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# Sound Communication in the Uinta Ground Squirrel

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# SOUND COMMUNICATION IN THE UINTA GROUND SQUIRREL

by

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Donna Mae Balph

# INTRODUCTION

Numerous investigators have studied sound communication in animals in recent years. Most of these studies have been on birds, insects, or cetaceans, particularly the dolphin. Most of the studies on terrestrial mammals have been of the natural history type, and the authors have given an orthographic rendition of any sounds produced by that particular species. Few definitive studies have been done. There have been a few attempts to determine cause and function of sounds in mammals (Arvola, Ilmen, and Koponen, 1962; Bartholomew and Collias, 1962; Rowell and Hinde, 1962; Andrew, 1963).

No quantitative studies on sound communication in Citellus have been made. Balph and Stokes (1963), Burnett (1931), Fitch (1948), Gordon (1943), Linsdale (1946), and Manville (1959) have described the natural history and ecology of various ground squirrels.

The purpose of my study was to catalog the sounds given by the Uinta ground squirrel (Citellus armatus), to determine the cause and function of each sound, and to see how these sounds represent adaptations to life in the animal's habitat.

# GENERAL LIFE HISTORY

For a more detailed account of the behavior of this species the reader should consult Balph and Stokes (1963). Most of the information for this section was taken from that paper and from personal communication with D. F. Balph. Balph and Stokes have described the ethology of the Uinta ground squirrel and are presently investigating the ecology of the species. Dr. Balph has also studied the behavioral response of the squirrels to a trap.

The Uinta ground squirrel is a diurnal, burrowing animal inhabiting brushy or grassy areas of the mountains and foothills. The animals live in aggregations but are not colonial. Their food consists mostly of succulent vegetation and occasional seeds. They do not require free water.

The annual cycle of the Uinta ground squirrel falls conveniently into two phenological periods. The first is the breeding period which in our area extends from April 1, the approximate date of emergence from hibernation, until May 1 when breeding ceases. The post-breeding period extends from May 1 until all the squirrels are in hibernation, about August 15.

During the first few days of the breeding period the animals are engaged mostly in maintenance behavior--feeding, moving about, grooming, or resting. The females do not defend any areas and tolerate other females. The males during this period do defend an area against other males but at high densities they are unable to completely exclude other males. When the males approach the females in courtship, the females generally threaten. The males persist until they chase the females down a burrow where copulation apparently occurs.

During the post-breeding period the above situation is reversed. Females defend areas for about 2 weeks before and after parturition. The males are subordinate to the females, are highly mobile, and do not defend any area. The young are born about May 15 but do not come aboveground until about June 1. At first there is little intolerance between or within litters. As the young grow older, however, the amount of play decreases and aggression increases. Some males are intolerant of the young, and the females become aggressive toward even their own litters after they are weaned. The dominance relationships between animals, individual distance, and learning are, no doubt, also important factors in the interactions between animals.

The Uinta ground squirrel has two main postures to which I shall refer. The upright posture consists of standing on the hind legs with the forelegs folded in front of the body (Figure 1). The down posture consists of standing on all four legs (Figure 2). It is possible that scent communication plays an important part in the life of the ground squirrel. There are two known scent glands. One is the anal gland, the papillae of which are everted in threat. A cheek gland (the function of which is being investigated by D. F. Balph) is used by the squirrels in the following manner: The animal paws

Figure 1. Uinta ground squirrel in upright posture.

Figure 2. Uinta ground squirrel in down posture.

at some loose dirt then rubs the sides of the head and body in the pawed area. This sequence is called wiping. It is done most often by males in the spring. It seems likely that wiping deposits a scent and is used for marking purposes.

# METHODS AND APPARATUS

This study was conducted at the Forestry Field Station 20 miles northeast of Logan, Utah (Figure 3). Additional observations were made on other populations near Logan and Mammoth, Wyoming. The density of the major population varied from 20 animals per acre in spring to 75 animals per acre after the young appeared aboveground. Most of the observations on the interactions of the squirrels with conspecifics were made on the 2-acre lawn of the Station.

I conducted field work for this study in 1962, 1963, and 1964, using a truck parked on the lawn as a blind from which I made tape recordings of the calls and recorded the behavior of the animals. Most of the squirrels had been trapped and numbers had been dyed on them for easy recognition of individuals.

An observation consisted of a call plus the situation in which it occurred. A situation consisted of the activities of the caller and respondent before, during, and after a call was given. Also recorded were such items as the distance between the interacting animals, or between the squirrels and a predator, the time, weather conditions, the location, and sex and age of each individual involved. I simultaneously tape-recorded any sound made during the interaction using a parabolic reflector and directional microphone. I made a

Figure 3. Forestry Field Station.

limited number of observations of the reaction of the squirrels to mounts of predators and to playbacks of the calls. I used the sound spectrograph to make graphs of the recorded sounds.

To determine the cause of a call I examined the activities of the caller and respondent before the call was given, as well as the environmental situation. This included such data as the distance between the animals or between the squirrel and a predator, the date, time, weather conditions, the location, and the sex and age of individuals involved. To determine the function of a call I examined the change in the behavior of the respondent from before the call to after the call.

# RESULTS

Uinta ground squirrels make six different sounds which I was able to detect: chirp, churr, squeal, squawk, teeth clatter, and growl. I shall discuss first the cause and function of calls used in interaction with conspecifics, then in interaction with other species.

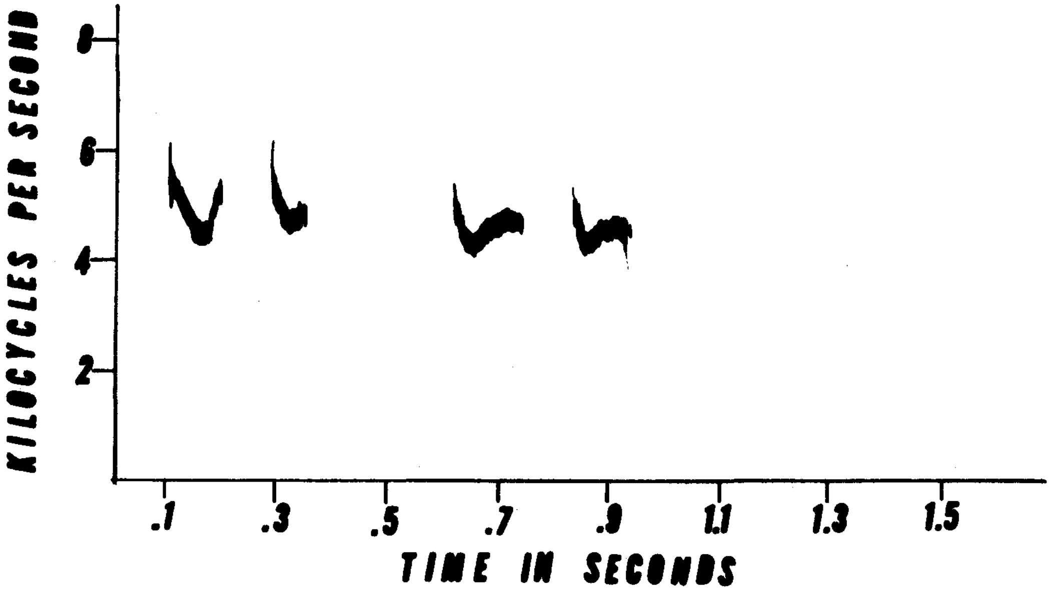
## Use of Calls in Interaction With Conspecifics

### Chirp

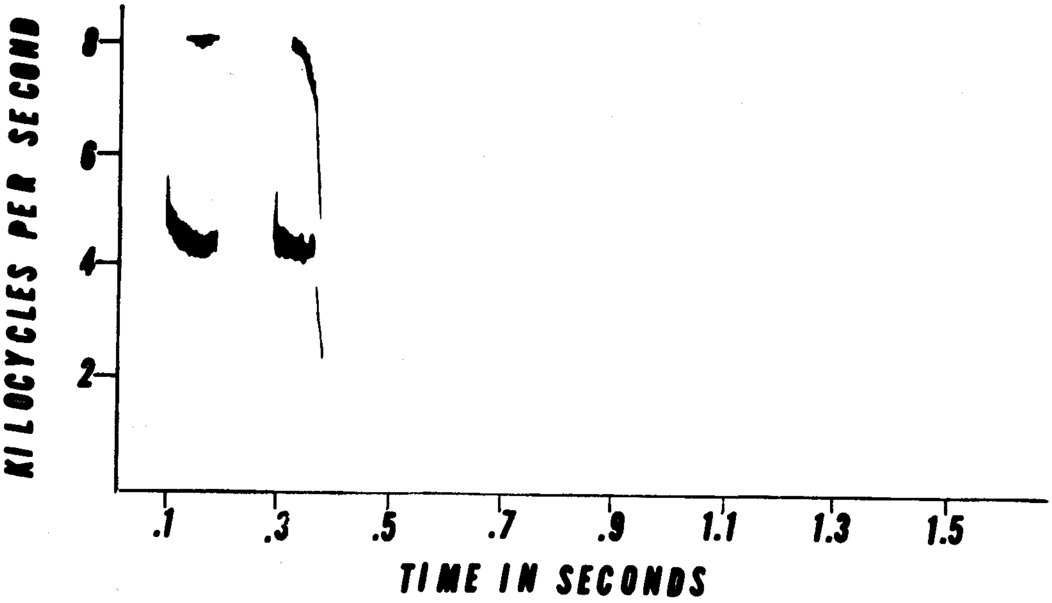
The chirp was a sharp sound, much like the chirps of some birds, from .01 to .1 seconds in duration. The frequency was usually 4,000 to 6,000 cycles per second. The chirp was given singly as well as in groups of 2 to 5 sounds. The interval between the chirps was approximately the same length as the chirps themselves (Figure 4).

Chirp by males.--The chirp call of the males had an average length of .08 seconds (n = 31, standard error = .005) and an average frequency of 4,500 cycles per second (n = 31, standard error = 58.5). The male almost always (98% of the observations) gave the chirp in groups of two to five sounds.

Before the chirp call was given by males to males in 35 situations, the respondent was usually attacking or approaching the caller (48%) or feeding and resting near the caller (35%). Sometimes the caller attacked or approached the respondent




(a) males




(b) females

Figure 4. The chirp call given in threat by (a) males and (b) females.

before giving the call (17%). In 54 percent of the observations the two animals were 6 to 25 feet apart; in 36 percent, 0 to 5 feet apart. In 93 percent of the situations no body contact occurred.

In 72 percent of the situations the males were inside their home ranges. I refer to home range as defined by Burt (1940):

> Home range . . . is that area about its established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for young. It excludes those areas traversed by vagrants or other individuals in search of home sites. (Burt, 1940, p. 25)

Therefore, the cause of the males' chirp call appears to be the approach or sight of another male closer than 25 feet. The call is given more by a male when he is inside his home range than outside. This difference is undoubtedly attributable to the fact that the animal is, by definition, inside his home range more often than not.

The function of the call was determined by examining the change in the behavior of the respondent from before the call to after. In Table 1, as in all the other tables in this section showing the function of a call, I have omitted the activities of the respondents after the call was given if the caller attacked as well as called. This was done to enable me to determine the function of the call only, not the call plus attack.

After a chirp call, the amount of attack or approach by the male respondents decreased from 32 percent to 0 percent (Table 1), and escape decreased from 11 percent to 0. Calling by the respondents increased from 11 percent to 26 percent.

Table 1. Change in activities of respondents after chirp call was given by males to males and females

| Activity | Percent of activity of respondents | | | |
|---|---|---|---|---|
| | Males | | Females | |
| | Before n=28 | After n=23 | Before n=21 | After n=14 |
| Maintenance | 46 | 74 | 57 | 71 |
| Attack or approach | 32 | 0 | 33 | 0 |
| Escape | 11 | 0 | 5 | 14 |
| Calling | 11 | 26 | 5 | 14 |

Most of the animals returned to or became engaged in maintenance activities after the call was given. Therefore, the function of the chirp appears to be to stop the approach of the respondent. It does not cause him to escape, however. He just moves off and begins to feed, sometimes returning the call. Of the calls given in response, 85 percent were also chirps.

The chirp call was also given by males to females in 16 situations mostly at the attack or approach of the respondent (50%), and to a lesser extent at the sight of the respondent nearby (37%). However, the females came closer in more situations before eliciting the call than the males. Females elicited the call at a distance of 0 to 5 feet 50 percent of the time; 6 to 25 feet 39 percent of the time. Therefore, one cause of the male to female chirp is the approach or sight of the female within 25 feet.

After the call was given by the male, no females ever continued to approach or attack. This behavior would be adaptive in that it would curtail the aggression of the female long enough for breeding to occur. Escape, calling, and maintenance increased (Table 1). Thus, the function of the chirp call is to stop approaching females. The female usually just moves off but sometimes escapes or calls in response.

The males gave the chirp call 52 percent of the time in an upright posture and 38 percent of the time while in the down posture or moving. The remaining 10 percent were given while attacking or escaping. The chirp may function to advertise the location of the male during the breeding season as well as to threaten and deter animals which come too close.

In April, during the breeding season, male ground squirrels gave the chirp call in a manner different from that described above. In 26 situations the call was elicited by the chirp calling of another male (50%), or by no apparent external stimulus (46%). The call was given in the upright posture 60 percent of the time; in down posture or moving, 26 percent; while attacking another, 6 percent. The call did not seem to be given at the boundaries of the male's home range or territory; instead it was given most often near the burrows he used most frequently. The apparent external cause of the male chirp in spring appears to be the sound of another animal chirping and, in the situations where no external stimulus was apparent, the calls were elicited by an internal stimulus. Since this type of calling did not occur outside the breeding season, and since this was the only time when the testes were in the scrota, it seems that the internal causation of the calls might well have been the high level of gonadotrophin. This high hormone level probably also acted to lower the level of the stimulus needed to elicit the call from the sight of another animal within 25 feet (which is the situation during the non-breeding season) to just the sound of another animal chirping.

The response of other squirrels to the males' chirps in spring may indicate the function of the call. The call did not attract females nor consistently repel those males which I saw and thought were responding to the caller (Table 2). Females either gave no response or looked up only momentarily. Males

Table 2. Response of other squirrels to male chirp in spring

| Response of males n=55 | | Response of females n=48 | |
|---|---|---|---|
| Activity | Percent of interactions | Activity | Percent of interactions |
| Returned the call | 40 | No response | 50 |
| Approached caller | 15 | Alert momentarily | 40 |
| Escaped | 15 | Escaped | 6 |
| Alert | 11 | Approached caller | 4 |
| No response | 9 | | |
| Wiped | 7 | | |
| Encounter with caller | 4 | | |

returned the call 40 percent of the time. This led to antiphonal calling which sometimes lasted for up to half an hour. The calling males tended to continue calling either from the same spot or while moving about and wiping (72% of 39 situations). This situation is similar to what Andrew (1964) has found in domestic chicks. There is a strong tendency to repeat the details of the immediately previous call, quite independent of the motivational state. Thus, the function of the chirp call given by males in spring seems to be epideictic. I use the term as defined by Wynne-Edwards (1962, p. 16): "Specially-timed communal displays . . ." The function of the epideictic display is to space out the population. If the males' chirp call did function to space out the males, this would benefit both the males and the females by reducing the number of encounters (which leaves more time for feeding), and increasing the amount of area available for feeding and burrows.

Chirp by females.--The chirp call given by females had an average length of .06 seconds (n = 43, standard error = .003). This was significantly shorter than the male call, .08 seconds in length (t = 3.85, df = 72, probability = .001) (Figure 5A). The average frequency of the chirp by females was 5,200 cycles per second (n = 43, standard error = 86.3). This was significantly higher pitched than the male call (t = 6.47, df = 72, probability is less than .001) (Figure 5B). Females gave the chirp call in groups of two to five sounds 61 percent of the time as opposed to the males 98 percent.

The stimuli eliciting the chirp call given by a female to

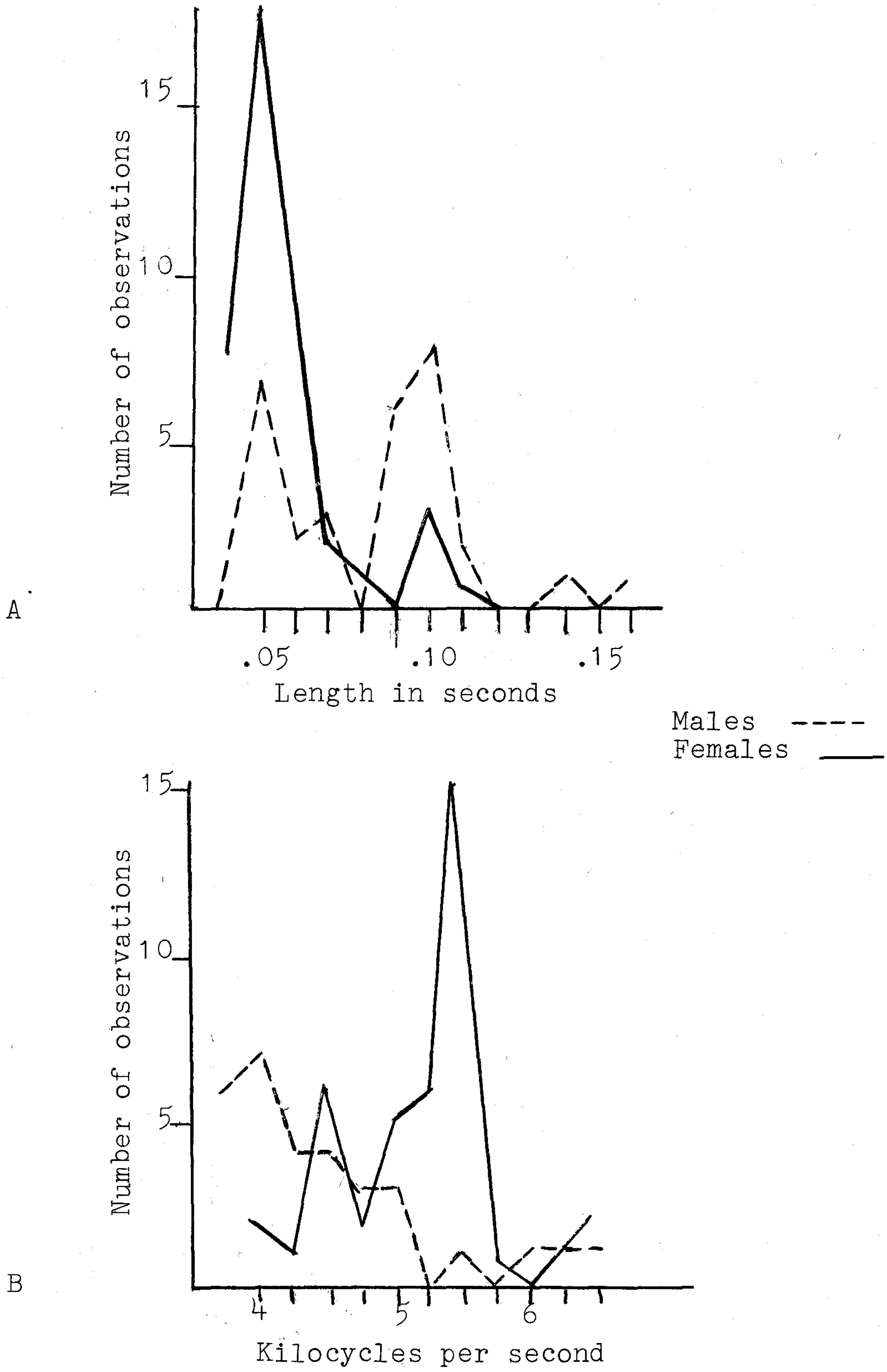



Figure 5. Frequency distribution of chirp calls given by males and females: A. length in seconds. B. pitch in kilocycles per second.

a female in 24 situations during the breeding season were mostly actual attack or approach of the respondent (71%) with some calls being given at the mere sight of another female nearby (21%). The respondent in most instances (85%) approached to within 5 feet before eliciting the call. Body contact occurred in only 10 percent of the interactions. Thus, the causation of the chirp given by females during the breeding season is the approach of the respondent to within 5 feet of the caller. The threshold of stimulation to calling appears to be very high.

After the breeding season the causation of the chirp was slightly different. The call was elicited (in 57 situations) as often by the sight of another female (46%) as by the approach of another female (42%). In this period only 49 percent of the calls occurred at a distance of 0 to 5 feet compared with 85% in the breeding period. Body contact occurred in only 4 percent of the interactions. Thus the apparent cause of the chirp given by females after the breeding season is the approach or sight of another female within 25 feet, not 5 feet as in the breeding season. Females become more intolerant after they have become pregnant. It is then that they select a nest burrow in which to give birth to their young. This greater intolerance is reflected in the greater distance at which females begin to interact; that is, their individual distance has increased. This would serve to space out the females and insure food and burrows for each litter.

In both seasons the chirp call causes the respondent to stop and a few may move away from the caller (Table 3). There

Table 3. Change in activities of respondent after chirp call was given in three different situations: (A) females to females during the breeding season; (B) females to females after the breeding season; and (C) females to males

| Activity | Percent of activity of respondents | | | | | |
|---|---|---|---|---|---|---|
| | A | | B | | C | |
| | Before n=29 | After n=19 | Before n=52 | After n=47 | Before n=30 | After n=23 |
| Maintenance | 48 | 89 | 58 | 79 | 30 | 78 |
| Attack or approach | 48 | 0 | 29 | 0 | 63 | 0 |
| Escape | 0 | 5 | 8 | 11 | 7 | 9 |
| Calling | 4 | 5 | 6 | 11 | 0 | 13 |

are slight increases in calling and escape by the respondent after the call was given. The immediate function is to keep other animals at a distance. The effect of the call is to space out the females and insure nest space and food for the young, as well as freedom from harassment by other females.

Chirp calls given by females to males in 33 situations were elicited mostly by the males approaching the females (72%), and to a lesser extent by the sight of the males nearby (21%). Most of the interactions occurred at 0 to 5 feet (69%) and 6 to 25 feet (28%). The chirp functioned to stop the approach of the male, as shown by the decrease in attack or approach (Table 3). The call also caused a small amount of escape. Body contact was noted in only 8 percent of the interactions. During the breeding season when the males made repeated sexual rushes at the females, the females did not always chirp. This may have indicated that the female was receptive at that particular time. After the breeding season females are more intolerant of males. I have few observations on the interactions between males and females because the males either move or are forced into the adjacent brushy areas and do not spend as much time on the lawn as in the breeding season.

The females gave the chirp in an upright posture only 25 percent of the time; 75 percent were given while in the down posture or moving. This and the fact that the females do not call for extended periods of time indicate that the chirp has no epideictic function in the females. The call has not been ritualized into a display and is not given communally by the females.

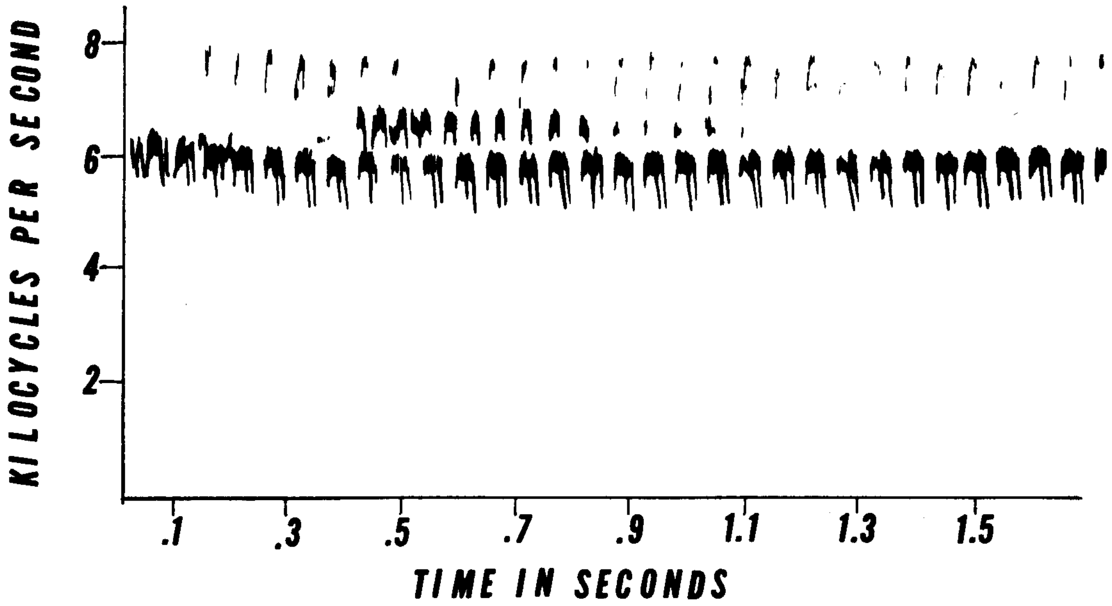
In summary, the chirp call in both sexes seems to be elicited by the approach of another squirrel to within 25 feet of the caller. The threshold of stimulation in the male in spring may be lowered by high hormone levels to the point that males may call merely at the sound of another male chirping.

Churr

The churr call was a trill of usually 20 syllables per second lasting 0.4 to 3.0 seconds (n = 24, standard error = .165). The average frequency of the highest point in the call was 6,100 cycles per second (standard error = 398.4) (Figure 6). The churr call was used intraspecifically only by females.

The stimuli eliciting the churr call given to females (in 56 situations) most often were the approach or attack by the respondent (53%) and the sight of the respondent feeding or resting near the caller (37%). Ninety percent of the calls were given when the two animals were 0 to 5 feet apart. Body contact occurred in 2 percent of the situations. The churr to males in 19 situations was elicited more by the attack or approach of the male (79%) than just by the sight of the male (16%). Seventy-one percent of the calls were given when the two animals were 0 to 5 feet apart. The causation of churrs given to both females and males is the approach of another animal or, to a lesser extent, the sight of another animal feeding or resting nearby.

The response of females to the churr was to stop



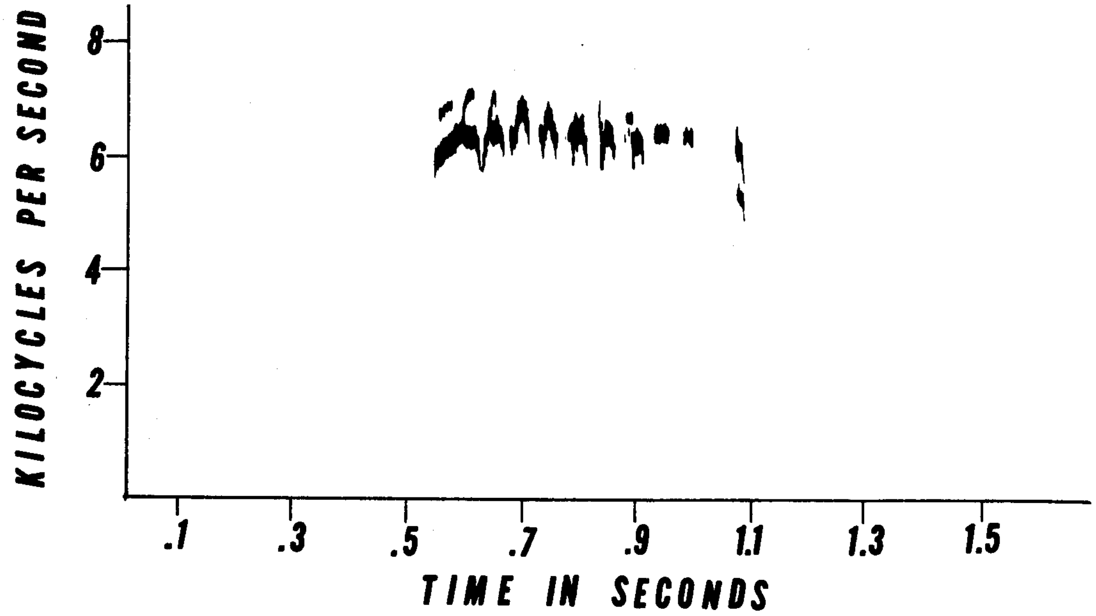




Figure 6. Churr call given in threat.

approaching or attacking, to call, and move off (Table 4). The response of the males was similar except that they tended to call and escape more.

## Squeal

The squeal was highly variable in structure, frequency, and length. It sounded much like the squeal of other mammals of the same size (Figure 7).

The squeal was almost always given when the caller was being attacked (96% of 24 situations). I recorded body contact, usually in the form of biting, occurred in 50 percent of the situations. It may have occurred more often. This is a much larger figure than for any of the other calls. In 96 percent of the interactions the squirrels were 0 to 5 feet apart when the squeal was given. Thus the squeal seems to be caused by actual body contact, usually biting. The squirrels sometimes squealed before contact actually occurred, anticipating the fight.

After the squeal was given, the attacker desisted and moved off (Table 5). I do not think the squeal caused the attacker to move off. The squeal has, in my opinion, no particular function, but is merely an involuntary expression of pain and fear.

## Squawk

The squawk was 0.01 to 2.0 seconds in length and averaged about 4,500 cycles per second as the frequency of the

Table 4. Change in behavior of respondent after churr call was given by females to females and males

| Activity | Percent of activity of respondents | | | |
|---|---|---|---|---|
| | Males | | Females | |
| | Before n=41 | After n=34 | Before n=17 | After n=13 |
| Maintenance | 32 | 71 | 12 | 62 |
| Attack or approach | 57 | 0 | 70 | 8 |
| Escape | 5 | 18 | 18 | 31 |
| Calling | 7 | 12 | 0 | 0 |

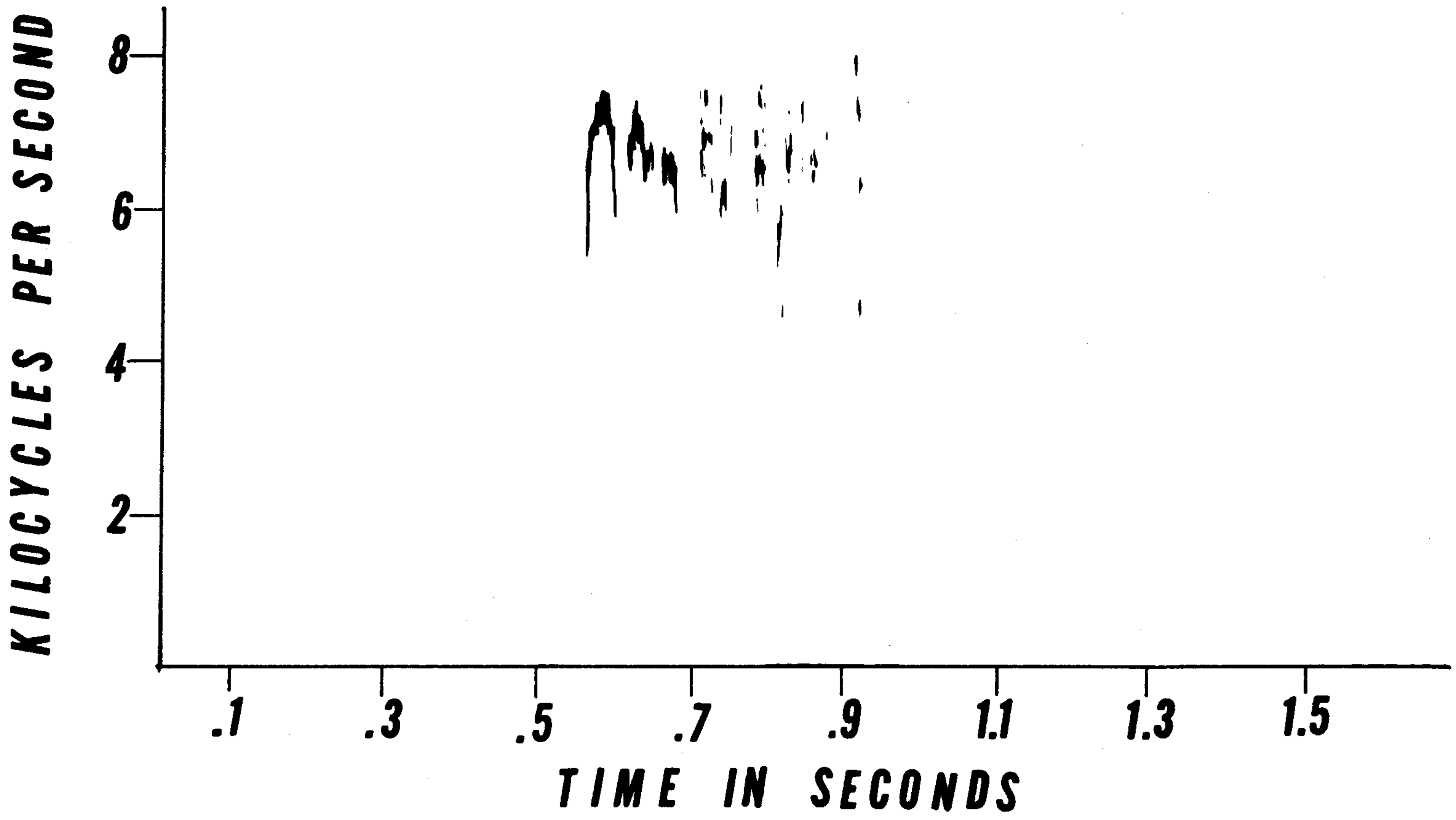



Figure 7. Squeal.

Table 5. Change in behavior of respondent after squeal was given

| Activity | Percent of activity of respondents<br>Before<br>n=24 | <br>After<br>n=22 |
|---|---|---|
| Maintenance | 25 | 77 |
| Attack or approach | 58 | 0 |
| Escape | 13 | 18 |
| Calling | 4 | 5 |

fundamentals (Figure 8). The sound itself is segmented.

Squirrels gave the squawk when held tightly by predator, human, or occasionally by another squirrel. Therefore, the cause of the squawk was being held tightly rather than just being bitten as in the squeal.

I determined the function of the squawk by observing the population response. The population did not usually respond to the squeals of a young or adult squirrel. When D. F. Balph and I began trapping early in the spring the squawks of the animals being handled elicited alarm churrs from the population. After a few days the animals became habituated to the squawks and no longer responded. We trapped very little during the last part of May, but began trapping intensively again when the young came aboveground in the first part of June. When the young squawked while being handled, animals within 150 feet gave churrs and females close by approached within 5 feet. When adults that were captured squawked, the population also responded with churrs. Thus, the squawk appears to function as a signal to inform other members of the population that one of their number has been caught. This call may induce some mobbing by the females, as evidenced by their approaching us.

Some calls are intermediate between the squeal and squawk (Figure 9). These were given during prolonged fights. One of these calls may have been derived from the other; i.e., the squawk may be a prolonged, sustained squeal, or the squeal a portion of the squawk. This would be consistent with the similarity in causation of the two calls.

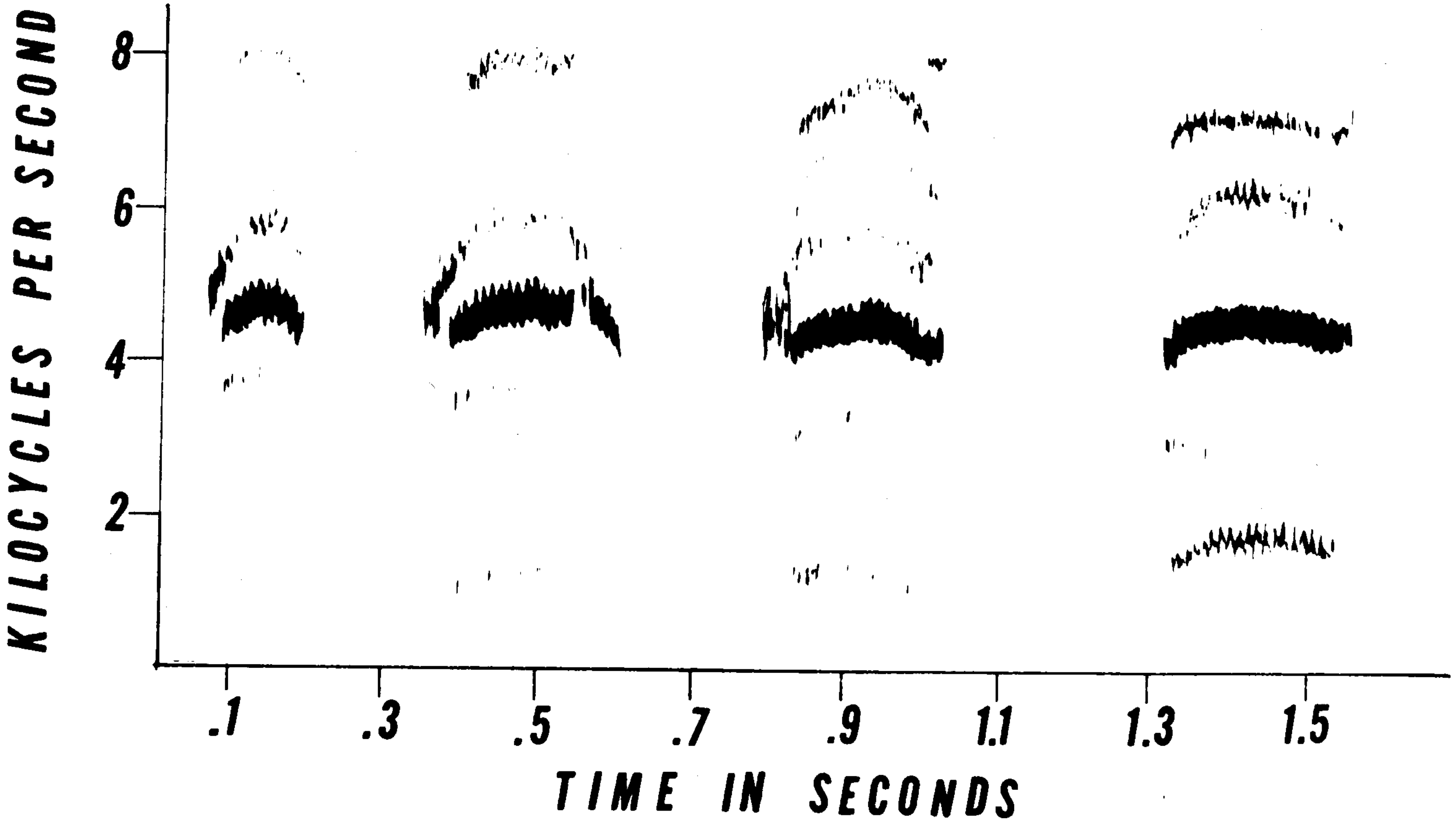



Figure 8. Squawk.

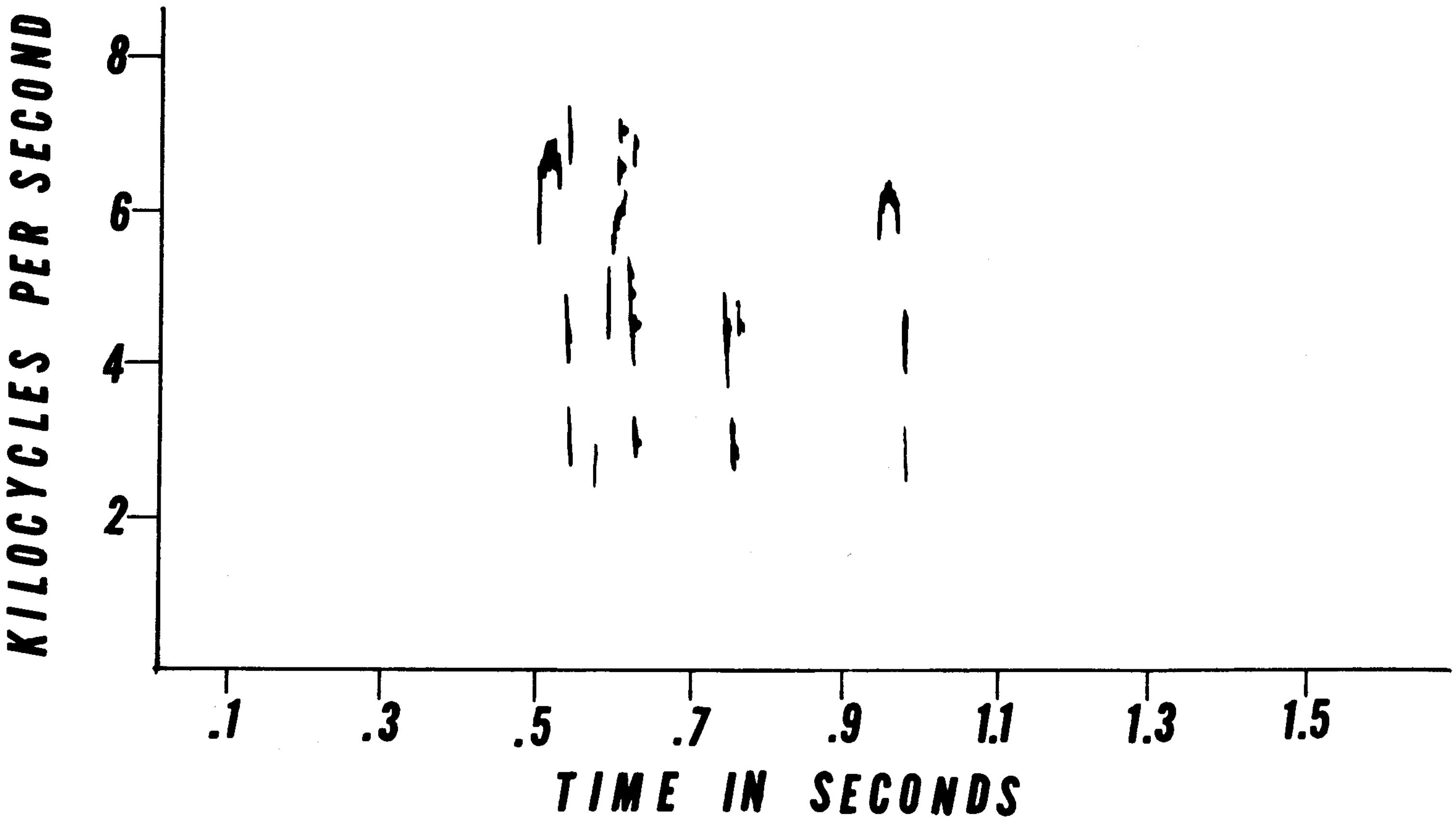



Figure 9. Call intermediate between squeal and squawk.

Teeth clatter

The ground squirrel makes a noise by clattering its teeth together. The speed of clattering is usually about 20 sounds per second. The length of the call varies from 1 to 3 seconds. The sounds made seem to cover all of the frequencies from 0 to 7,500 cycles per second, although this does not show in the accompanying tracing because the lower frequencies (less than 6,000) were very faint on the spectrograms (Figure 10).

In 67 percent of 20 situations the teeth clatter occurred after a fight between two squirrels; the rest of the calls were given when two animals met. The calls were also given by animals after we had tried unsuccessfully to remove them from the traps. The teeth clatter was never given when we grasped them or as we approached them sitting in the traps. Most of the calls (86%) were given when the animals were 0 to 5 feet apart with no body contact. Tooth-chattering occurs in the heteromyid rodents during encounters or when defending the nest (Eisenberg, 1963). Thus the teeth clatter appears to be given after the animal has been attacked.

The change in the activity of the respondent from before the call to after the call showed a decrease in attack and escape from 36 percent to 0, and a decrease in calling from 21 percent to 7 percent. Maintenance behavior increased from almost none of the animals to almost all (7% to 93%) (Table 6). The teeth clatter seems to signal that the caller would rather return to its maintenance activities than either attack or escape.

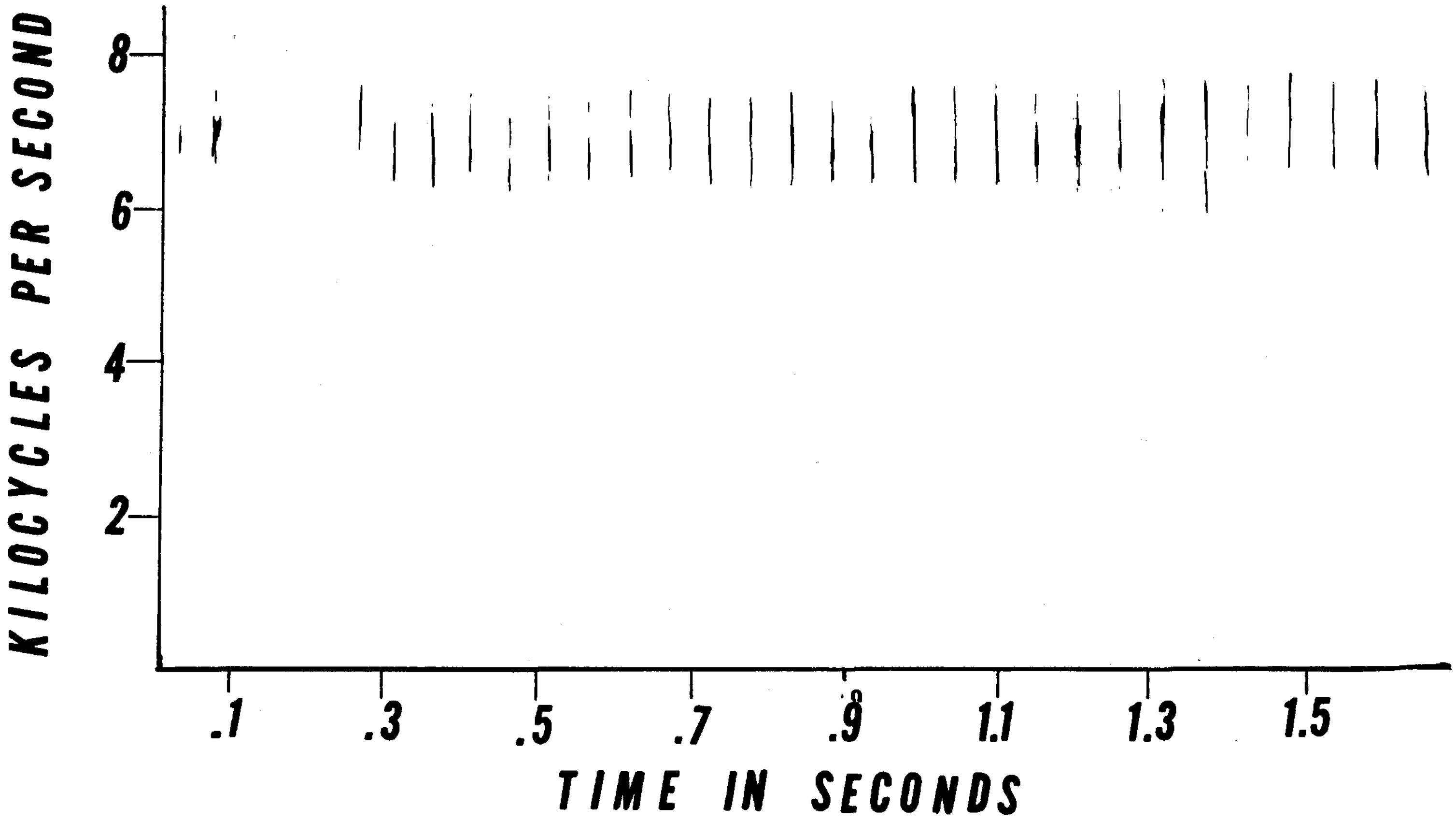


Figure 10. Teeth clatter.

Table 6. Change in activities of respondents after teeth clatter was given

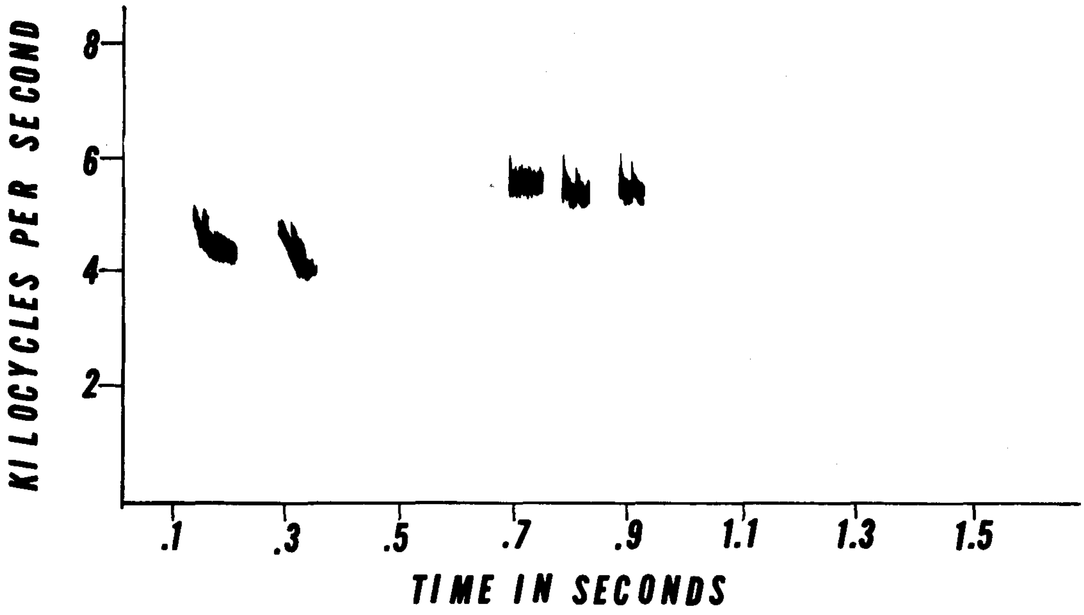
| Activity | Percent of activity of respondents Before n=14 | After n=14 |
|---|---|---|
| Maintenance | 7 | 93 |
| Attack or approach | 36 | 0 |
| Escape | 36 | 0 |
| Calling | 21 | 7 |

## Growl

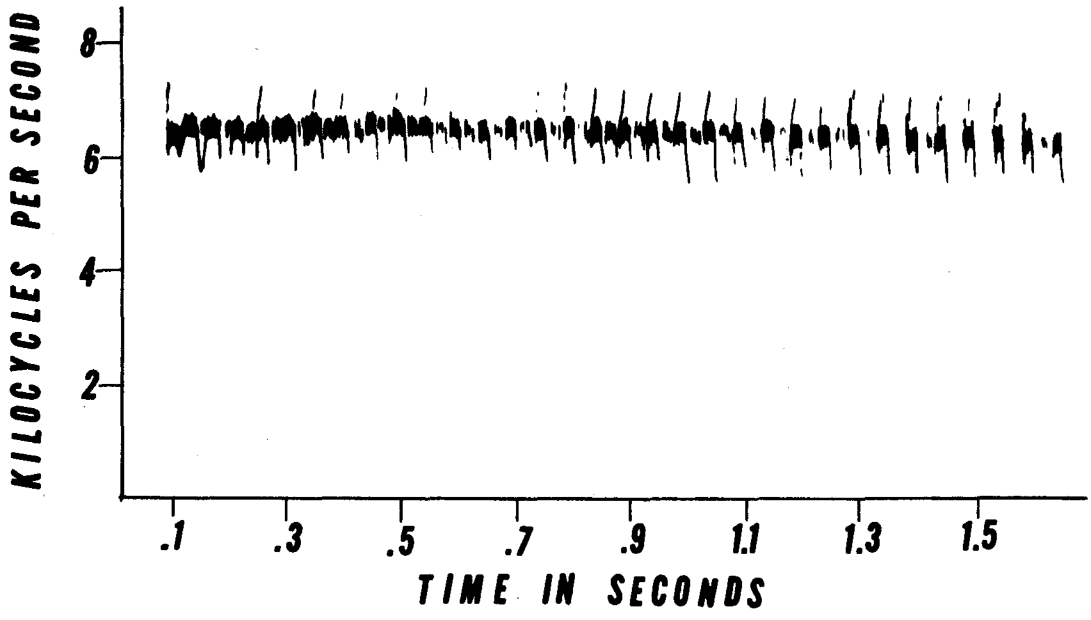
The Uinta ground squirrel produced a growl similar to that of other rodents and small carnivores. I heard the growl given only twice in the free-ranging animals. In these instances the calling animal was being harassed by another squirrel. I heard it more often when removing animals from traps. In heteromyid rodents the growl is given in a thwarting context as when the animal is being harassed by a conspecific or is defending the nest (Eisenberg, 1963). The cause of the growl in the ground squirrel is perhaps harassment by a conspecific or another animal. I have no theories as to its function.

## Use of calls by juveniles

When the young appeared aboveground about June 1 their repertoire of calls was complete and fully developed (Figure 11). At first the young gave the chirp and churr with no apparent external stimulus as the littermates clustered about their burrow. This indicated that the threshold of stimulation for the young was low. As they ranged farther from their home burrow they interacted more with adults and young. At this time the cause and function of their calls appeared to be the same as for adults except in a few details. Chirps given between two young were usually elicited when the animals were 2 feet apart, rather than 6 to 25 feet as in the adults. This may indicate more tolerance between the young than between adults. The young gave the call from the down position only, whereas the adults called from both the down and upright. Chasing,




(a) chirp




(b) churr

Figure 11. Calls given by the young: (a) chirp and (b) churr.

after the chirp was given, seemed to be more frequent in young than adults. Perhaps the young had not learned the signal value of the calls as threat. The churr was given by young when an adult approached within 2 or 3 feet, but if the adult continued to approach the young often squealed, although no body contact occurred. Again, the level of stimulation may be lower for the young. By the end of July the use of calls by juveniles was identical to that of adults.

Comparison of chirp and churr

The fact that the chirp and churr seem to be used in exactly the same type of situation indicates the same cause and function. This is in contrast to the specificity of the calls of many animals. I felt that there should be some difference in the situations in which these two calls were used. Having two calls used in exactly the same type of situation would not be consistent with the simple and limited number of calls in this species. A number of factors might influence which call was given. Whether the respondent was a stranger or a neighbor, the prior activity of the caller and respondent, and the activity of the respondent after the call might show some differences in function. The distance between the caller and respondent might give an indication of the relative intensity of the calls.

A comparison of the number of chirps and churrs given to strangers and neighbors shows no significant difference (chi-square = 2.73, df = 1, probability = approximately .10)

(Table 7). I compared the prior activity of the caller and respondent before the chirp and churr calls, and have used this comparison as an indication of prior motivation. There is no significant difference between the activities of either the caller or respondent before the chirp or churr was given (Tables 8 and 9). A comparison of the amount of change in the various categories of behavior of the respondent before the call was given to after the call (Table 10) shows that there is no difference in the effect the two calls have on the respondent.

Table 11 shows the percentage of chirps and churrs which were given at various distances. The differences between the two calls are highly significant, more churrs being given at the closer distances than chirps. Figure 12 shows that, as the distance between the caller and respondent increased, fewer churrs and more chirps were given. The churr may be a lower intensity threat call since the caller permits the respondent to approach closer before giving threat. On the other hand, the churr may be considered high intensity threat since the two animals were closer together and caller was more intolerant. I think this explanation is more nearly correct. The caller does not change from chirps to churrs as the respondent approaches because either call usually stops the approach of the respondent.

Table 7. Comparison of number of chirps and churrs given to neighbors and to strangers[a]

| | Number of calls given | |
|---|---|---|
| | Chirp | Churr |
| To neighbor | 43 | 32 |
| To stranger | 13 | 3 |

[a]Chi-square=2.73, df=3, chi-square at the 90 percent level is 2.71.

Table 8. Comparison of activities of callers before giving chirp and churr to conspecifics[a]

| | Percent of activity before calling | |
|---|---|---|
| Activity | Chirp n=84 | Churr n=41 |
| Maintenance | 65 | 73 |
| Attack or approach | 23 | 15 |
| Escape | 11 | 7 |
| Calling | 1 | 5 |

[a]Chi-square=.93, df=3, chi-square at 10 percent level is .584.

Table 9. Comparison of three types of activities of respondents before chirp and churr calls. Escape and calling are excluded[a]

| The call type | Percent of activity of respondent before the call | | |
|---|---|---|---|
| | Feeding & moving | Attacking | Approaching |
| Female to female chirp, n=84 | 12 | 12 | 22 |
| Female to female churr, n=41 | 17 | 15 | 42 |
| Female to male chirp, n=30 | 30 | 7 | 57 |
| Female to male churr, n=17 | 12 | 12 | 59 |

[a]Female to female calls, chi-square=1.37; female to male calls, chi-square=3.07. Chi-square at 90 percent level is 4.61.

Table 10. Comparison of amount of change (in percent) in various activities of respondent from before call to after call[a]

| Activity | Female to female Chirp n=84 | Female to female Churr n=41 | Female to male Chirp n=30 | Female to male Churr n=17 |
|---|---|---|---|---|
| Maintenance | 28 | 39 | 48 | 50 |
| Attack or approach | 36 | 57 | 63 | 62 |
| Escape | 4 | 13 | 2 | 13 |
| Calling | 4 | 5 | 13 | 0 |
| | Chi-square=1.43, df=3 | | Chi-square=3.57, df=3 | |

[a]Chi-square at the 50 percent level is 2.37; at the 25 percent level, 4.11.

Table 11. Comparison of distance between caller and respondent when chirp and churr calls were given[a]

| Distance between caller and respondent | Percent of calls given Chirp n=99 | Churr n=65 |
|---|---|---|
| 0-1' | 31 | 47 |
| 1-2' | 12 | 24 |
| 2-3' | 11 | 5 |
| 3-4' | 8 | 8 |
| 4-5' | 7 | 2 |
| 6-25' | 25 | 11 |
| 26-100' | 5 | 2 |

[a]Chi-square=15.7, df=7, probability=approximately .025.

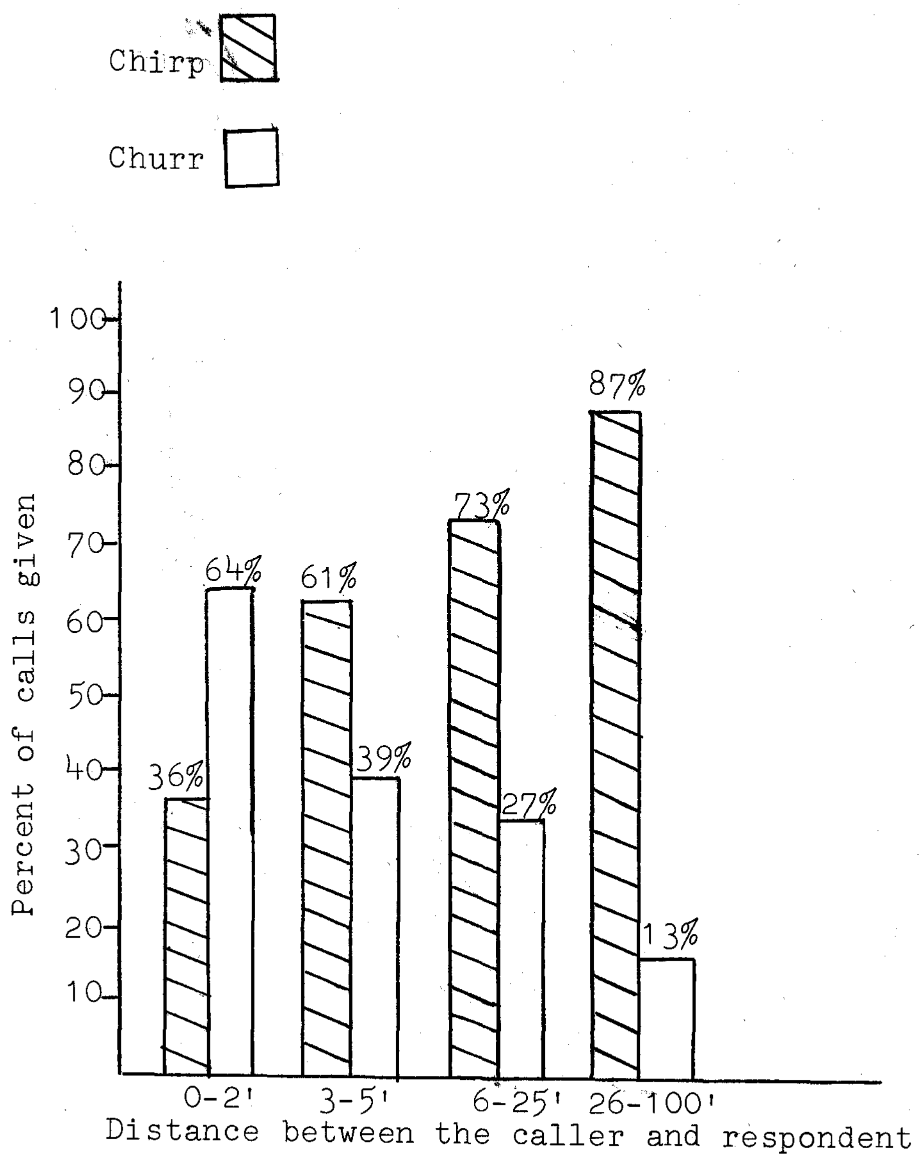



Figure 12. A comparison of the percent of chirps and churrs given when two animals were various distances apart.

## Use of Calls in Interaction With Other Species

### Reaction to airborne predators

The response of the squirrels to airborne predators was primarily alertness (Table 12). When a large hawk or eagle was soaring high in the air, the squirrels became very alert, sometimes ran to their burrow entrances before adopting an alert posture. If the bird started to dive, the squirrels in the bird's path gave two to four chirps. The caller escaped down his burrow only if the hawk came within 25 to 150 feet, the distance depending on the speed and height of the bird. The response of nearby squirrels to the chirp was also one of alertness but not necessarily escape. At the sound of the chirp most of these animals became alert in either the upright or down posture. If a squirrel was far from his burrow entrance he ran to it. The chirp is not repeated by other squirrels unless the hawk also flies over them. No "all-is-well" call is given as is the case in the black-tailed prairie dog (_Cynomys ludovicianus_) (King, 1955, p. 74).

The response of the squirrels to a small raptor such as the sparrow hawk (_Falco sparverius_) was somewhat different. The squirrels showed only mild interest as the hawk flew overhead or perched nearby. They continued to feed, glancing up occasionally at the bird. If the bird swooped down a few feet over the head of the squirrel, this elicited chirps and escape as in the case of the larger hawks (Table 12). Possibly the squirrels were responding to the angle subtended by the hawk's

Table 12. Response of Uinta ground squirrels to large and small hawks at various distances

| The response | Percent of response to | | | | | |
|---|---|---|---|---|---|---|
| | Large hawk | | | Small hawk | | |
| | close (0-25') | medium (26-150') | far (over 150') | close | medium | far |
| Chirp, then escape | 0 | 25 | 0 | 14 | 0 | 0 |
| No call, then escape | 0 | 0 | 0 | 43 | 0 | 0 |
| Chirp, no escape | 100 | 75 | 37 | 43 | 11 | 33 |
| Alert and orient to hawk | 0 | 0 | 62 | 0 | 78 | 67 |
| No apparent response | 0 | 0 | 0 | 0 | 11 | 0 |
| Number of situations | 3 | 4 | 8 | 7 | 9 | 3 |

outline; that is, the smaller the bird the closer it can get to the squirrel before eliciting chirps or escape. The spectrograms of the chirp given as alert look the same as the chirps given in threat (Figure 13); however, the chirps given to predators seem louder to me.

I observed the reaction of the squirrels to a large hawk which landed on the ground near where several animals were feeding. One squirrel in down posture beside her burrow entrance chirped in groups of two and three until the hawk flew off. No squirrel escaped when the hawk flew. This suggested that the squirrels were responding to the movements of the hawk rather than its shape. To determine whether this was true, I presented a stuffed hawk with the wings spread from behind a screen at a distance of 25 to 50 feet from some squirrels. The adults showed only mild interest in the hawk, no alertness or calls. The young escaped, but gave no calls. The young tend to escape more from a strange object whereas the adults regard the object with mild interest. The movements of flying or swooping seemed to be important in eliciting the hawk response from squirrels. The animals in the previous situation watched the hawk land and did not rely merely on its shape. In several instances, I saw the squirrels chirp at large airplanes overhead. Evidently the airplane sufficiently resembled a soaring hawk to elicit the airborne predator response.

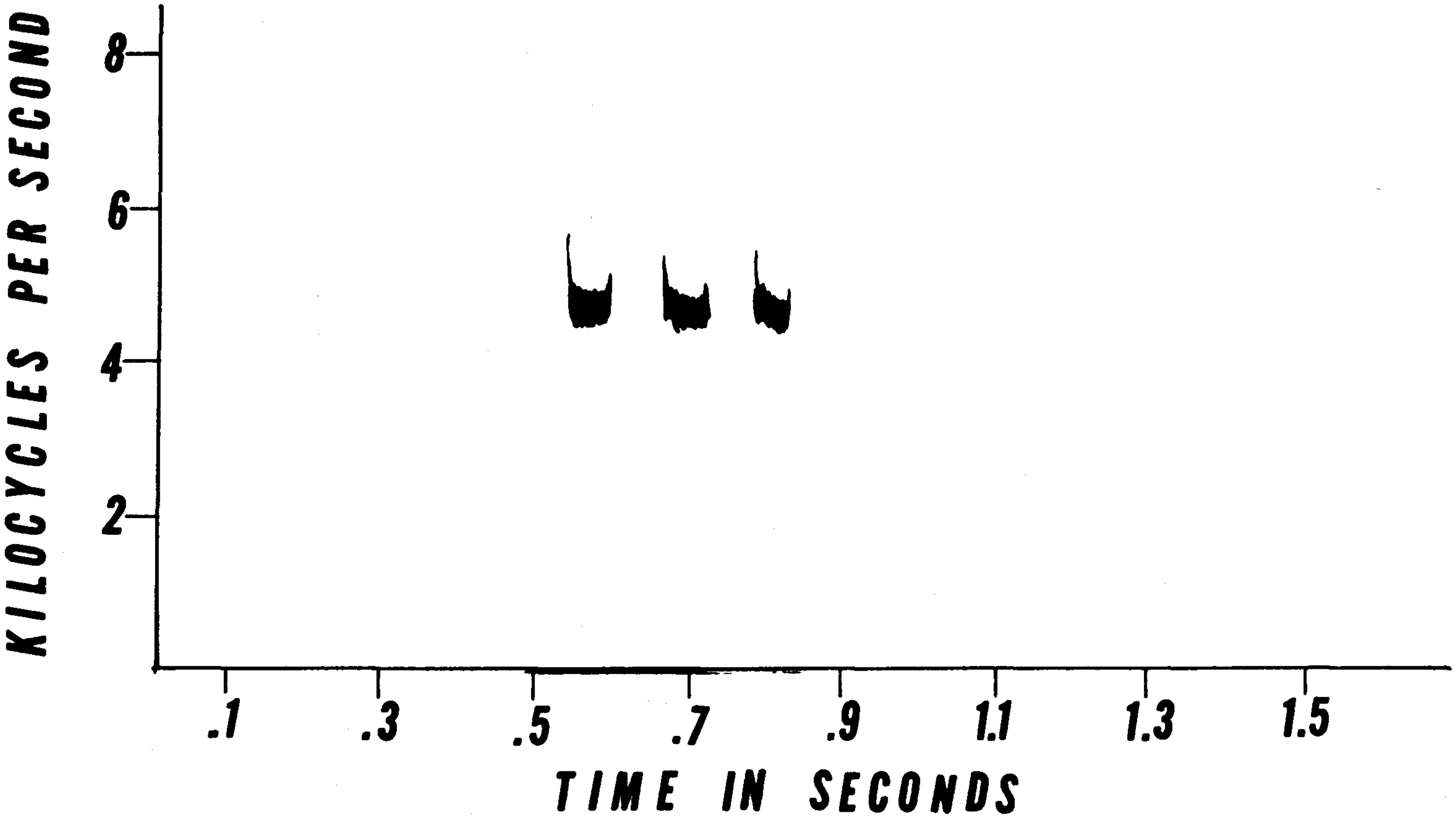



Figure 13. The chirp call given in alert to a hawk.

Reaction to predators on the ground

My conclusions on the reaction of ground squirrels to predators on the ground are based on observations of squirrels responding to humans, dogs, cats, weasels (Mustela frenata), mink(Mustela vison), badger (Taxidea taxus), and cattle.

The response of the squirrels to ground predators is generally the same as for raptors except for the calls given (Table 13). At the appearance of the predator the squirrels often adopted an upright posture, probably to see better through the tall grass. At some variable distance, which I shall discuss later, the squirrels began to give the churr call (Figure 14). They churred repeatedly, sometimes continuing long after the predator was gone. The squirrels did not escape down their burrows unless the predator approached to within 25 feet. The churr was not repeated or passed on by the other squirrels. The population response was to stand up, locate the predator, then call.

The distance between a squirrel and a predator at which the first churr call was given (Table 14) was affected by many factors such as the direction of the predator and how long it had been in the area. If the predator was merely wandering about, the squirrel was less alarmed than when the predator was charging directly toward him. If the predator had been in the area for an hour or so and there had been many churrs given, the squirrels began to ignore the alert and resume their other activities. However, when this did occur, they were extremely "jumpy" and would call and/or

Table 13. Response of Uinta ground squirrels to ground predators at various distances

| The response | Distance between squirrel and predator | | | |
|---|---|---|---|---|
| | 0-5' | 6-25' | 25-150' | over 150' |
| Churr with escape | 25% | 40% | 14% | 20% |
| No call, escape | 0% | 8% | 14% | 0% |
| Churr, no escape | 75% | 31% | 54% | 60% |
| Alert, orient to predator | 0% | 6% | 14% | 20% |
| Give chirp | 0% | 14% | 4% | 0% |
| Number of situations | 8 | 35 | 44 | 5 |

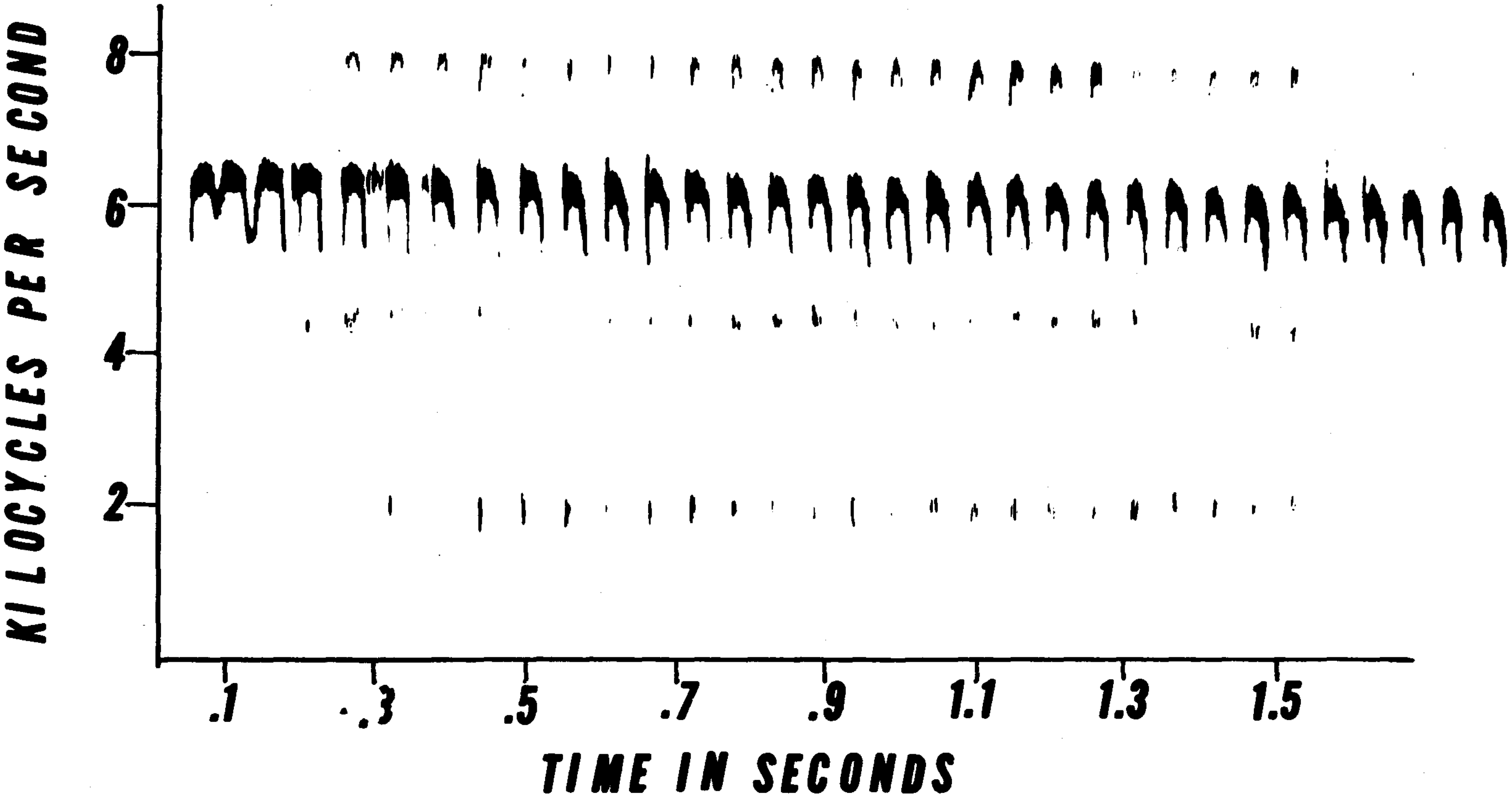



Figure 14. The churr call given in alert to a ground predator.

Table 14. Distance from ground predator when churr call was given (n=92)

| Distance | Percent of interactions |
|---|---|
| 0-5' | 11 |
| 6-25' | 41 |
| 26-150' | 43 |
| over 150' | 5 |

escape at any sudden movement or sound.

The response of ground squirrels to a weasel varied with the season. Early in the spring they churred at weasels but did not give chase. In May they churred and chased the weasels. Late in the summer the squirrels would ignore a weasel which was attacking a juvenile squirrel. The response of the squirrels may be linked with the female's maternal behavior. The squirrels that I saw attacking the weasel were females with young not yet aboveground. Late in the summer the young are capable of defending themselves against weasels; until then, they appear to be easy prey.

The response of ground squirrels to humans varied with the amount of exposure to them. Other populations of ground squirrels may have more or less contact with humans than the population at the Field Station. The response to humans of squirrels in those populations with less contact was the same response as to any ground predator. However, with continuous or repeated exposure to humans the response changed. The first change was that the distance between the human and the squirrel when the churr call was given decreased from 150-200 feet to less than 25 feet. As the squirrels became even more accustomed to humans they would escape when the predator was 15 to 25 feet away without calling. This demonstrated clearly the habituation of the squirrels to an alerting stimulus.

After observing the squirrels at close range without a blind for about 1 month, I noted a second change in their response to humans. When I was sitting quietly near some females they often would chirp at me. These chirps did not elicit alertness or escape in any of the other animals, so they did not appear to be an alert call. The cause and function appeared to be the same as a chirp used in interaction with conspecifics. The squirrels appeared to be threatening me as they would a conspecific who came too close.

I also observed the response to humans in a population which has more contact with humans than the population at the Field Station. This population was located on the lawns of the residences in Mammoth, Wyoming. The call these squirrels always gave in response to the approach of humans was the chirp. The residents there told me they had heard the churr given to coyotes. It appears, then, that habituation plays a part in determining whether an animal is treated as a conspecific or as a predator.

Reaction to snakes

The California ground squirrel (Citellus beecheyi) has a special response to rattlesnakes (Crotalus) (Linsdale, 1946). They wag their tails horizontally and bark, all within a few feet of the snake. Although rattlesnakes and gopher snakes (Pituophis catenifer) do prey on Uinta ground squirrels when their ranges overlap (A. Woodbury, personal communication), I have observed only one snake-squirrel interaction. The snake involved was about 3 feet long. The squirrel was about 3 feet from the snake and facing it through the grass. The squirrel gave no calls and remained motionless beside its hole. My approach frightened the snake away.

To ascertain the response of ground squirrels to snakes, I placed two ground squirrels in a pen about 20' x 30' and turned a large garter snake (Thamnophis ordinoides) loose in the pen. The squirrels gave no apparent response to the snake although they passed within several inches of it while trying to escape from the enclosure. Since putting the squirrels in an enclosure seemed to make them interested only in getting out and not in investigating strange objects, I put a gopher snake in a 10-gallon aquarium with a screen top and set the aquarium in an area where several squirrels were feeding. Three adults and three juveniles investigated the aquarium, some even putting their noses on the glass. No calls were given and no squirrels showed any fear of the snake, which was moving around.

If the interaction which I saw showed the typical response to a snake (freezing), I think the response would be highly adaptive since many snakes strike only at moving objects. Perhaps the reason why the Uinta ground squirrel does not have a stereotyped display to snakes is that it does not encounter snakes as often as the California ground squirrel. This may be comparable to the situation in the Northern elephant seal (Mirounga angustirostris) which has no alarm call, perhaps because it has had no terrestrial predators except man for thousands of years (Bartholomew and Collias, 1962). The Uinta ground squirrel may have had a response to the rattlesnake similar to that of the California ground squirrel, but there is no remnant of it now. It is more likely that there is a consistent long-term difference between the California and Uinta ground squirrels.

# DISCUSSION

## Unspecific Nature of Calls

All calls I have described which are used by the Uinta ground squirrels in aboveground interactions are associated with agonistic behavior. I know of no calls to attract the female to the male or young to the mother. There are no care-giving or care-soliciting calls. In the light of what has been discovered about sound communication in birds, the limited number of ground squirrel calls and their unspecific nature may seem unusual. The results are not unusual, however, considering the social organization, behavior, habitat, and particularly the reliance on the eyes and nose which characterize this animal. The Uinta ground squirrel is an intolerant animal that occurs at high densities up to 75 per acre. There is little interaction between mother and young aboveground. Pairing does not occur, as this species is promiscuous. While the squirrels are engaged in any activity, they constantly look up and around them. Unlike birds, ground squirrels depend on scent, as well as sight and sound, for information about their environment.

The unspecific nature of the calls is reflected in the use of the churr and chirp for both threat to conspecifics and alarm at the approach of predators. The reaction of the squirrels to the churr, for example, shows that they sometimes confuse the alarm and threat. They will sometimes become alert after hearing a threat churr during an encounter between two other squirrels or completely ignore a churr given in alert if it is not very loud. The typical response to the alert churr is a very general one. The squirrel stands up and looks around. This response is similar to that of many other rodents: Columbian ground squirrel (Citellus columbianus) (Manville, 1959); black-tailed prairie dog (King, 1955); and the California ground squirrel (Fitch, 1948). Other ground squirrels and rodents may use the same sounds for threat and alert: the mantled ground squirrel (Citellus lateralis) (Gordon, 1943), Columbian ground squirrel (Manville, 1959), the Norwegian lemming (Lemmus lemmus) (Arvola et al., 1962), the woodchuck (Marmota monax) (Anthony, 1962), and the yellow-bellied marmot (Marmota flaviventris) (Armitage, 1962).

Andrew (1964) states that different calls are evoked by stimuli different in intensity and contrast. Therefore, if the same call is evoked by two different stimuli, these stimuli must have the same amount of stimulus contrast. Therefore, a conspecific approaching to within 5 feet of a ground squirrel should, according to Andrew, have the same amount of stimulus contrast as a ground predator approaching to within 200 feet.

It is difficult to compare the results of my study with previous work on sound communication in mammals. Previous authors have described calls in terms of some common sound such as a whistle, trill, or chirp. It is impossible to determine how similar such sounds are to the sounds of Uinta ground squirrels. Further, the repertoire of a species' vocalizations based on a few observations may lead to error both in the number of vocalizations and their cause and function. Spectrograms of the same type of call given by the same individual look different depending on whether the animal is stationary or running or whether his mouth is empty or full of food. There are differences between individuals in the configuration and length of a call. The source of these differences is not apparent without a quantitative approach based on known individuals using the relatively objective technique of taping and graphing the sounds.

## Ease of Location of Calls

Marler (1956) has suggested that whether or not a sound conveys information about the location of the caller depends on the structure of the call. His criteria are as follows:

> . . . the most readily located notes should have a wide range of pitch, with many sudden changes in pitch, or with repeated breaks in the sound, all tending to encourage mainly vertical spectrograms. Notes located with difficulty will be the opposite, with a rather narrow range of pitch, not too low or too high, and without sudden changes in pitch, having therefore mainly horizontal spectrograms. (Marler, 1956, p. 254)

The chirp call (Figure 4) fits Marler's description of a readily located call. The churr call (Figure 6) has a rather narrow range of pitch, repeated breaks in the sound, many sudden changes in pitch, and decidedly horizontal spectrograms. This is a composite of the hard- and easy-to-locate types. The churr is readily located, probably because of its length and segmented nature.

A readily located call brings both advantages and disadvantages to the species. The advantage to the threat chirp is most obvious. This call is usually given after the respondent has approached too close to the caller or his area. The call would be valuable in pinpointing the exact position of the caller and its territory, especially if the interaction took place in an area where the vegetation was dense and sight communication failed. If the respondent learned the location of the caller's territory then he could avoid actual physical combat. One disadvantage would be the susceptibility of the caller to predators while chirping.

The advantage of the alert churr being readily located is in informing all members of the population of the approximate location of the predator in the area. I can see no particular advantage or disadvantage in advertising the location of a hawk by means of the alert chirp, since a soaring bird would be visible to all animals in the area. Likewise, I can see no particular advantage or disadvantage in indicating the position of the caller when the threat churr is given since the animals are usually less than 5 feet apart.

# CONCLUSIONS

I have been able to identify five major calls in the Uinta ground squirrel: chirp, churr, squeal, squawk, and teeth clatter. A growl is heard infrequently. In interaction with conspecifics the chirp, churr, and teeth clatter are elicited by the approach or attack of another animal. These calls function to stop the approach, and infrequently cause escape. The squeal and squawk are given on contact with a conspecific or member of another species. The growl appears to be used in threat.

The reaction to predators is one of alertness. The squirrels who first notice a predator on the ground or those in the path of a swooping raptor give the alert. A churr is given for predators on the ground and a chirp for airborne predators. The rest of the population responds to the alert call by looking around for the cause. Some animals which are far from their burrow entrances may run to their holes before looking around. The population response to the alert call is the same. The alert call is not immediately passed on. Other members of the population may give the alert when the predator gets close.

Sound communication in this species consists of a few calls which are highly unspecific in cause and function. They are neither received nor given in a stereotyped manner. An explanation for this may be found in the habitat and social behavior of the animal. The habitat is usually open grassy areas with good visibility. The animals rely on their eyes and nose more than birds do. The animals repeatedly stop and look about them while engaged in their daily activities. This keeps them aware of not only potential predators but also the activities of their neighbors. The reliance on visual and scent communication makes an elaborate sound communication system unnecessary.

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