal rubbing the sole of its foot along the moist fur around the gland and then planting the foot on the

ground to apply the scent from the gland. Jannett and Jannett (1974) also suggested that M. arvalis, M. agrestis and M. oeconomus which all have hip glands may mark runways or burrow systems by walking backwards and rubbing their hips along the sides of the runway. Thus, microtines may not be responding to acoustic messages alone, but to a combination of acoustic plus olfactory information.

Vocalizations may be useful for taxonomic comparisons. The taxonomic status of Microtus richardsoni is still speculative. The glans penis of M. richardsoni is structurally most similar to that of Arvicola terrestris (Hooper and Hart, 1962), and this similarity was used as ground for placing the two species of water voles in the same genus by these authors. The use of drum-marking by M. richardsoni and A. terrestris has been argued as a reason for placing both species in the genus Arvicola (Jannett and Jannett, 1974). On the other hand, the physical properties of the calls emitted by M. richardsoni are more similar to those emitted by M. agrestis than to those emitted by A. terrestris (Johst, 1973). In her study on ultrasounds in neonatal rodents, M. A. Colvin (1973) found that the differences in physical characteristics of the ultrasounds produced by M. ochrogaster correspond to morphological differences of this species in relation to other species of the genus Microtus. Thus, vocalizations in rodents, along with other taxonomic characteristics, may aid in determining the relationships of one species to another. Future research and comparison of acoustic communication in mammals may reveal new taxonomic relationships and prove interesting and useful to phylogeneticists.

This study reveals that microtine vocalizations are similar and that the repertoire of sounds produced by these animals is small. That

these rodents use sound in the field is probable. Field studies on vocalizations are lacking because of lack of equipment to record sounds emitted in the field and lack of observation of such in these secretive animals. Laboratory studies, however, are necessary to control physiological factors such as sexual receptivity which may affect the results of an experiment. Such studies provide a foundation for further research in the field.

SUMMARY

This study found that Microtus richardsoni produces ten different call types or sounds. According to their similarities in physical properties, six of these call types were classified as Group I or Group II calls. Group I included the squeal, squawk, grind and complex. The voiced whimper and voiceless whimper constituted the Group II calls. The Group I calls appeared to communicate the degree of submissiveness of the vocalizing animal. A high degree of submissiveness was probably indicated by an animal emitting the grind. The squawk and complex may indicate the intermediate degrees. The graded differences of the calls in Group I supported this idea. Group II calls appeared to be modified Group I calls and thus may communicate the same message. Inhibition of aggression by the recipient of a Group I or II call was probably an effect of these calls. Another sound produced by these voles was the tooth-chatter. It was a nonvocal sound and was found to communicate threat. Finally, miscellaneous sounds including ultrasounds, audible peeps and "whooping" calls were emitted by the North American water vole, but the functions of these sounds was not known. The physical properties of sounds produced by microtines have been found to be species-specific. A comparison of differences of the sounds produced by different species may be useful for determining taxonomic relationships.

LITERATURE CITED

- Anderson, J. W. 1954. The production of ultrasonic sounds by laboratory rats and other mammals. *Science* 119:808-809.
- Arvola, A., M. Ilmen, and T. Koponen. 1962. On the aggressive behavior of the Norwegian lemming (Lemmus lemmus), with special reference to the sounds produced. *Arch. Soc. Zool.-Bot. Fennicae 'vanamo,' Helsinki* 17(2):80-101.
- Bailey, V. 1924. Breeding, feeding, and other life habits of meadow mice (Microtus). *J. Agric. Res.* 27:523-536.
- Balph, D. M. and D. F. Balph. 1966. Sound communication of Uinta ground squirrels. *J. Mamm.* 47:440-450.
- Brooks, R. J. and E. M. Banks. 1973. Behavioural biology of the collared lemming (Dicrostonyx groenlandicus (Traill)): An analysis of acoustic communication. *Anim. Behav.* 6:1-80.
- Clarke, J. R. 1956. The aggressive behavior of the vole. *Behavior* 9:1-23.
- Clough, G. C. 1965. Lemmings and population problems. *Amer. Sci.* 53:199-212.
- Colvin, D. V. 1973. Agonistic behavior in males of five species of voles Microtus. *Anim. Behav.* 21:471-480.
- Colvin, M. A. 1973. Analysis of acoustic structure and function in ultrasounds of neonatal Microtus. *Behavior* 44:234-263.
- Dunford, C. 1970. Behavioral aspects of spatial organization in the chipmunk, Tamias striatus. *Behavior* 36:215-231.
- Getz, L. L. 1962. Aggressive behavior of the meadow and prairie voles. *J. Mamm.* 43:321-358.
- Gould, E., N. C. Negus, and A. Novick. 1964. Evidence for echolocation in shrews. *J. Exper. Zool.* 156:19-38.
- Hart, F. M. and J. A. King. 1966. Distress vocalizations of young in two subspecies of Peromyscus maniculatus. *J. Mamm.* 47:287-293.
- Hatfield, D. M. 1935. A natural history study of Microtus californicus. *J. Mamm.* 16:261-271.
- Hooper, E. T. and B. S. Hart. 1962. A synopsis of recent North American microtine rodents. *Mus. of Zool., Univ. Mich.* 120:1-68.

- Hooven, E. F. 1973. Notes on the water vole of Oregon. *J. Mamm.* 54: 751-753.
- Itani, J. 1963. Vocal communication of the wild Japanese monkey. *Primates* 4:11-66.
- Jannett, F. J. and J. Z. Jannett. 1974. Drum-marking by *Arvicola richardsoni* and its taxonomic significance. *Amer. Midl. Nat.* 92:230-234.
- Johst, V. 1973. Struktur und funktion akustischer signals der Schermaus *Arvicola terrestris* (L.). *Forma et Functio* 6:305-321.
- Koplin, J. R. and R. S. Hoffman. 1968. Habitat overlap and competitive exclusion in voles (*Microtus*). *Amer. Midl. Nat.* 80:494-507.
- Kummer, H. 1971. Primate societies. Aldine-Atherton, Chicago. 160 pp.
- Marler, P. R. and W. H. Hamilton III. 1966. Mechanisms of animal behavior. John Wiley and Sons, Inc., New York. 771 pp.
- Murie, J. O. 1971. Behavioral relationships between two sympatric voles (*Microtus*): relevance to habitat segregation. *J. Mamm.* 52: 181-186.
- Negus, V. E. 1949. The comparative anatomy and physiology of the larynx. Grune and Stratton, New York. 230 pp.
- Noirot, E. 1966. Ultrasound in young rodents. I. Changes with age in albino mice. *Anim. Behav.* 14:459-462.
- Noirot, E. 1968. Ultrasound in young rodents. II. Changes with age in albino rats. *Anim. Behav.* 16:129-134.
- Noirot, E. 1974. Nest-building by the virgin female mouse exposed to ultrasound from inaccessible pups. *Anim. Behav.* 22:410-420.
- Noirot, E. and D. Pye. 1969. Sound analysis of ultrasonic distress calls of mouse pups as a function of their age. *Anim. Behav.* 17:340-349.
- Ognev, S. I. 1964. Mammals of USSR and adjacent countries. Vol. II: Rodents. Israel Program for Scientific Translations, Inc.
- Okon, E. E. 1970a. The effect of environmental temperature on the production of ultrasounds by isolated non-handled albino mouse pups. *J. Zool.* 162:71-83.
- Okon, E. E. 1970b. The ultrasonic responses of albino pups to tactile stimuli. *J. Zool.* 162:485-492.
- Quay, W. B. 1968. The specialized posterolateral sebaceous glandular regions in microtine rodents. *J. Mamm.* 49:427-445.

- Roberts, L. H. 1975. Evidence for the laryngeal source of ultrasonic and audible cries of rodents. *J. Zool.* 175:243-258.
- Rosenzweig, M. R., D. A. Riley and K. Kreck. 1955. Evidence for echolocation in the rat. *Science* 121:600.
- Rowell, T. E. and R. A. Hinde. 1962. Vocal communication by the rhesus monkey (Macaca mulatta). *Proc. Zool. Soc. Lond.* 138:279-294.
- Sales, G. D. 1972. Ultrasound and auditory discrimination in rats and other mammals. *Anim. Behav.* 20:88-100.
- Sewell, G. D. 1968. Ultrasound in rodents. *Nature* 217:682-683.
- Sewell, G. D. 1970. Ultrasonic signals from rodents. *Ultrasonics* 8:26-30.
- Sherman, R. A. W. 1974. Demonstration of the hamster alarm pheromone. *Dissert. Abstr. B*, 34(8):3656.
- Smith, W. J. 1969. Messages of vertebrate communication. *Science* 165:145-150.
- Stoddart, D. M. 1972. The lateral scent organs of Arvicola terrestris (Rodentia, Microtinae). *J. Zool.* 166:49-54.
- Tembrock, G. 1968. Land mammals. Pp. 338-404 in *Animal Communication*. (T. A. Sebeok, ed.), Indiana Univ. Press, Bloomington, Indiana. 686 pp.
- Waring, G. H. 1966. Sounds and communication of the yellow-bellied marmot (Marmota flaviventris). *Anim. Behav.* 14:177-183.
- Waring, G. H. 1970. Sound communications of black-tailed, white-tailed and Gunnison's prairie dogs. *Amer. Midl. Nat.* 83:167-185.

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