5-1979

An Experimental Analysis of the Alarm Calls of Captive Uinta Ground Squirrels (*Spermophilus armatus*)

Marion Barch Cherry
Utah State University

AN EXPERIMENTAL ANALYSIS OF THE ALARM CALLS OF CAPTIVE UINTA GROUND SQUIRRELS *(SPERMOPHILUS ARMATUS)*

by

Marion Barch Cherry

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

of

MASTER OF SCIENCE

in

Wildlife Science

Utah State University
Logan, Utah

1979

ACKNOWLEDGEMENTS

I would like to extend a special thanks to Dr. David F. Balph for his assistance throughout this project. I would also like to thank Dr. Frederick F. Knowlton and Dr. James A. Gessaman for their constructive criticism and interest in this project.

I would like to express my appreciation to Dr. Carl D. Cheney of the Psychology Department for the loan of a red fox, Tanya, who was the predator in this research. Thanks also go to Dr. David L. Turner and Mary Veronica Kolesar of the Applied Statistics and Computer Science Department for their assistance in data analysis.

This project was supported in part by a Sigma Xi grant-in-aid for research.

I am indebted to friends who occasionally assisted in this study, especially Bruce C. Hastings, Deborah L. Mueller, Shirley S. Badame, Sandra W. Knight, Lynn A. Maguire, and Mary Sue Fisher.

Had it not been for the assistance and encouragement of my family, this project would never have been completed. Special thanks go to my parents, Mary and William Barch, and my grandparents, Mary and Ernest Carter. Thanks also go to my husband, Steve, for his unfailing support throughout my thesis program.

Marion B. Cherry

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

An Experimental Analysis of the Alarm Calls of Captive

Uinta Ground Squirrels *(Spermophilus armatus)*

by

Marion Barch Cherry, Master of Science

Utah State University, 1979

Major Professor: Dr. David F. Balph
Department: Wildlife Science

This study investigated alarm calls given by Uinta ground squirrels *(Spermophilus armatus)* in the presence of a ground predator. I observed predator responses of 18 groups of three to four squirrels each for an average of three trials apiece. My objectives were: (1) to describe prey-predator interactions resulting in alarm calls, and (2) to test the following hypotheses:

1. Each Uinta ground squirrel (by sex and age) has an equal probability of giving an alarm call at any time of the season.
2. All Uinta ground squirrels are equally likely to call regardless of their distance to a burrow, closest conspecific, and the predator.
3. Alarm calls are as likely to occur in the search stage of predation as in the pursuit stage.
4. Callers and noncallers are equally vulnerable to predation.

I found that: (1) each Uinta ground squirrel (by sex and age) in the experimental population had an equal probability of giving an alarm call in the presence of a predator through the season, (2) callers and noncallers were equally close to burrows at the time of the call, (3) the caller was typically located farther away from its closest conspecific than noncallers at the time of the call, (4) the caller was significantly closer to the predator than were noncallers at the time of the call, (5) alarm calls occurred significantly more often in the pursuit stage of predation than in the search stage, and (6) noncallers suffered significantly more predation than did callers.

There appeared to be little risk and energetic cost associated with calling. Squirrels that called usually were being pursued by the predator and were very close to a burrow when they called. The callers had little to lose and could increase their inclusive fitness by warning relatives of the presence of danger.

This study dealt only with responses to ground predators. Squirrels are likely to respond differently to avian predators. It is suggested that responses of animals to avian and terrestrial predators should vary with the potential threat that the predator poses.

The apparent inhibition of secondary calls is discussed. Once animals are aware of the presence of danger, there is no need for another animal to repeat the message and reveal its location to the predator.

(36 pages)

INTRODUCTION

Alarm calls often warn other animals of danger and therefore have been discussed in terms of altruism. The findings of Sherman (1977) and Dunford (1977) on ground squirrels indicate that alarm calls may function to assist relatives, while Charnov and Krebs (1975) suggest that alarm calls may have evolved through direct individual selection.

A few studies have dealt extensively with alarm calls, but most observations on alarm calls have been made in the course of other studies. Recent research in the literature primarily discusses the sex, age, and reproductive status of callers versus noncallers (Dunford 1977, Sherman 1977).

A major reason for the lack of quantitative information on alarm calls is that observations of prey-predator interactions are rare. More information is necessary to determine causes and functions of alarm calls. Data are needed regarding the caller and noncaller relationships in space to important environmental parameters such as cover, the predator, and the closest conspecific. An animal's location in the environment may determine whether or not that animal will give an alarm call when it perceives a predator. The stage of predation (i.e. search, pursuit) may influence the likelihood of an animal to give an alarm call.

This study on alarm calls was conducted in an experimental situation to facilitate observation of predation situations and manipulation of numbers, age, and sex of the prey population. The

Uinta ground squirrel *(Spermophilus armatus)* was chosen as the study animal because its general biology is well understood (Balph and Stokes 1963, Burns 1968, Slade and Balph 1974, Paul 1977), and because work has been conducted on its vocalizations (Balph and Balph 1968).

My objectives were: (1) to describe prey-predator interactions resulting in alarm calls, and (2) to test the following hypotheses:

1. Each Uinta ground squirrel (by sex and age) has an equal probability of giving an alarm call at any time of the season.
2. All Uinta ground squirrels are equally likely to call regardless of their distance to a burrow, closest conspecific, and the predator.
3. Alarm calls are as likely to occur in the search stage of predation as in the pursuit stage.
4. Callers and noncallers are equally vulnerable to predation.

METHODS

Uinta ground squirrels were taken from the Utah State University Forestry Field Station (USUFFS), located approximately 35 km east of Logan, Utah. The mean elevation at this site is 1921 m, and the general habitat is open lawn surrounded by sagebrush *(Artemesia tridentata)* and aspen *(Populus tremuloides)*. Terrestrial predators of the squirrels in this area include domestic and feral dogs *(Canis familiaris)*, coyotes *(Canis latrans)*, weasels *(Mustela frenata)*, badgers *(Taxidea taxus)*, and humans.

Squirrels were trapped for experimentation approximately every 5 to 7 days from 22 April to 3 August 1978. Captured squirrels were transported to the Green Canyon Ecology Research Station in North Logan, Utah, where they were toe-clipped for permanent identification and dyed for temporary individual identification. Squirrels were then placed in an outdoor experimental pen (approximately 10 m x 10 m) which had solid side walls and a chickenwire top. The bottom of the pen was covered with chickenwire and a layer of earth. The pen included brush, logs, and rocks, simulating natural cover, and six 50 cm x 5.1 cm artificial burrows constructed of ABS pipe (Fig. 1). The observation point was located on the outside of the north side of the pen, and the predator entrance was located on the center of the west side of the pen.

Each group of squirrels was given 24 to 48 hours to habituate to

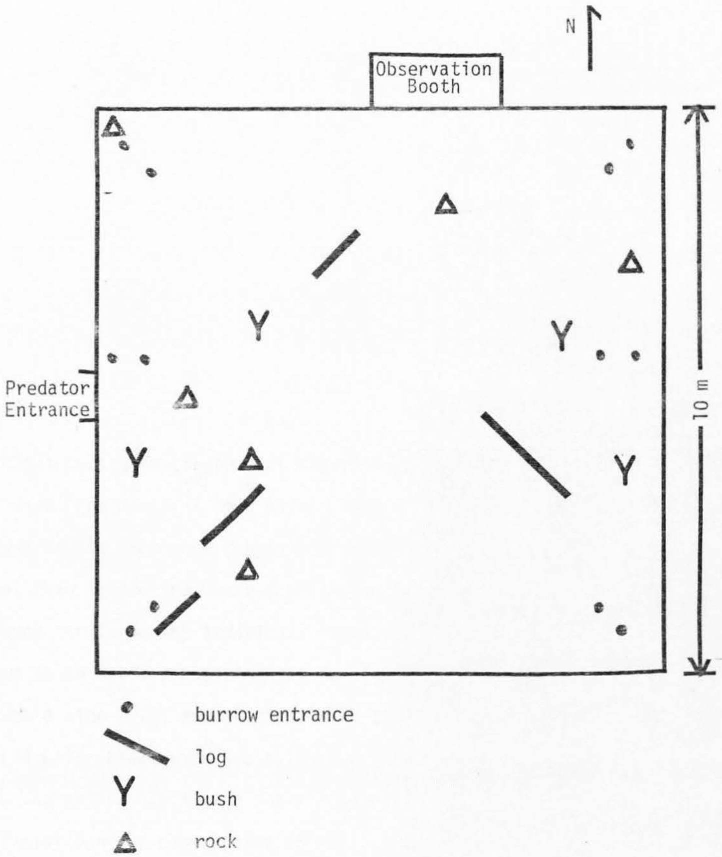

Figure 1. Experimental pen located at the Green Canyon Ecology Research Station, North Logan, Utah.

the experimental arena. During this period squirrel exploratory behavior decreased and normal feeding behavior resumed.

A red fox *(Vulpes fulva)* was used to elicit squirrel alarm calls. The animal was born in captivity and was relatively tractable.

A total of 18 different groups of squirrels was used. Each group was initially composed of four squirrels (two males and two females), except for groups 17 (two males, one female) and 18 (three females). Each group went through three trials, except for groups 4 and 11 which experienced two and four trials respectively. A total of 54 trials were conducted. Squirrels that survived the trials were returned to the approximate site of their capture, and no squirrels were members of more than one group. A total of 69 individual squirrels were used in the research.

Trials commenced when the fox entered the pen and ended either when the fox captured a squirrel or when the first chase of a squirrel ended. For each trial, data were collected on the following parameters: (1) group number; (2) trial number; (3) numbers of squirrels present at the time of the trial; (4) initial caller number; (5) sex and age of initial caller; estimated distance (to the nearest 0.1 m) from callers and noncallers to (6) closest conspecific, (7) a burrow, and (8) the predator at the time of the call; (9) predation stage at the time of the call; (10) whether the caller was moving or stationary when it called; (11) whether or not there were other callers; (12) whether or not any squirrel(s) were killed, and if so, sex and age of the squirrel(s).

RESULTS

Description of Squirrel-Fox Interactions

A trial commenced when I opened a connecting door between the predator and squirrel pens. The time it took for the fox to enter the squirrel pen varied from trial to trial. Squirrels that were above ground at the time of the predator's entry usually oriented toward the fox and then became motionless (Fig. 2). The fox meandered about the perimeter of the pen until it appeared to me to perceive a squirrel. The squirrel often remained motionless until the fox was very close before running to the nearest burrow. The escaping squirrel usually was the animal that gave the alarm call [the churr call (Balph and Balph 1966), a vocalization often given by a Uinta ground squirrel perceiving a ground predator]. The squirrel was almost always in motion and very close to a burrow entrance when it called.

Sometimes the fox walked around the burrows and occasionally stopped near one of them. If the fox sensed a squirrel in a burrow, it dug around the entrance and often uncovered the plastic burrow. In this situation, the squirrel in the burrow usually called only after the fox began to dig. Other squirrels present in the pen made no observable responses to the alarm calls, but many of them had apparently perceived the predator by the time an initial alarm call was given.

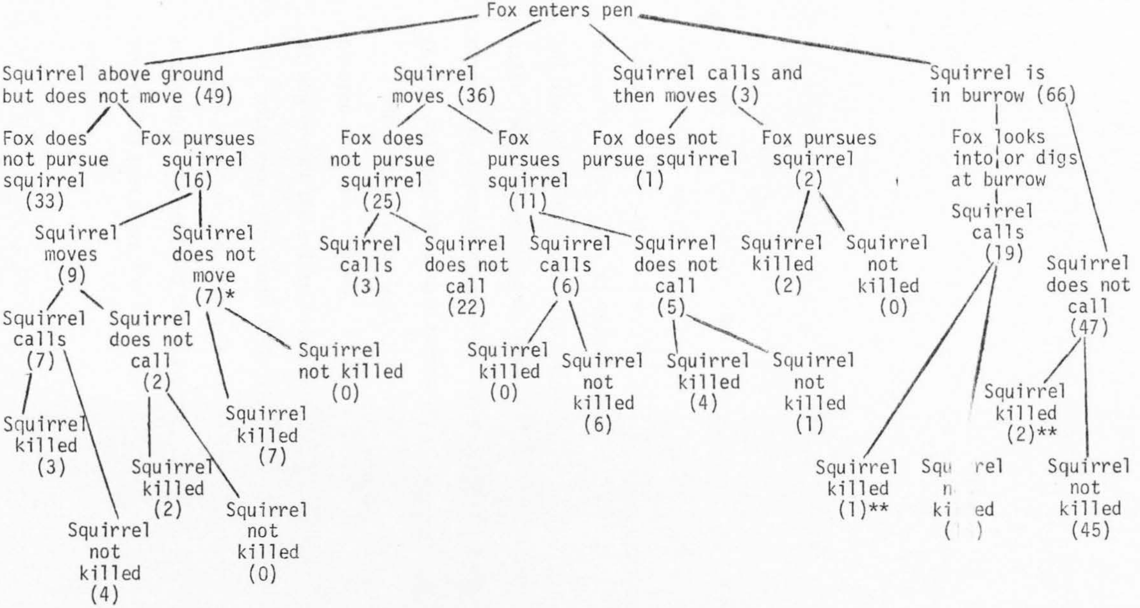

Figure 2. Squirrel-fox interactions during trials. Numbers in parentheses refer to frequencies of behaviors of 154 squirrels on 50 trials.

* Squirrels were in a semi-torpid state and could not respond.

** Squirrels killed were not completely inside burrows because burrows were already occupied.

Tests of Hypotheses

The first hypothesis considered was that each Uinta ground squirrel (by sex and age) had an equal probability of giving an alarm call in the presence of the predator throughout the season. For this analysis, expected values were computed by assuming that animals called in direct proportion to the number of times they were present when a predator appeared. The data analysis indicated no significant difference between initial alarm callers by sex and age and what was expected by chance ($P > 0.20$, $df = 3$, $\chi^2 = 2.01$, Table 1, Fig. 3). There was also no significant difference between callers by sex and age and sexes and ages of pursued squirrels ($P > 0.20$, $df = 3$, $\chi^2 = 2.03$). Nor was there a significant difference between the first and second halves of the season ($P > 0.20$, $df = 3$, $\chi^2 = 1.30$ for sex, $\chi^2 = 1.32$ for age, Fig. 4, 5).

The second hypothesis considered was that all squirrels were equally likely to call regardless of their distance to (1) a burrow, (2) closest conspecific, and (3) the predator. For this analysis the STATPAC/BMDO8V Analysis of Variance program was used on the eight groups of squirrels in which alarm calls occurred on all three trials (to meet the assumptions of the statistical test).

The mean distance from the caller to the closest burrow at the time of the call was 0.3 m (SD = 0.6 m), and the average distance for noncallers was 0.4 m (SD = 0.5 m) (Table 2, p. 13). There was no significant difference between the distance from the caller to a burrow and the average distance of noncallers to a burrow at the time of the call ($P > 0.20$, $df = 1,7$, $F = 0.54$).

Table 1. Initial alarm callers by sex and age on 43 trials in which alarm calls occurred.

Sex and Age of Caller	Number of Possible Callers	Number of Expected Callers	Number of Observed Callers
Adult Male	43	10.9	9
Adult Female	46	11.6	9
Juvenile Male	43	10.9	11
Juvenile Female	38	9.6	14
All Males	86	21.7	20
All Females	84	21.3	23
All Adults	89	22.5	18
All Juveniles	81	20.5	25
TOTAL	170		43 ? 129

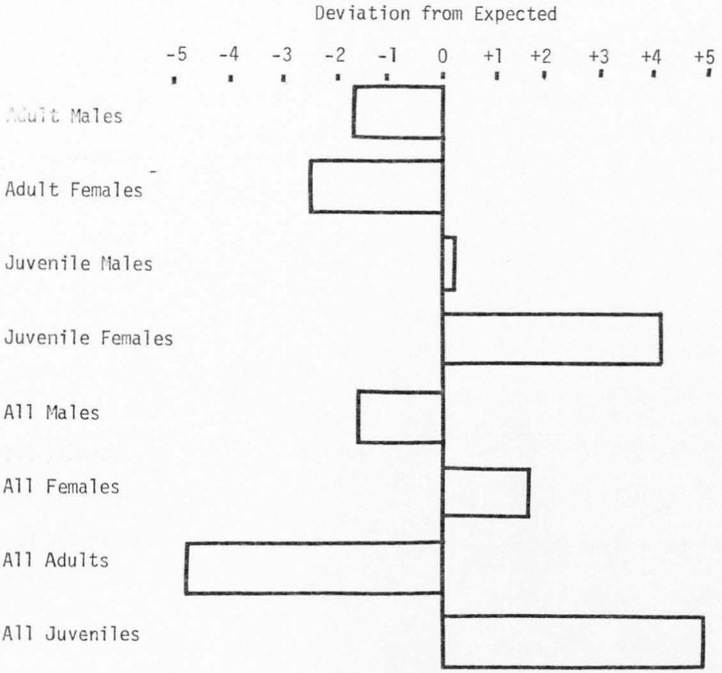

Figure 3. Initial alarm callers by sex and age on 43 trials in which call occurred.

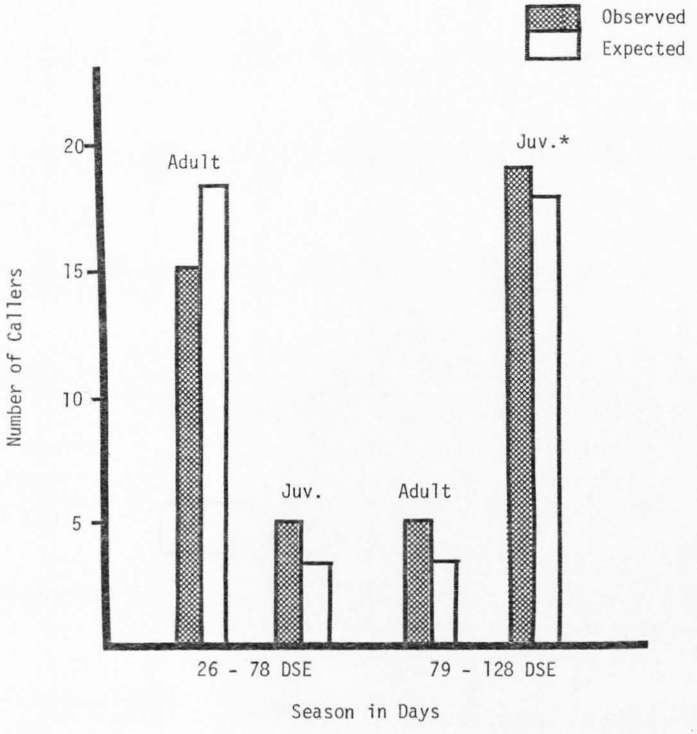

Figure 4. Observed and expected initial callers by age through the season. (DSE = days since emergence from hibernation.)

* The increase in juveniles relative to adults in the last half of the season was caused by a shift in the relative availability of the two age classes.

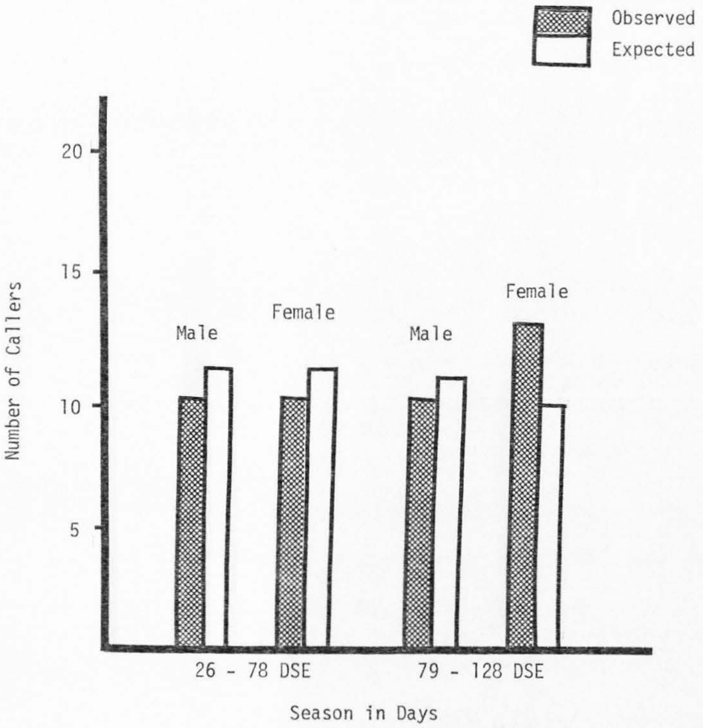

Figure 5. Observed and expected initial callers by sex through the season. (DSE = days since emergence from hibernation.)

Table 2. Distances (m) from callers and noncallers to (1) a burrow, (2) closest conspecific, and (3) the predator at the time of the call for the eight groups in which calls occurred on all three trials (N = 24).

	Burrow			Conspecific			Predator		
	$\bar{x}$	SD	Sig.	$\bar{x}$	SD	Sig.	$\bar{x}$	SD	Sig.
Callers	0.3	0.6	ns	5.4	2.9	0.01	1.4	2.2	0.001
Noncallers	0.4	0.5		4.3	2.3		6.2	3.1	

The distances from callers and noncallers to environmental parameters for all groups and trials are also presented (Table 3).

The mean distance from the caller to the closest conspecific at the time of the call was 5.4 m (SD = 2.0 m), and the average distance for noncallers was 4.3 m (SD = 2.3 m). There was a significant difference ($P < 0.05$) between the distance from the callers to their closest conspecific and the average distance from noncallers to their closest conspecific at the time of the call; noncallers were closer to their nearest conspecific than were callers ($P < 0.01$, df = 1,7, F = 15.71).

The mean distances from the callers and noncallers to the predator at the time of the call were 1.4 m (SD = 2.2 m) and 6.2 m (SD = 3.1 m), respectively. There was a highly significant difference ($P < 0.005$) between distance from the caller to the predator at the time of the call and the average distance from noncallers to the predator at the time of the call; callers were closer to the predator than were noncallers ($P < 0.001$, df = 1,7, F = 39.94).

The median test was used to determine if the median distances from callers and noncallers to the three environmental parameters were significantly different between the sample of eight groups and all trials. It was found that these two samples did not differ significantly from each other ($P < 0.20$, df = 1, $\chi^2 < 1.0$ for all parameters). Thus, both of these samples were taken from a population with the same median.

The third hypothesis was that alarm calls were equally likely to occur in either the search or pursuit stages of predation. On trials in which alarm calls occurred, the initial alarm call was given in

Table 3. Distances (m) from callers and noncallers to (1) a burrow, (2) closest conspecific, and (3) the predator at the time of the call for all groups and trials.

	Burrow			Conspecific			Predator		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
Callers	0.2	0.4	42	5.1	2.8	41	1.1	1.8	43
Noncallers	0.3	0.5	41	4.8	2.3	41	6.4	2.8	41

35 (81 %) of the trials while the predator was in pursuit (the predator had perceived and was rapidly approaching the prey) of the animal that called, and in 7 (16 %) of the trials the initial alarm call occurred while the predator was in the search phase (the predator had apparently not yet perceived the prey) of predation. On one trial (3 %) a squirrel called after the predator had already caught another squirrel. The Fisher's exact test for independence (Sokal and Rohlf 1969) was used to test the above hypothesis. The null hypothesis, that alarm call occurrence was independent of the stage of predation, was rejected ($P < 0.001$).

A fourth hypothesis was that animals that gave alarm calls and those that did not call were equally vulnerable to predation. An analysis was conducted on squirrels that both moved and were pursued. Of these squirrels 13 of 20 called, and only 3 of the callers were killed while 6 of the 7 noncallers were killed. The Fisher's exact test for independence was used and revealed that noncallers were significantly more vulnerable to predation than were callers ($P < 0.05$).

DISCUSSION

Most biologists assume that alarm calls serve some beneficial function. Disagreements arise concerning who gains from these calls. There seem to be four possible beneficiaries: (1) self, (2) self and predator, (3) nonrelatives, or (4) relatives. In this section I shall relate my findings to each of these possibilities.

Self Benefit

Alarm calls may divert the attention of the predator to other prey (Charnov and Krebs 1975). Charnov and Krebs (1975) hypothesized that the caller's chances for survival are greater than its flockmates, because the caller knows both that there is a predator and the location of the predator, whereas those hearing the call merely know that there is a predator. They suggest that animals that hear the call may react in such a way as to be detected by the predator.

In this study, noncallers suffered significantly more predation than callers. Animals that heard a call usually remained motionless, and animals that called usually called only after the predator had located them and began pursuit. Callers were generally in safe locations when they called. If callers manipulate their conspecifics by calling, responses to calls that lead to predation would be selected against.

Turner (1973) found that Belding's ground squirrels *(Spermophilus beldingi)* hearing a call reacted in the same manner as those that gave the alarm call. These squirrels did not suffer a higher rate of predation.

If an animal does not call until it is in a relatively safe location, its own chances for survival are high. Why should this animal call at all since it may draw the attention of a predator to the area or species?

Benefit to Self and Predator

Smythe (1970) suggested that it may be to the prey's advantage to let a predator know that it has been perceived, but only when the prey has an excellent chance to escape the predator. This behavior would minimize the amount of time the animal must spend in predator surveillance and not involved in normal activities. Whether or not this tactic works depends upon the type of habitat in which the animals live and the hunting strategies of the predator (Hirth and McCullough 1977), and would be most likely to occur only in open situations where predators cannot successfully ambush prey.

There was no evidence in this study that alarm calls reduced the likelihood of predator attack. Alarm calls occurred late in the predation sequence, and did not deter the predator. Sherman (1977) had similar findings for Belding's ground squirrels. If the calls occurred when the predator was some distance away, and the prey had good visual coverage of their habitat, alarm calls might deter the predator. If an alarm call is reinforcing to a predator in search of food, however, calling may attract a predator. The alarm call becomes associated with the probability of receiving food reinforcement.

Benefit to Nonrelatives

Animals may warn others who are likely to return that favor in the future. Reciprocal altruism would require that the animals associate with one another long enough to exchange risks (if there is a risk involved in calling) (Trivers 1971). As emphasized by Rohwer et al. (1976), cheaters are likely to have an advantage if there is a risk involved in the act of calling. These nonreciprocaters must be recognized and penalized or they will become predominant in the population.

Most populations of animals are composed of at least some genetically related individuals, and therefore it is difficult to distinguish between reciprocal altruism and kin selection. Certainly the two factors were confounded in the present study.

Benefit to Relatives

Callers may increase their inclusive fitness by consistently warning relatives of danger at some risk to themselves (Hamilton 1963, Maynard Smith 1965). Risk to the caller may not be a necessary assumption for the evolution of alarm calls through kin selection (Harvey and Greenwood 1978).

In Uinta ground squirrels, males tend to disperse while females remain near their natal burrows (Walker 1968), therefore, one might expect females to give alarm calls proportionately more often than males (because females have more relatives nearby) if kin selection operates on the evolution of these calls. This study revealed no significant differences between callers and noncallers by sex and age throughout the season although all squirrels were taken from the same population. The predator generally pursued the first animal that it perceived, with the sex and age of that animal being a matter of chance. The call was usually given by a moving squirrel that was being closely pursued by the predator. These results may be due to the fact that the predator appeared suddenly in close proximity to the squirrels because of the size of the experimental arena.

Some other *Spermophilus* species have a population biology similar to that of the Uinta ground squirrel with males dispersing more than females (Dunford 1977, Sherman 1977). These squirrels have promiscuous mating systems so that male genetic relationships are less certain than female genetic relationships. Adult females called significantly more often than adult males in round-tailed ground squirrels *(Spermophilus teriticaudus)* (Dunford 1977). Sherman (1977) found that reproductively active female Belding's ground squirrels with living kin called more than reproductively active females without living kin, and these females called more than nonreproductively active females. Males were the most consistent noncallers. Females with living kin called whether or not those kin were present when the predator appeared. Transient squirrels called less than expected (Carl 1971, Sherman 1977). Similar findings have been reported in others species that have audible responses to predators (Barash 1975, Hirth and McCullough 1977, Tenaza and Tilson 1977). Researchers concluded that the probability of an animal giving an alarm call in the presence of a predator is greatest when neighbors are closely related (Dunford 1977, Hirth and McCullough 1977, Sherman 1977, Tenaza and Tilson 1977).

Several other results of my research have implications for the kin selection hypothesis in the evolution of alarm calls. A significant difference was found between the distance from callers to their closest conspecific and the average distance from noncallers to their closest conspecific with callers being farther from their nearest neighbor at the time of the call. The more isolated the squirrel, the more likely it was to call.

An isolated animal is slower to perceive danger than a group of animals (Lazarus 1972, Pulliam 1973, Siegfried and Underhill 1975) and may not freeze as quickly in the presence of a predator as animals in a group. This single animal is more likely to continue with its activities after a group of animals has already perceived danger and reacted. The movement of the single animal may draw the attention of the predator. Since a single animal is more likely to be pursued by the predator, it is more likely to call than a member of a group.

This study showed no significant difference between distance from callers to a burrow and the average distance from noncallers to burrows. However, all squirrels were very close to burrows when calls were given. The mean distance for both callers and noncallers was less than 0.5 m from a burrow. Other researchers (Barash 1975, Dunford 1977, Hirth and McCullough 1977, Sherman 1977) noted that callers were usually in safe locations when they called. If the caller is in a relatively safe place when it calls, the actual risk to the caller is slight while it may increase its inclusive fitness by warning relatives.

There was no significant risk associated with calling in this study. Callers suffered less predation than noncallers. It should be noted that alarm calls of Uinta ground squirrels are probably localizable by predators due to the call characteristics (Balph and Balph 1966) and the hearing ability of red foxes (Isley and Gysel 1975). Sherman (1977) also found no significant risk involved for the caller.

Hamilton (1963) theorized that if the risk is slight or the average neighbor is closely related, alarm call behavior will become prevalent in a population. Since studies have revealed no significant risk involved for the animal giving the call (Barash 1975, Dunford 1977, Sherman 1977, this study) then calling should evolve through kin selection as it would increase the caller's inclusive fitness. In situations in which callers have been vulnerable to predation, alarm calls have evolved that are difficult for a predator to locate (Marler 1955, 1957).

The only cost known to exist for the caller is the actual energetic cost of giving the call. This cost is slight in comparison with the possible benefits that the caller may gain in terms of increasing its fitness by warning relatives of danger.

There are some questions that remain to be answered. How does an animal know when its kin are nearby? Is familiarity with neighbors a more important determinant of whether or not an individual will call than genetic relatedness? Is benefit to kin an artifact of an act which would occur whether or not kin are present? If kin selection is operating on the evolution of alarm call behavior in squirrels, why do not males, who are successful breeders, call? Further research with populations of known relatedness is needed to answer these questions.

Avian versus Ground Predation

This study dealt only with ground predation. Animals are likely to respond differently to an avian predator.

The Uinta ground squirrel "chirp" and "churr" calls given in response to predators also occur in intraspecific agonistic encounters (Balph and Balph 1966). The generalized response of Uinta ground squirrels to either call is alertness (Fig. 6). Squirrels hearing a call orient toward the caller, thus obtaining further information on the elicitor of the call. Some researchers suggest that characteristics of squirrel calls may indicate what elicited the calls (Leger and Owings 1978). Once the elicitor of the call is perceived, then a squirrel may react. If another squirrel elicited the call, those hearing the call may continue with their previous activities.

If a predator elicited the call, then squirrel responses vary with the potential threat that the predator poses (Table 4). "Chirp" calls are emitted in the presence of an aerial predator. Raptors are capable of rapid attack, and alarm calls generally occur when the raptor is a considerable distance away from the caller (45 - 50 m). "Churr" calls are given in the presence of a ground predator which is usually not a threat unless it is relatively near the colony (Balph and Balph 1966).

Before the predator has been located by squirrels hearing an alarm call, these squirrels tend to remain motionless or move to nearby cover. If the predator has been perceived at a considerable distance from the squirrels, the squirrels will probably move to a secure location. However, if the predator is very near, prey probably freeze

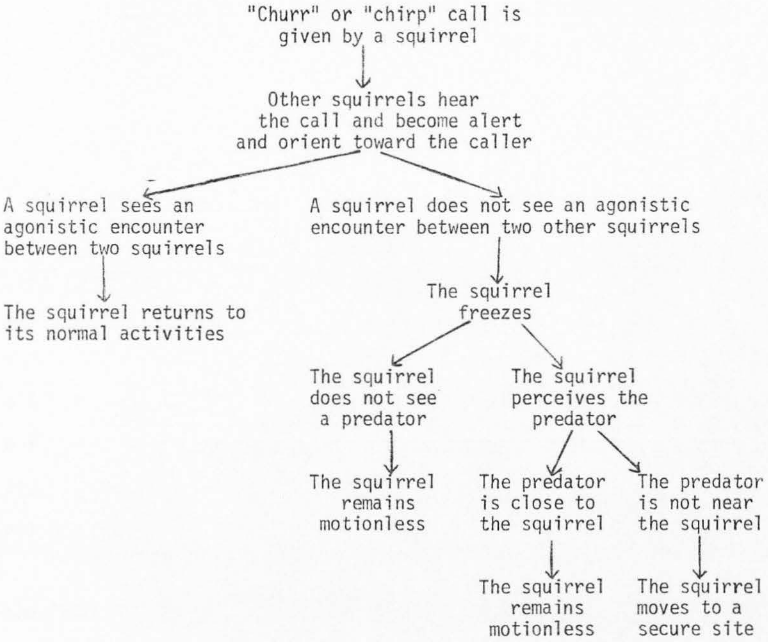

Figure 6. Reactions of Uinta ground squirrels to an alarm call.

Table 4. Responses of Uinta ground squirrels to avian and ground predators.

Relative Distance from the Squirrel to the Predator	Uinta Ground Squirrel Responses to a Large Aerial Predator	Uinta Ground Squirrel Responses to a Ground Predator
Near	"Chirp" call is given by one to two squirrels who perceive the predator and are close to cover, the call is repeated until the raptor leaves, those hearing the call may become alert and some may move to cover if they are close to cover	Animals perceiving the predator freeze, "churr" given usually only if squirrel is perceived and pursued by the predator, squirrels hearing the call that had not perceived the predator become alert and may move to cover
Far (moving toward squirrels)	No audible response, some animals perceiving the predator become alert	Usually one squirrel gives the "churr" call, other squirrels may become alert and move to safety
Far (not moving toward squirrels)	No call is given, squirrels may become alert briefly	No callis given, squirrels may become alert briefly

unless they are very close to cover. The predator response system of squirrels may be refined so that squirrels respond slightly differently depending upon the species of predator and its method of hunting as suggested by Turner (1973).

Calling Inhibition

In some species that give alarm calls in the presence of a predator, usually only one or a few individuals in the population call (Balph and Balph 1966, Sherman 1977, this study). It seems that there may be an inhibitory mechanism operating on animals that hear an alarm call which keeps them from giving a second call.

Once animals are aware of the presence of danger, there is no need for another animal to repeat the message and reveal its location to the predator. It would not be adaptive for an animal to call unless it is in a relatively safe location and/or it is already being pursued by the predator. In this study, calls seemed to occur only when the caller risked little and could gain by warning others of danger.

LITERATURE CITED

Balph, D. M. and D. F. Balph. 1966. Sound communication of Uinta ground squirrels. J. Mammal. 47(3):440-450.

Balph, D. F. and A. W. Stokes. 1963. On the ethology of a population of Uinta-ground squirrels. Amer. Midl. Natur. 69(1):106-126.

Barash, D. P. 1975. Marmot alarm-calling and the question of altruistic behavior. Amer. Midl. Natur. 94(2):468-470.

Burns, R. J. 1968. The role of agonistic behavior in regulation of density in Uinta ground squirrels *(Citellus armatus)*. M.S. Thesis, Utah State University. 50 pp.

Carl, E. A. 1971. Population control in arctic ground squirrels. Ecology 52(3):395-413.

Charnov, E. L. and J. R. Krebs. 1975. The evolution of alarm calls: altruism or manipulation? Amer. Natur. 109(965):107-112.

Dunford, C. 1977. Kin selection for ground squirrel alarm calls. Amer. Natur. 111(980):782-785.

Hamilton, W. D. 1963. The evolution of altruistic behavior. Amer. Natur. 47(896):354-356.

Harvey, P. H. and P. J. Greenwood. 1978. Anti-predator defence strategies: some evolutionary problems. pp. 129-151 in J. R. Krebs and N. B. Davies (eds.). Behavioural ecology: an evolutionary approach. Sinauer Associates, Inc., Sunderland, Massachusetts. 494 pp.

Hirth, D. H. and D. R. McCullough. 1977. Evolution of alarm signals in ungulates with special reference to white-tailed deer. Amer. Natur. 111(977):31-42.

Isley, T. E. and L. W. Gysel. 1975. Sound-source localization by the red fox. J. Mammal. 56(2):397-404.

Lazarus, J. 1972. Natural selection and the functions of flocking in birds: a reply to Murton. Ibis 114(4):556-558.

Leger, D. W. and D. H. Owings. 1978. Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. Behav. Ecolo. Sociobiol. 3:177-186.

Marler, P. 1955. Characteristics of some animal calls. Nature 176 (4470):6-8.

Marler, P. 1957. Specific distinctiveness in the communication signals of birds. Behaviour 11:13-39.

Maynard Smith, J. 1965. The evolution of alarm calls. Amer. Natur. 99(904):59-63.

Paul, R. T. 1977. Social behavior and social organization in an unconfined population of Uinta ground squirrels. M.S. Thesis, Utah State University. 75 pp.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings *(Sturnus vulgaris)* in relation to predation and foraging. Anim. Behav. 22(2):501-505.

Pulliam, H. R. 1973. On the advantages of flocking. J. Theor. Biol. 38(2):419-422.

Rohwer, S., S. D. Fretwell and R. C. Tuckfield. 1976. Distress screams as a measure of kinship in birds. Amer. Midl. Natur. 96(2):418-430.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. Science 197(4310):1246-1253.

Siegfried, W. R. and L. G. Underhill. 1975. Flocking as an anti-predator strategy in doves. Anim. Behav. 23:504-508.

Slade, N. A. and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology 55(5):989-1003.

Smythe, N. 1970. On the existence of "pursuit invitation" signals in mammals. Amer. Natur. 104(939):491-494.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco, Calif. 776 pp.

Tenaza, R. R. and R. L. Tilson. 1977. Evolution of long-distance alarm calls in Kloss's gibbon. Nature 268(5617):233-235.

Trivers, R. L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46(1):35-57.

Turner, L. W. 1973. Vocal and escape responses of *(Spermophilus beldingi)* to predators. J. Mammal. 54(4):990-993.

Walker, R. E. 1968. Local distribution in a population of Uinta ground squirrels. Ph.D. Thesis, Utah State University. 71 pp.

VITA

Marion Barch Cherry

Candidate for the Degree of

Master of Science

Thesis: An Experimental Analysis of the Alarm Calls of Captive Uinta Ground Squirrels *(Spermophilus armatus)*

Major Field: Wildlife Science

Biographical Information:

Personal Data: Born in Allentown, Pennsylvania, December 7, 1951, daughter of William T. and Mary C. Barch; married John Steven Cherry August 19, 1972.

Education: Attended elementary and secondary school in Allentown, Pennsylvania, graduated from Louis E. Dieruff High School in 1969; received A.B. degree from Catawba College, Salisbury, North Carolina with a major in Psychology in 1973; 1979 completed requirements for M.S. degree at Utah State University with a major in Wildlife Science.

Professional Experience: 1978-79, Student Assistant on Natural History Project at Utah State University; 1978 Teaching Assistant in the Department of Wildlife Science and Utah State University; 1977-78, Research Assistant in the Department of Wildlife Science at Utah State University; 1976-77 Teaching Assistant in the Department of Wildlife Science at Utah State University.