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# ANTIPREDATOR BEHAVIOUR IN THE COLUMBIAN GROUND SQUIRREL, *Spermophilus columbianus*: VIGILANCE, ALARM CALLING AND ESCAPE RESPONSES

by

ROBERT BRUCE MACWHIRTER ©

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS
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(SIGNED) R. Bruce McWhirter

PERMANENT ADDRESS:

3 Boulderwood Road
Halifax, Nova Scotia
B3P 2J3 Canada

DATED 8 September, '89

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ANTIPREDATOR BEHAVIOUR IN THE COLUMBIAN GROUND SQUIRREL, *Spermophilus columbianus*: VIGILANCE, ALARM CALLING AND ESCAPE RESPONSES submitted by ROBERT BRUCE MACWHIRTER in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

Jan. O Murie
Supervisor

Linda Marie Fedigan

Date 8 September, 1989

# Abstract

Several aspects of antipredator behaviour in Columbian ground squirrels were studied at two colonies in southwestern Alberta during spring and summer of 1987 and 1988. I examined the effects of several variables on vigilance and the distance from burrows at which ground squirrels foraged. I also quantified ground squirrel antipredator calling behaviour and escape responses to simulated aerial (flying disc) and terrestrial (stuffed badger) predator attacks. As well, I compared the activity and foraging behaviour of parous and nonparous adult females to test the hypothesis that the energetic demand of reproduction results in exposure to a greater risk of predation for parous females.

Environmental variables that were significant predictors of time spent vigilant differed somewhat between colonies and among age classes. In general, ground squirrels reduced their vigilance and spent more time feeding with the head down when foraging among conspecifics. At Dyson Creek, an area surrounded by forest, ground squirrels increased their vigilance when foraging in close proximity to the forest edge. At Meadow "B", an "open" habitat, ground squirrels increased their vigilance when foraging in areas providing relatively poor visibility for the detection of predators. Ground squirrels decreased their vigilance when foraging farther from burrows. There was a seasonal decline in time spent vigilant by foraging ground squirrels at Meadow "B", but not at Dyson Creek, where observations ceased shortly after juvenile emergence. There were no consistent age or sex class differences in time spent vigilant.

Ground squirrels in direct line of the flying disc ran to, and entered, the nearest burrow, and rarely gave a nonrepetitive call; squirrels distant from the flying disc often called, usually while running or after reaching a burrow. In contrast, ground squirrels were less likely to run or call in response to the badger, rarely ran to the nearest burrow, and were more likely to call before running or while remaining stationary. The frequency of nonrepetitive and repetitive calling in response to the flying disc did not vary significantly across age, sex, parity, or kin classes. Parous females were much more likely than nonparous females to give nonrepetitive and repetitive calls in response to the badger, but the presence/ absence of non-juvenile close kin had no apparent effect.

Parous adult females had a longer active season, spent more time above ground, and more time foraging than nonparous females. Parity differences in activity patterns suggest that parous females foraged at nearly a maximum rate throughout the reproductive season, whereas nonparous females may have delayed accumulating sufficient fat stores for hibernation. Parous females did not reduce their level of vigilance or forage farther from burrows in order to increase their rate of food intake. Relative to nonparous females, parous females likely experience greater exposure to predators.

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In keeping with the adage that "no 'gopherologist' is an island", it is with pleasure (and humility) that I thank those individuals and agencies that helped to bring this thesis to fruition. Dr. David Boag secured a permit to access the road into Dyson Creek, kindly allowed me to study the ground squirrels at Meadow "B", and made available the facilities of the R. B. Miller Biological Station. I appreciate the able field assistance provided by Heather Dundas and Kathy Duffield. Thanks also to Susan Hatfield for mapping burrows and trapping juveniles at Dyson Creek in 1987. Jim Hare and Paul Young provided technical advice and assistance, both in the field and in the lab. Jim Hare offered advice on statistics. Special thanks to two altruists, Craig Daniels and Dawn McArthur, who assisted me in various ways during the latter stages of the preparation of this thesis. As members of my supervisory committee, Drs. David Boag and Bev Mitchell provided numerous helpful suggestions throughout the study. Dr. Steve Dobson also contributed insightful comments on my research. I am grateful to Dr. Linda Fedigan for stepping in late in the "game" and pinch-hitting for Dr. Mitchell, on my examining committee. Dr. Stan Boutin kindly agreed to serve as committee chairman and examiner for my thesis defense. Dr. Lawrence Wang kindly provided me with access to his Laser printer to produce the final version of the thesis.

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# I. Introduction

A reduction in the risk of predation has been advanced as one of the primary advantages of living in groups (Bertram 1978). That advantage has been invoked as a major selective factor in the evolution of sociality in general (e.g., Alexander 1974, Treisman 1975, Caraco and Pulliam 1984), and group-living in ground-dwelling squirrels in particular (Hoogland 1981).

Although there are a number of possible mechanisms through which animals may gain increased protection from predators by virtue of living in groups (see reviews by Bertram 1978, Pulliam and Caraco 1984), two of these have received particular attention from behavioural ecologists: (1) the role of vigilance for the detection of predators, and (2) antipredator calling behaviour.

Most studies have viewed group-living as an adaptation to increase foraging efficiency without compromising risk of predation (Bertram 1978), and researchers have sought the proximate factors that mediate the trade-off between foraging and vigilance. The general consensus is that vigilance, for a wide array of species, is influenced by a variety of ecological and social factors that reflect changing degrees of risk of predation (reviewed by Lima 1987).

With the advent of the sociobiological approach to animal behaviour (Wilson 1975, Barash 1977), researchers became particularly intrigued by the seemingly altruistic behaviour of alarm calling and sought to determine whether kin selection or individual selection hypotheses best explain the mechanisms by which this behaviour has evolved.

Among the ground-dwelling sciurids, studies of antipredator behaviour have been limited primarily to the highly social marmot (Marmota) and prairie dog (Cynomys) species (e.g., Hoogland 1979, 1981; Holmes 1984, Carey and Moore 1986). However, for most species within the genus Spermophilus (ground squirrels), predator avoidance behaviours have received limited attention. Although the question of alarm calling has been reasonably well-studied, information is particularly lacking regarding the influence of social and ecological factors on vigilance behaviour.

Given the important function that antipredator behaviour may play in influencing the survivorship of ground-dwelling sciurids and the paucity of data regarding such behaviour, I initiated this study with the following objectives:

(1) To examine the extent to which social and ecological factors, including estimates of relative predation risk, influence the foraging and vigilance behaviour of Columbian ground squirrels.

(2) To examine the antipredator calling behaviour and escape responses of Columbian ground squirrels to simulated

aerial and terrestrial predator attacks.

(3) To examine the effects of reproductive condition on the activity and foraging behaviour of adult female Columbian ground squirrels.

In chapter 2 I examine whether Columbian ground squirrels respond to changes in predation risk when making decisions regarding the allocation of time to vigilance and the distance from escape burrows at which animals forage. Specifically, ground squirrel foraging and vigilance behaviour is examined in relation to the number of conspecifics visible to foraging animals, the distance from escape burrows, an estimate of the squirrels' visibility for detecting aerial and terrestrial predators, and the animals' proximity to habitat that may conceal predators. Also, I examine the possibility of seasonal, age and sex differences in the foraging-vigilance trade-off.

Harvey and Greenwood (1978) advocated two approaches to address questions of the evolutionary and functional significance of antipredator calling behaviour. First, a comparison of such behaviour in related species, and second, given the rarity of observations of natural predation in the field, an experimental approach. In chapter 3 I heed the latter suggestion and assess the antipredator calling and escape behaviour of Columbian ground squirrels by exposing them to simulated aerial (a flying disc) and terrestrial (a stuffed badger) predators. The central aims are to determine whether age, sex, reproductive status, and kinship influence the propensity to call in order to evaluate the extent of "nepotistic" calling (Sherman 1977) and whether it differs for aerial and terrestrial predators. In addition, I also examine the influence of the squirrel's proximity to the predator model and proximity to escape burrows on the tendency to give antipredator calls. A comparative approach to the question of the evolutionary and functional significance of antipredator calling behaviour has been used most extensively in ground-dwelling sciurids (e.g., Hoogland 1983, Davis 1984, Sherman 1985, Owings et al. 1986). My study represents an extension of the comparative approach for understanding the adaptive significance of antipredator calling in ground-dwelling squirrels.

The fourth chapter compares the activity and foraging behaviour of parous and nonparous adult female Columbian ground squirrels in order to determine the extent to which the energetic demands of reproduction influence the foraging and activity of females. Using Barash's (1980) study of hoary marmots as a point of departure, I tested several predictions based on the assumption that reproductive females have greater foraging needs and will accept a greater risk of predation.

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# II. Foraging and Vigilance in the Columbian Ground Squirrel

## Introduction

For many animals the maximization of fitness involves the objectives of averting starvation (in either the short or long term) and avoiding predation. Often these objectives are largely mutually exclusive, such that foragers cannot simultaneously maximize rate of energy intake and scan their surroundings for predators. Researchers have recognized that conventional optimal foraging models, which assume that animals are selected to maximize their net rate of energy intake (e.g., see reviews by Schoener 1971, Pyke et al. 1977), may be insufficient for determining the major factors shaping the foraging patterns of animals that are vulnerable to predators (e.g., Sih 1980, Werner and Mittelbach 1981, Cerri and Fraser 1983, Holmes 1984, Schneider 1984, Lima et al. 1985, Lima and Valone 1986). Consequently, many recent studies have viewed animal foraging behaviour from a cost-benefit perspective, with observed patterns interpreted in the context of a trade-off between foraging efficiency and predation risk (e.g., Grubb and Greenwald 1982, Holmes 1984, Lima 1985, Lima et al. 1985, Carey and Moore 1986, Godin 1986, Newman and Caraco 1987, Valone and Lima 1987, Morgan 1988). If, as selection theory predicts, foraging animals behave in a manner that maximizes their fitness, it is expected that an animal's behaviour will be responsive to aspects of their social and ecological environment that alter their risk of predation. Studies of the environmental factors mediating the feeding-vigilance trade-off often have been framed within the context of the adaptive significance of group living, most notably in flocking birds (e.g., Powell 1974; Smith 1977; Lazarus 1979a,b; Elgar and Catterall 1981; Studd et al. 1983; Lima 1985; Beverage and Deag 1987), and herd-living ungulates (e.g., Berger 1978; Underwood 1982; Berger et al. 1983; Alados 1985; Berger and Cunningham 1988; Fitzgibbon 1989, Prins and Iason 1989). A general consensus from those and numerous additional studies is that the time spent being vigilant while foraging is influenced by a variety of ecological and social factors that reflect changing degrees of predation risk (see review by Lima 1987a). More specifically, animals foraging in the presence of conspecifics may gain increased protection from predators through a "dilution effect" (Hamilton 1971), predator "confusion effect" (Curio 1976), and/or by virtue of increased corporate vigilance and consequently, enhanced predator detection capabilities of the group (e.g., Lazarus 1979b, Hoogland 1981, van Schaik et al. 1983, Magurran et al. 1985). An individual's risk of predation may be reduced in large groups, such that time devoted to predator surveillance per individual can decrease, without sacrificing safety (Caraco 1979a). A decrease in individual vigilance with increasing group size has been documented for many avian and mammalian species (e.g, see references in Hoogland 1979, Gluck 1987, Jarman 1987, Lima 1987a,b,; Phelan 1987, Berger and Cunningham 1988, Hogstad 1988).

Individuals in close proximity to habitat that provides concealment for predators (e.g., forest) may be at a greater risk of predation relative to conspecifics farther away because (1) predator detection distance (and possibly time to escape) is reduced and/or (2) predators may preferentially attack individuals near the periphery of a group. For instance, cheetahs (*Acinonyx jubatus*) tend to select Thomson's gazelles (*Gazella thomsoni*) at the edge of a group (Fitzgibbon 1989). Furthermore, cheetahs are more likely to chase and kill individuals with lower vigilance levels than their neighbors (Fitzgibbon 1989). Prins and Iason (1989) found that a buffalo's (*Syncerus caffer*) likelihood of falling victim to lions is greatest at the ecotone between structurally closed and open vegetation and decreases rapidly with distance from potential cover for lions. Hackett (1987) reported that significantly more yearling Columbian ground squirrels (*Spermophilus columbianus*) living near shrub cover were killed than those occupying open-meadow habitat. An individual's risk of predation is probably greater near habitat that may conceal predators, and, for several species, vigilance has been shown to increase with increasing proximity to such areas (e.g., Underwood 1982, Lendrem 1983, Knight and Knight 1986). Similarly, individuals on the periphery of foraging groups are presumably at greater risk of predation relative to central individuals, and often exhibit higher vigilance levels (e.g., Jennings and Evans 1980; Inglis and Lazarus 1981; Robinson 1981; Berger et al. 1983; Alados 1985; Petit and Bildstein 1987; Phelan 1987; Berger and Cunningham 1988, Prins and Iason 1989).

Among animals that elude predators by fleeing to cover, an individual's vulnerability to predation is likely greater when foraging away from versus close to protective because escape distance and the time needed to escape once a predator is sighted is increased (e.g., Holmes 1984). Numerous studies have shown that time spent vigilant increases as a function of increasing distance from safety refuges (e.g., Barnard 1980, Caraco et al. 1980, Holmes 1984, Mayhew 1987; but see Barnard and Stephens 1983, Lima 1987b).

Animals foraging in physically complex habitats may experience a change in their risk of predation if topographic relief imposes restrictions on the animal's view of its surroundings. If visibility is limited, there will be a reduction in the distance at which animals can detect predators, such that less time is available for escape, and vulnerability to predation may increase. Reduced habitat-specific visibility is known to increase vigilance in shorebirds (Metcalfe 1984) and marmots (Carey and Moore 1986).

Vulnerability to predation also may vary among age classes. Young animals may, relative to older animals, lack the full complement of physical or behavioural attributes necessary to rapidly detect, respond to and escape a predator, may be less familiar with the location of safety refuges, or may simply have yet to learn to recognize potential predators. For example, Holmes (1984) found that young hoary marmots (Marmota caligata) were slower to respond to predators, and reached protective cover later than adults. Young marmots also exhibited higher levels of vigilance than older animals (Holmes 1984). However, despite the possibility that certain classes of animals may be more vulnerable to predators, the energetic demands of growth and the need to accumulate sufficient nutrient reserves to avoid starvation, may produce a compromise between foraging and vigilance such that animals increase feeding and reduce vigilance when energetic demands are relatively high. (e.g., migrating birds, Metcalfe and Furness 1984). If energetic demands vary seasonally, time devoted to vigilance for predators may decrease without a concomitant seasonal decrease in the risk of predation (e.g., Metcalfe and Furness 1984), particularly if there are constraints on the amount of time that energy can be accumulated, as seems likely for hibernating ground squirrels.

From a comparative standpoint, the ground-dwelling sciurids (marmots, prairie dogs, and ground squirrels) provide an excellent group with which to examine the factors mediating vigilant behaviour during feeding, given the wide range of ecological and social environments that species within this taxon occupy (Armitage 1981; Michener 1983; Murie and Michener 1984). However, to date, studies that rigorously examine the factors mediating vigilance and foraging are limited to black-tailed (Cynomys ludovicianus) and white-tailed prairie dogs (C. leucurus)(Hoogland 1979, 1981; Devenport 1986, 1989), hoary marmots (Holmes 1984), and yellow-bellied marmots (Marmota flaviventris)(Carey and Moore 1986). In this chapter I evaluate the importance of age, sex, the presence of conspecifics, and several ecological factors that may alter predation risk and influence the feeding-vigilance trade-off in the Columbian ground squirrel (Spermophilus columbianus). If several factors are operative, it is expected that the relative importance of factors will differ in different ecological situations. More specifically, I address the following questions. (1) Does vigilance decrease with an increase in the number of conspecifics present within visible range? (2) Does time spent vigilant decrease with an increase in an individual's distance from the forest edge? (3) Does time spent vigilant increase with an increase in the distance from the nearest escape burrow? (4) Does reduced visibility for the detection of predators result in increased vigilance? (5) Does vigilance decrease as the active season progresses? (6) Are younger animals, particularly juveniles, more vigilant than older animals? Furthermore, if Columbian ground squirrels are capable of assessing environmental variables that reflect their risk of predation, and modify their behaviour accordingly, then the distance from escape burrows at which ground squirrels forage may be influenced by one or more of the environmental factors described above. Therefore, the influence of the number of conspecifics present, the proximity of the forest edge, visibility for detecting predators, age, sex, and season on the distance from a burrow at which ground squirrels forage is examined.

## Study Animal

Columbian ground squirrels are group-living rodents which occupy montane and subalpine meadows throughout much of west-central North America (Hall and Kelson 1959). They have a short (3-4 month) active season in which to breed, grow and store fat before entering hibernation in late summer (Boag and Murie 1981a, Young 1988). In southwestern Alberta sexually mature, typically adult (> 1 yr old), Columbian ground squirrels emerge in April and May, and breed shortly thereafter. Both males and females typically mate with >1 individual; consequently, many litters are multiply sired (J. O. Murie, pers. comm.). Each female produces one litter of 1 to 6 young (Wroot et al. 1987). The gestation period lasts 24 d (Shaw 1925, Murie and Harris 1982) and litters emerge from natal burrows 24 to 32 days after birth (Murie and Harris 1982) during June and July. Both a male-biased dispersal of yearlings and strong natal philopatry of females promotes a social system based on female kin clusters (Festa-Bianchet and King 1984; Michener 1983; Harris and Murie 1984; Murie and Harris 1984; King and Murie 1985; King 1989). Columbian ground squirrels in southwestern Alberta usually do not attain sexual maturity until 2 years of age (Murie and Harris 1982), although some females breed as yearlings (Festa-Bianchet 1981, Dobson and Murie 1987; pers. obs.; see also Dobson and Kjelgaard 1985a).

Columbian ground squirrels in southwestern Alberta are exposed to a wide variety of terrestrial predators including grizzly bear (*Ursus arctos*), coyote (*Canis latrans*), American badger (*Taxidea taxus*)(Dobson and Kjelgaard 1985b, Hackett 1987), weasel (*Mustela* spp.), and a number of avian species, particularly northern goshawk (*Accipiter gentilis*), golden eagle (*Aquila chrysaetos*) (Boag 1977), red-tailed hawk (*Buteo jamaiciensis*), prairie falcon (*Falco mexicanus*), and common raven (*Corvus corax*).

Individuals that detect predators usually emit vocalizations which warn other colony members (Betts 1976, Harris et al. 1983, Lickley 1984; chapter 3) and, under conditions of immediate danger (i.e., aerial predator attack), ground squirrels usually run to the nearest escape burrow (chapter 3).

## Study Sites

Columbian ground squirrels were observed on two grassy meadows situated within the Sheep River Wildlife Sanctuary of southwestern Alberta, 32 km west of Turner Valley (50° 39′ N, 114° 39′ W). Site 1: Dyson Creek (elevation 1570 m) is a 1.06 ha meadow almost entirely surrounded by aspen (Populus spp.) and mixed coniferous woodland. A detailed description of the area is provided in Festa-Bianchet (1981) and Festa-Bianchet and Boag (1982). Site 2: Meadow "B" (elevation 1500 m), located 3 km north of Dyson Creek, is a 2.39 ha split-level meadow with two flat benches separated by a steep, south-facing slope, and borders the north side of the Sheep River Canyon (Fig. 1 in Wiggett et al. 1989). Elsewhere the meadow is surrounded by aspen and mixed coniferous forest. Columbian ground squirrels were first introduced to the meadow in 1983 (Wiggett and Boag 1986) and, by 1987, the colony occupied much of the slope and the lower bench. Meadow "B" is grazed by bighorn sheep (Ovis canadensis) between mid-April and late June (Festa-Bianchet, pers. comm.), and both areas are grazed by cattle during July and August. In order to maintain uniform observer visibility throughout the colony, portions of Meadow "B" were mowed once in late June. Grazing and mowing resulted in a relatively uniform height of vegetation throughout the season.

## Methods

### General procedures

All squirrels were live-trapped weekly using live traps (National and Tomahawk) baited with peanut butter and, if previously unmarked, tagged through each ear with a numbered metal band (National Band and Tag Co., Monel No. 1). For ease of identification the fur of each squirrel was marked with an individually distinct pattern using human hair dye (Lady Clairol Nice N' Easy blue-black, No. 124). At each capture location, identity, body mass, head width, and reproductive condition was recorded. Body mass was recorded to the nearest 5 g with a spring balance (Pesola 1500 g). Head width was measured to the nearest 0.1 mm using a modified dial caliper. Reproductive status of males was assessed primarily by the degree of black pigmentation of the scrotum (Wells 1935), and secondarily by the size and protrusion of the testes (Murie and Harris 1978). Reproductive status of females was determined from the degree of swelling of the vulva during the breeding season and from swelling of the nipples during lactation (Murie and Harris 1982, 1988). Kin relationships were determined by trapping each litter on emergence at or near the natal burrow associated with the mother. Age and genealogical data were available for individuals first captured as juveniles in previous years, inhabiting both study areas (D. A. Boag and D. W. R. Wiggett, unpubl. data). Unmarked immigrant squirrels were assigned to an age class (yearling or 2+) based on their weight, the time of year (Boag and Murie 1981b), and head width (unpubl. data). The location of captures was noted and recorded as the coordinates of a grid marking the study area. The location and entrance diameter of all known burrow entrances available to ground squirrels for escape from predators was recorded as they were opened. Each entrance was labeled with a uniquely numbered aluminum tree tag (Canadian Forestry Supplies), and rechecked at least once per week. Locations were later plotted on 1/157 scale maps of the areas. It is unlikely that many escape burrows were undetected; during simulated aerial predator attacks squirrels that ran to burrows (n = 68) always ran to one that was open and marked (see also chapter 3).

Each study area was subdivided by means of a 10 x 10 m grid with colour-coded surveyors flags on wire stakes used to mark grid coordinates. To increase the accuracy of estimates of squirrel locations small (20 cm high), uniformly colored flags were placed halfway between grid coordinates.

To assess the visual complexity of each area, a measure of visual distances was calculated. At each coordinate of the 10 x 10 m grid, called sample points, visual distance measures were taken in 8 directions (along grid axes and diagonals). There were 114 sample points at Dyson Creek, and 78 at Meadow "B". Distance measures were made from the approximate eye level of an upright Columbian ground squirrel, using the following procedure. While lying prostrate, with my eyes approx. 20 cm from the ground, I noted the point at which various portions of an assistant's body disappeared from view as she paced from the coordinate along grid lines and diagonals. Ankle sock height (0.25 m) was taken as the maximum distance at which a conspecific could be visible, assuming that both the focal animal and conspecifics were in a vertical posture; the visibility with regard to terrestrial (e.g., coyote) and aerial (e.g., goshawk) predators were taken at the top of the thighs (0.75 m) and, with one arm raised above the head, fingertip height (2.2 m), respectively. The resulting 8 distances for each coordinate were recorded and later mapped to produce a visibility "octagon" at that point. The maximum possible number of conspecifics visible to the focal animal was estimated using the number of squirrels within a given "octagon". The data are analyzed and presented as the number of conspecifics present, including the focal animal. Visibility estimates for each predator type were produced by summing the distances of the eight directions to yield a "score" for each sample point. Also, the distance between each sample point and the surrounding forest was measured in the 8 directions, the shortest of which was used as the distance to the forest edge for each sample point. Bighorn sheep and cattle grazing activities and mowing by me prevented vegetation from becoming very long, and squirrels in a slouched posture (i.e., sitting with forebody slouched on hindquarters) were usually able to see above the immediately surrounding vegetation. For that reason, visual distances were measured once during the summer.

### Behavioural observations

Observations of ground squirrel behaviour were made from 2-3 m high wooden platforms using 10 x 40 or 10 x 50 binoculars. To minimize disturbance, focal observations did not begin until 10-15 minutes after arriving, except when squirrels had yet to emerge in the morning. Data were dictated into a taperecorder and later transcribed for analyses. Observations at Dyson Creek were made from 11 May to 23 June for 70 h on 19 days, and at Meadow "B" from 3 May to 29 July, 1987, for 115 h on 34 days. Consequently, data are for the post-breeding period only. Daily observation periods of approximately 4 hr in length were randomly distributed between morning (0700-1100), afternoon (1100-

1500), and evening (1500-2030).

Feeding and vigilance activities were recorded using focal-animal sampling (Altmann 1974). During each observation period animals were sampled according to a randomly generated list of all individuals present on the study area. An account of the focal animal's activity over 5-min (or until lost from sight) was dictated into a tape recorder and later transcribed. The time devoted to each behaviour was recorded to the nearest 0.1 s, cumulatively with a digital stopwatch. Animals frequently moved more than 1 m during a 5-min period; therefore, to reduce the potential confounding effects of changes in position and to maximize sample size, I restricted the analysis of feeding and vigilance to the first min of each focal observation. Foraging bouts were excluded if the animal moved >1 m within the one minute period. Further, the analysis is restricted to only those 1 min periods during which animals were engaged in behaviours associated with foraging (searching for, and ingesting food), and does not include periods when animals were running, grooming, interacting directly with conspecifics, or were vigilant for a period of >10 s at a time (typically in response to an alarm vocalization, or just before a change from feeding to another behaviour, e.g., social interaction, c.f. Holmes 1984). Thus, the analysis of foraging and vigilance behaviour is based on observations of concentrated feeding "bouts" rather than modal feeding (see also Holmes 1984). Although the vigilance capabilities of Columbian ground squirrels when feeding with the head down are unknown, I assume that a squirrel's ability to observe its surroundings is reduced when the head is down compared to when it is up. For the purposes of this study time spent feeding with the head down is considered inversely proportional to the time spent vigilant. I assume that an increase in amount of time spent with head down provides an individual with a greater rate of food intake, an assumption supported by other studies of animals feeding on immobile prey (e.g., Powell 1974, Abramson 1979, Caraco 1979b, Goldman 1980, Jennings and Evans 1980). Immediately before each focal observation, the area was scanned and the identity and location to the nearest 0.25 m of conspecifics was recorded. Later, an estimate of the number of conspecifics visible to the focal animal was made using the "octagon" of visibility for the nearest sample point as a measure of the squirrel's field of view. The location of the focal animal was assessed relative to the locations of open burrows to determine the animal's proximity to the nearest escape burrow.

For the analysis of ground squirrel feeding and vigilance the dependent variable was the amount of time (seconds per minute) spent with the head raised above the horizontal axis, including head up, slouched, or vertical postures (for diagrams and detailed descriptions of vigilant postures see

Harris et al. 1983, and Lickley 1984). Independent variables recorded include; age and sex of the focal animal, date, estimate of the number of conspecifics visible to the focal animal, distance to the nearest escape burrow, distance to the surrounding forest, and visibility scores for observing terrestrial and aerial predators. Additionally, the distance from the nearest burrow at which the focal squirrel foraged was treated as a dependent variable, with the remaining variables used as independent variables.

The analysis of Columbian ground squirrel foraging and vigilance is based on 117 focal observations of 32 individuals at Dyson Creek, and 197 focal observations of 33 individuals at Meadow "B". Individuals at Dyson Creek were used three times on average (range = 1-9), and those at Meadow "B" five times (range = 1-15), in the analysis. To reduce the likelihood of statistical dependence between focal observations, individuals were not used more than once per day. The ground squirrels used at Dyson Creek include 16 adults (>1 yr old)(7 males and 9 females), 14 yearlings (6 males and 8 females), and 2 juveniles (1 male and 1 female). At Meadow "B" data were recorded for 11 adults (8 males and 3 females), 10 yearlings (7 males and 3 females), and 12 juveniles (1 male and 11 females). Juveniles included in the analyses were observed from 14 days (approximately 7 weeks old) to 45 days post-emergence (approx. 11 weeks old). Observations at Dyson Creek ceased shortly after juveniles emerged from natal burrows; consequently, the sample of observations of foraging juveniles was too small for a separate analysis of this age class at Dyson Creek.

### Statistical procedures

Time spent vigilant was converted to percent of the 1-min sample period and then arcsine transformed for statistical analysis. Distance to the nearest escape burrow was log (X+1) transformed when treated as a dependent variable. Measures of time spent vigilant and distance from burrows have been converted back to proportions and metres, respectively, in all summary tables. Untransformed data are presented in figures.

An analysis of covariance was used to test the null hypotheses that there are no significant differences between males and females or among age classes. The analysis controls for the effects of the covariates (date, number of squirrels present, distance to the nearest burrow, visibility scores (terrestrial and aerial), distance to the forest edge) while testing for sex and age differences. The test provides means that are adjusted for all of the independent covariates.

Data for juvenile, yearling and adult vigilance and foraging distances were tested separately and in combination using simple and multiple linear regression. Some of the independent variables are undoubtedly intercorrelated (multicollinearity); thus estimates of partial correlations and significance levels may be unstable. However, multicollinearity tends to inflate the variance of regression coefficients, thereby making significant t-values more difficult to obtain (Neter and Wasserman 1974, see also Carey and Moore 1986). Therefore, the significance values of each of the independent variables is a conservative estimate of its effect on ground squirrel vigilance and foraging distances.

Statistical analyses were performed using the Michigan Interactive Data Analysis System (MIDAS)(Fox and Guire 1976) at the University of Alberta.

## Results

### Factors Influencing Vigilance

Most of the variables examined were significantly correlated with the proportion of time spent vigilant by foraging Columbian ground squirrels (Table 1a,b.). However, the suite of variables that were significant predictors of vigilance time varied among age classes and between colonies (Table 1a,b). Several of the independent variables were intercorrelated, therefore, partial correlations were generated to assess the combined and individual effects of each factor.

When the data are pooled for all age classes the overall regression was highly significant, accounting for 48% and 20% of the variance in ground squirrel vigilance at Meadow "B" and Dyson Creek, respectively (Table 2a and 3a). Many of the significant simple linear correlations between time spent vigilant and the independent variables disappeared, however, when partial correlations were calculated (Table 2a-d, and 3a-c), reflecting the high degree of multicollinearity among variables. The relationship between each of the variables and Columbian ground squirrel vigilance behaviour during foraging is considered below.

### Presence of conspecifics

The mean proportion of foraging time spent vigilant decreased significantly with an increase in the number of conspecifics visible to foraging ground squirrels at Meadow "B" and Dyson Creek (Fig. 1., Table 2a and 3a). The greatest benefit of reduced individual vigilance appears to be realized at relatively small "group" sizes, with the time spent vigilant reaching an asymptote when 4-6 conspecifics are present (Fig. 1). Solitary ground squirrels at Meadow "B" spent an average of 55.7% of their foraging time being vigilant, whereas foragers with >4 conspecifics visible spent 17.9% of their time being vigilant, a 68% reduction compared to solitary animals. At Dyson Creek solitary foragers devoted an average of 40% of their time to vigilance compared to 28.3% for animals feeding in the presence of >4 conspecifics, a reduction of 29%. The decrease in vigilance with increasing numbers of conspecifics visible was significant for all age classes at Meadow "B" (Table 2b-d). At Dyson Creek, however, the correlation between time spent vigilant and number of conspecifics was no longer statistically significant when yearlings and adults were analyzed separately (Table 3b-c.). That may be partly a consequence of small sample sizes for "groups" containing >4 animals.

### Distance from the forest edge

The proportion of time spent vigilant during foraging was negatively correlated with the distance from the surrounding forest edge at which ground squirrels foraged at Dyson Creek (Fig. 2, Table 3a). That trend remained significant for adults (Table 3c), but not yearlings (Table 3b), when the those age classes were analyzed separately. Yearlings at Dyson Creek foraged farther from the surrounding forest than adults (yearling median = 30 m; adult median = 20 m); however, it is unclear whether this spatial difference contributed to the lack of a significant effect of distance from the forest on yearling vigilance. At Meadow "B", time devoted to vigilance was not significantly correlated with proximity to the forest edge for any age class (Table 2a-d).

### Distance from the nearest escape burrow

Contrary to expectation, time spent vigilant during foraging generally decreased, rather than increased, when ground squirrels foraged farther from escape burrows. Time spent vigilant was negatively correlated with distance from the nearest burrow at Meadow "B" (Table 1a). That trend was significant for juveniles (Fig. 3) and adults (Fig. 4), but not for yearlings (Table 1a). Vigilance during foraging also decreased with increasing distance from escape burrows for ground squirrels at Dyson Creek (Table 1b and 3a), particularly for adults (Fig. 5, Table 3c). However, because foraging distance was intercorrelated with other independent variables (see below), once the effects of the other variables were controlled, the distance from the nearest burrow no longer accounted for a significant amount of the variance in time spent vigilant for the entire data set (Table 2a) and juveniles (Table 2b) at Meadow "B". Multiple regression analysis revealed that the distance from burrows at which adults at Meadow "B" foraged influenced negatively the amount of time spent vigilant (Table 2d). Paradoxically, when the effects of other independent variables were controlled, yearling vigilance increased with an increase in foraging distance at Meadow "B" (Table 2c).

### Visibility

At Meadow "B", time devoted to vigilance was negatively correlated with the visibility for terrestrial predators (= minimum visibility), but not the visibility for aerial predators (Table 1a). It was largely the vigilance behaviour of juveniles that accounted for the significance of the overall data set (Fig. 6, Table 1a and Table 2a-d). Time spent vigilant by ground squirrels at Dyson Creek decreased significantly with an increase in visibility scores for both terrestrial and aerial predators, particularly for yearlings (Table 1b). At Dyson Creek, aerial and terrestrial visibility scores were often similar, which may explain why both terrestrial and aerial visibility scores were significant in the simple linear regression. The statistical significance of visibility scores disappeared, however, when the effects of the other independent variables were controlled for in the partial regression analysis (Table 3a-c.).

### Season

Ground squirrels foraging at Meadow "B" spent less time vigilant as the active season progressed (Fig. 7, Table 1a). Adults accounted for much of that seasonal trend (Fig. 8, Table 1a), but the trend was significant for all age classes when the effects of the other independent variables were controlled (Table 2a-d). At Dyson Creek, there was no strong trend for vigilance to decrease as the season progressed (Table 1b and Table 3a-c). However, observations at Dyson Creek spanned a shorter time period compared to those at Meadow "B" (8 vs 14 wks) and, for the most part, did not include the period of post-juvenile emergence, the period when the most pronounced decline in vigilance occurred at Meadow "B" (Fig. 7).

### Age

Juvenile ground squirrels at Meadow "B" were significantly less vigilant than yearlings and adults; adults were somewhat less vigilant than yearlings (Table 4). At Dyson Creek, adults were more vigilant than yearlings (Table 4). However, the mean proportion of foraging time spent vigilant did not vary significantly across age classes at Meadow "B" and Dyson Creek when the effects of the covariates were controlled for (Table 5). That suggests that there are no inherent age-specific differences in time devoted to vigilance during foraging.

### Sex

There were no sex differences in the percent of time spent vigilant within age classes at Meadow "B" (Table 6a) and Dyson Creek (Table 6b). The absence of significant sex differences persisted when the effects of the covariates were controlled for (Table 7a-b).

## Factors Influencing Foraging Distance From Burrows

The distance from burrows at which ground squirrels foraged was significantly correlated with several of the independent variables (Table 8a,b.). As with time spent vigilant, the combination of variables that were significant predictors of the dependent variable (foraging distance) varied among age classes and between colonies (Table 8a,b). Again, partial correlations were generated to assess the combined and individual effects of each factor.

At Meadow "B", the overall multiple regression was highly significant, with the combination of the five variables accounting for 16% of the variance in the distance at which ground squirrels foraged (Table 9a). The five variables did not explain a significant amount of the variability in foraging distance at Dyson Creek (6%)(Table 10a). Most of the significant simple linear correlations between foraging distance and the independent variables remained significant when partial correlations were calculated (Table 9a-d, and 8a-c). The relationship between each of the variables and the distance from burrows at which ground squirrels foraged is examined more fully below.

## Presence of conspecifics

At Meadow "B", juveniles foraged farther from burrows with an increase in the number of conspecifics present and visible above ground (Fig. 9, Table 8a and 9b); such a trend was not apparent among yearlings and adults (Table 8a and Table 9c-d). At Dyson Creek yearlings, but not adults, foraged farther from escape burrows with an increase in the number of conspecifics visible (Fig. 10, Table 8b and 10b,c).

## Distance from the forest edge

There was a trend for ground squirrels to forage at greater distances from escape burrows when farther from the forest edge at Meadow "B" (Fig. 11, Table 8a and 9a).

However, when age classes were analyzed separately, proximity to the forest edge did not account for a significant amount of the variability in foraging distance within age classes (Table 9b-d). At Dyson Creek, the distance from burrows at which yearlings, but not adults, foraged increased as they moved away from the surrounding forest (Fig. 12, Table 8b and 10b,c).

### Visibility

At Meadow "B", ground squirrels of all age classes foraged at greater distances from escape burrows with an increase in "terrestrial" predator visibility, but not with estimates of visibility to aerial predators (Fig. 13, Table 8a and 9a-d). The distance at which yearlings, but not adults, at Dyson Creek foraged from escape burrows was significantly correlated with visibility, whether measured with respect to terrestrial, aerial (Table 8b), or a minimum combination of the two (Fig. 14). Visibility did not, however, account for a significant amount of the variability in the foraging distance of ground squirrels at Dyson Creek when these variables were included in the overall regression equation (Table 10a-c). Intercorrelation between the two measures of visibility for predators and distance from the forest edge may have obscured any significant influence that visibility, per se, may have on foraging distances.

### Season

No strong seasonal pattern in the distance at which Columbian ground squirrels at Meadow "B" foraged from burrows was apparent for any age class (Table 8a and 9a-d). However, adults at Dyson Creek foraged farther from escape burrows as the season progressed (Table 10c). That trend was not apparent among yearlings (Table 10b).

### Age

An analysis of variance did not reveal significant age class differences in the distance at which animals foraged from escape burrows at Meadow "B", but there was a trend for adults to forage farther from burrows than yearlings at Dyson Creek (Table 11). When the effects of other independent variables were controlled in an analysis of covariance, adults at Dyson Creek foraged significantly farther, on average, than yearlings (Table 12); at Meadow "B", a trend for older animals to forage farther from burrows was not significant (Table 12).

### Sex

There were no significant differences between males and females of each age class in the mean distance from the nearest escape burrow at which they foraged at Meadow "B" (Table 13a) and Dyson Creek (13b). The absence of significant sex differences persisted when the effects of the covariates were controlled for (Table 14a-b).

## Discussion

The patterns in foraging and vigilance behaviour observed in this study suggest that Columbian ground squirrels are responsive to several elements of their social and physical environment, several of which likely reflect changes in relative risk of predation. The general behavioural response was an increase in the amount of time allocated to vigilance during foraging and a decrease in foraging distance from escape burrows as a function of presumed increased risk of predation. However, younger animals appeared to be more sensitive to changes in relative risk of predation. Recent studies of the feeding-vigilance trade-off for other ground-dwelling sciurids have concluded that predation risk plays a major role in shaping foraging and vigilance behaviour patterns (Holmes 1984, Carey and Moore 1986). Moreover, animals of different ages may vary in responsiveness to the social and physical factors that mediate vigilance behaviour (Carey and Moore 1986). The present study differs from the marmot studies in two important respects. First, Columbian ground squirrels exhibited between-site variation in the relative importance of each risk factor in explaining the observed variability in vigilance and foraging distance from escape burrows. Second, for one variable examined, foraging distance from a burrow, ground squirrels adjusted their level of vigilance in a manner opposite to that predicted by an increase in predation risk; vigilance time decreased when squirrels foraged farther from burrows. These apparent discrepancies reflect the considerable behavioural complexity of the foraging and vigilance response of Columbian ground squirrels to aspects of the risk of predation, and underscore the importance of conducting correlational field studies at more than one colony.

## Factors Influencing Vigilance

### Presence of conspecifics

The amount of time that individual foraging ground squirrels devoted to vigilance decreased with an increase in the number of conspecifics visible, although the relationship was less pronounced at Dyson Creek compared to Meadow "B". Decreased predator surveillance time when foraging in the presence of visible conspecifics permits individuals to devote more time to feeding with the head down, searching, cropping and ingesting vegetation. Moreover, an increase in rate of energy intake may reduce the absolute amount of time spent exposed to potential predation while foraging. It appears that the greatest benefits of reduced individual vigilance are realized at relatively small "group" sizes, with time spent vigilant reaching a minimum asymptote with 4-6 ground squirrels present. Several studies have shown that the presence of conspecifics influences the vigilance behaviour of ground-dwelling squirrels. Hoogland (1979, 1981) reported that individual alertness correlated negatively with effective increases in prairie dog ward size. Hoary marmots, *Marmota caligata*, (Holmes 1984) and Olympic marmots, *M. olympus*, (Barash 1973) scanned less frequently when feeding in the presence of conspecifics than when foraging alone, and yellow-bellied marmots, *M. flaviventris*, exhibited a decrease in individual vigilance with an increase in the number of conspecifics present (Svendsen 1974, Carey and Moore 1986).

### Distance from the forest edge

Ground squirrels at Dyson Creek, but not Meadow "B", were significantly more vigilant when feeding near the surrounding forest than when foraging farther from it. The absence of a significant "forest edge" effect at Meadow "B" likely relates, in part, to site differences in the extent to which the meadow is enclosed by forest. The meadow at Dyson Creek is almost completely enclosed (approx. 90%) by forest; consequently, predators can attack squirrels over a very short range from virtually all points surrounding the meadow. By contrast, Meadow "B" is relatively "open", with the entire south border facing a canyon. Elsewhere, forested areas are localized, or distant from the areas of the meadow occupied by ground squirrels. Thus, at least at Dyson Creek, foragers appeared to perceive a greater risk of predation with increasing proximity to habitat that provides concealment for predators. Greater vigilance is expected if marginal predation is more intense than central predation. The seven successful attacks by northern goshawks observed during this study were all made within 20 m of the surrounding forest (unpubl. data), providing indirect evidence that foraging Columbian ground squirrels may experience a greater risk of danger from encounters with predators when feeding close to the forest. That an individual's foraging behaviour is sensitive to cover that may harbour predators has been documented for African antelopes (Underwood 1982) and bald eagles (Knight and Knight 1986). Hoogland (1979, 1981) for prairie dogs, and Svendsen (1974) and Armitage (1962) for yellow-bellied marmots, reported that individuals at the periphery of a colony or ward are more vigilant than those located in the centre. Particularly at Dyson Creek, and to a lesser extent at Meadow "B", the distance to the forest perimeter and the degree to which animals were peripheral coincided; hence, proximity to the forest edge was equivalent to being peripheral.

### Distance from the nearest escape burrow

A decrease in time spent vigilant with an increase in the density of, or a decrease in the distance from, escape burrows has been demonstrated for foraging hoary and yellow-bellied marmots (Holmes 1984, Carey and Moore 1986) and black-tailed prairie dogs (Devenport 1986), suggesting that marmots and prairie dogs adjust their vigilance levels relative to increased risk of predation away from burrows. That response is explicable if increased vigilance favors earlier predator detection, and escape is less likely if attacks occur while feeding farther from protective cover (Lima 1987a,b). Contrary to previous studies, with the exception of Meadow "B" yearlings, Columbian ground squirrels significantly decreased, rather than increased, the time spent scanning when foraging farther from escape burrows. That pattern persisted even when changes in number of conspecifics present was controlled in the analysis. That trend was strongest for adults of both colonies. Thus, as Lima (1987a,b) emphasized, vigilance may not necessarily increase with the risk of predation. One possible explanation for this apparent anomaly is that ground squirrels foraging distant from burrows decrease vigilance in order to increase feeding rate, such that a desired absolute amount of food is obtained more quickly, thus minimizing the amount of time vulnerable to predators (Lima 1987a). Andrusiak and Harestad (1989) showed that under experimental conditions Columbian ground squirrels had a significantly higher feeding rate when far (2.5 m) from burrows than when close (0.5 m) to them. Extended observation of individual ground squirrels under natural conditions is required to test that hypothesis. That yearlings at Meadow "B", (but not those at Dyson Creek), spent more time vigilant when foraging farther from escape burrows is compatible with the presumption of an increase in risk of predation with increasing distance from burrows. It is not clear, however, why juveniles, which are presumed to be at least equally vulnerable to predators, do not adjust their vigilance behaviour in a similar manner. Perhaps yearlings increase vigilance for reasons unrelated to predator avoidance. Adult ground squirrels behave aggressively toward yearlings, particularly yearling males (Festa-Bianchet and King 1984); thus, in addition to an antipredator function, vigilance likely serves to monitor the location and behaviour of older animals. If the availability of preferred foods is generally greater far from burrows, and ground squirrels are attracted to these areas, the potential for aggressive interactions between adults and yearlings may be increased. In contrast to yearlings at Meadow "B", those at Dyson Creek exhibited a non-significant trend of decreasing vigilance with increasing distance from burrows. However, during the period of peak aggression by parous females (late gestation/lactation), yearlings at Dyson Creek appear to reduce spatial overlap and minimize aggressive encounters with adults by moving to the central area of the meadow, an area not used extensively by adults (Festa-Bianchet and King 1984, pers. obs.). Data used in the present analysis indicate that yearlings on average foraged significantly farther from the surrounding forest than adults (30 m vs 20 m, Median test, $p < 0.0015$). Such an age-class spatial separation was not apparent at Meadow "B" (adults and yearlings, both medians = 36 m, $p > 0.15$).

It should be kept in mind, however, that interspecific differences in the manner in which ground squirrels alter their vigilance behaviour when foraging farther from burrows (i.e., whether it conforms to predictions based on the assumption of increased risk of predation with increasing foraging distance), may reflect differences in their foraging behaviour. Unlike yellow-bellied marmots, who frequently forage more than 40 m from a burrow (Frase and Armitage 1984), or hoary marmots, whose average foraging distance ranges from 5-11 m (Barash 1980), Columbian ground squirrels usually fed <4 m from a burrow (Figs. 3 to 5; see also Table 10, chapter 4). It is possible that a stronger negative relationship would be evident at greater distances from a burrow.

### Visibility

Juveniles, and to a lesser extent yearlings, at Meadow "B" appeared to be responsive to changes in the extent of visibility afforded by their physical surroundings. They increased the amount of time spent vigilant when foraging in areas with lower visibility. Individuals in visibility-poor areas may be confronted with shorter predator detection distances and, hence, be at a greater risk of predation.

Juvenile yellow-bellied marmots increased the time devoted to vigilance with an increase in the volume of vegetation (assumed to limit visibility for predator detection). Similar to the present study, Carey and Moore (1986) found that the vigilance behaviour of older animals (yearlings and adults) was less responsive to changes in visibility than that of juveniles. Metcalfe (1984) found that purple sandpipers increase the time spent vigilant with decreasing visibility. African antelopes exhibit greater vigilance in poor-visibility habitats (Underwood 1982).

### Season

Seasonal trends in vigilance during foraging have not been previously described for any ground-dwelling squirrel. Amount of time spent vigilant decreased significantly as the active season progressed for all age classes at Meadow "B", but not at Dyson Creek. However, observations at Dyson Creek ceased shortly after juveniles emerged from natal burrows in June, whereas those at Meadow "B" continued until shortly before hibernation. The necessity of accumulating sufficient fat to ensure overwinter survival during hibernation (see Murie and Boag 1984), coupled with the comparatively short active season of Columbian ground squirrels in southwestern Alberta, may promote a shift in behavioural priorities during foraging as hibernation approaches. That is, Columbian ground squirrels may place greater emphasis on meeting long-term nutrient requirements and accept a higher degree of predation risk as the active season progresses. In addition, a seasonal decrease in time spent vigilant by juveniles may reflect a progressive improvement in their antipredator capabilities (e.g., predator recognition, knowledge of escape routes, running speed), as they grow.

### Age

For the Columbian ground squirrels observed in the present study the time devoted to vigilance during foraging did not vary appreciably among age classes. Carey and Moore (1986) found that young (juvenile and yearling) yellow-bellied marmots spent significantly more time vigilant than did adults, and Holmes (1984) noted that foraging yearling hoary marmots were significantly more vigilant than older animals. They suggested that greater vigilance by young marmots may be an adaptive response to a greater inherent vulnerability to predators, given that juvenile yellow-bellied marmots are more likely to be preyed upon than older animals (Carey 1985) and yearling hoary marmots responded more slowly to a predator, and were slower in reaching safety compared to adults (Holmes 1984). The lack of differences in vigilance among age classes of Columbian ground squirrels might reflect earlier development of antipredator capabilities relative to marmots.

## Factors Influencing Foraging Distance From Burrows

### Presence of conspecifics

Juveniles at Meadow "B" and yearlings at Dyson Creek foraged farther from escape burrows as the number of conspecifics visible increased. Devenport (1989) found a significant positive correlation between the density of black-tailed prairie dogs and the distance from burrows at which animals foraged in one colony, but not another (Devenport 1986).

### Distance from the forest edge

There was a trend for ground squirrels at Meadow "B" to forage farther from burrows when they were located away from the forest perimeter. That trend was not significant when age classes were analyzed separately. At Dyson Creek, yearlings, but not adults foraged significantly farther from the nearest escape burrow with increasing distance from the surrounding forest. That response is expected if predation risk decreases with increasing distance from forest cover and increases with increasing distance from escape burrows. Again, as with vigilance, site differences in the responsiveness of squirrels to their proximity to the surrounding forest when foraging from burrows may relate to the differences in the openness of the meadows.

### Visibility

Ground squirrels at Meadow "B" foraged farther from burrows when in areas affording greater visibility for predators. Multiple regression analysis indicated that increased visibility had the strongest influence on the foraging distances of juveniles and adults. Although the foraging distances of yearlings at Dyson Creek was positively correlated with habitat visibility, this factor did not contribute significantly to the overall regression.

### Season

Columbian ground squirrels may exhibit forage preferences (Lambeth and Hironaka 1982; Elliot and Flinders 1985; Harestad 1986; Andrusiak and Harestad 1989) and preferred plant species may become depleted near burrows (Andrusiak and Harestad 1989). Consequently, ground squirrels may be compelled to forage away from burrows where preferred foods are more abundant (Leger et al. 1983). If preferred foods become depleted with time, grounds squirrels may forage farther from burrows as the active season progresses (Leger et al. 1983). However, in the present study, with the exception of adults at Dyson Creek, there was no strong indication that ground squirrels foraged farther from burrows as the season progressed. The lack of a seasonal influence on foraging distance could have been the result of a variety of factors. For one, Columbian ground squirrels may indeed deplete vegetation near burrows, but use resources in previously unexploited areas by opening burrows in these areas (c.f., Holmes 1984). Also, Columbian ground squirrels may respond to decreases in preferred plant species near burrows by including less-preferred species in their diet (Andrusiak and Harestad 1989). Alternatively, an increase in foraging distances with season may not occur in the meadows studied, owing, in part, to the high density of burrows. Ground squirrels at Meadow "B" and Dyson Creek may seldom have to forage far from burrows to find suitable food.

### Age

The distance from escape burrows at which Columbian ground squirrels foraged did not differ significantly among age classes at Meadow "B", although the average foraging distance for adults was significantly greater than that of yearlings at Dyson Creek. Foraging distances from a talus slope (providing refuge from predators) increased significantly with increasing age of hoary marmots (Holmes 1984). Holmes (1984) suggested that the inverse relationship between foraging distance and age may reflect an adaptive response of younger marmots to a greater vulnerability to predators than for adults. The absence of detectable age differences in foraging distance and vigilance among ground squirrels at Meadow "B" argues against an age-dependent vulnerability to predators. However, young Columbian ground squirrels, particularly juveniles, may indeed be at a greater relative risk of predation, but are more responsive than older animals to features of their social and physical environment that influence the distance from burrows at which they forage. That appears to be true for ground squirrels studied here. The social and physical factor variables included in the multiple regression analyses accounted for 30-39% of the variance in the distance at which juveniles and yearlings foraged from burrows, compared to 7 and 13% for adults at Dyson Creek and Meadow "B", respectively.

### Conclusions

Comparisons between sites and among age classes indicate that the relationship between the foraging and the vigilance behaviour of Columbian ground squirrels and measures of apparent predation risk is a complex one. As demonstrated by both univariate and multivariate analyses, several similarities and differences existed between sites. The presence of conspecifics resulted in a decrease in time devoted to vigilance, particularly at Meadow "B". A decrease in vigilance with an increase in "group size" has been demonstrated for all ground-dwelling squirrel species in which it has been examined, and may represent an important foraging and antipredator advantage of group-living in social ground squirrels.

Proximity to the surrounding forest, which may provide cover for predators, was a significant predictor of vigilance at Dyson Creek, a "closed" habitat, but not at Meadow "B", which is more "open". Similarly, Underwood (1982) noted that the magnitude and relative importance of several environmental variables in influencing antelope vigilance differed between 'open' and 'closed' habitats. For instance, the influence of position within the herd (and proximity to predator cover) was less pronounced in open habitat, and was significant for fewer antelope species. Further studies of foraging and vigilance in other ground squirrel species in open and closed habitats are required to confirm the generality of this interpretation from the present study.

Contrary to predictions, vigilance decreased with an increase in the distance from burrows at which ground squirrels foraged. That suggests that either risk does not increase appreciably with increasing distance from burrows, or ground squirrels alter their foraging behaviour when farther from burrows, perhaps compromising vigilance in order to increase their rate of food intake. Moreover, the relationship between vigilance and foraging distance may be determined, in part, by the influences of other risk-related variables that are correlated with foraging distance (see below).

Reduced visibility for predators, particularly terrestrial predators at Meadow "B", was negatively correlated with vigilance. However, in most cases, that variable did not contribute significantly to the overall multiple regression. Multicollinearity among visibility scores and proximity to the forest edge, particularly at Dyson Creek, may have obscured any effects of visibility on vigilance.

Seasonal patterns in vigilance have not previously been described for ground squirrels. A seasonal decline in vigilance during foraging may be attributable to increased foraging demand in order to accumulate fat as hibernation approaches. Also, if the availability of suitable forage declines as the active season progresses, ground squirrels may have to devote proportionately more time to searching for food in order to maintain a reasonable rate of energy intake. Again, further comparative studies with other ground squirrel species and other Columbian ground squirrel populations are required to confirm the generality of the pattern observed in the Columbian ground squirrel.

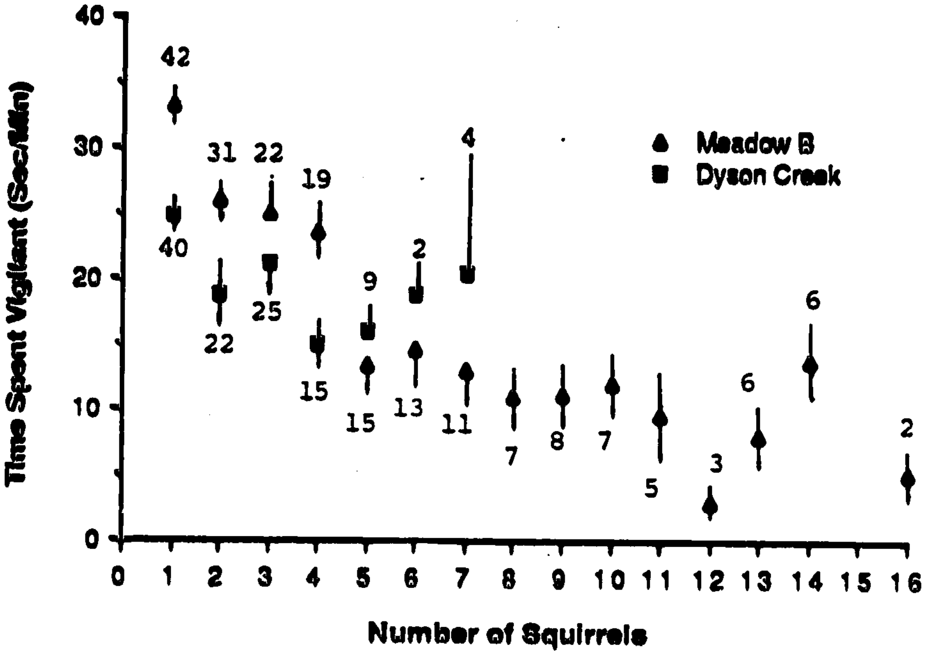
The distance from burrows at which ground squirrels foraged was correlated with several of the risk-related variables examined. However, younger animals, particularly juveniles at Meadow "B" and yearlings at Dyson Creek, appeared to be more strongly influenced by those variables. In particular, younger animals appeared responsive to the presence of conspecifics, foraging farther from burrows when more squirrels were visible.

The central aim of my study was to determine the extent to which measures of relative risk of predation were important predictors of Columbian ground squirrel foraging and vigilance behaviour. Although I have demonstrated that ground squirrel foraging and vigilance behaviour is significantly correlated with several environmental variables that are likely reasonable measures of risk of predation, at best the combination of variables examined explained <50% of the variability in time spent vigilant. What factors not examined in this study may account for the residual variability?

The spatial distribution and availability of food may be combined with predator risk factors in affecting the foraging and vigilance trade-off in Columbian ground squirrels (e.g., Holmes 1984, Carey 1985, Carey and Moore 1986). Changes in the foraging patterns of Columbian ground squirrels may parallel spatial and seasonal changes in the abundance and distribution of preferred foods (see also Holmes 1984). Extended observation of individual animals, coupled with vegetation analyses may help to explain some of the variability in ground squirrel foraging and vigilance behaviour. Socially-mediated factors such as relative dominance, familiarity with neighbours, and kinship (e.g., Davis 1984) also may contribute to the observed residual variability in vigilance behaviour. The relative importance of such factors are likely to vary spatially and temporally for different classes of individuals, e.g., spatial patterns and seasonal changes in territorial behaviour (Murie and Harris 1978, 1988; Festa-Bianchet and Boag 1982). Studies that examine additional social and ecological variables not directly related to predator avoidance, such as those outlined above, should improve our understanding of the factors mediating the trade-off between foraging and vigilance in Columbian ground squirrels, and ground-dwelling sciurids in general. The present paper provides a point of departure for such studies.

Figure 1. Average time spent vigilant by foraging ground squirrels (all age classes combined) at Meadow "B" and Dyson Creek in relation to the number of squirrels present and visible to focal animals (focal animal included). Numbers above and below SE bars represent the number of focal observations.

Figure 2. Time spent vigilant by foraging ground squirrels (all age classes combined) at Dyson Creek in relation to the focal animal's distance from the forest edge.


Time Spent Vigilant (Sec/Min)
Number of Squirrels
Meadow B
Dyson Creek
0
10
20
30
40
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
42
40
31
22
22
25
19
15
9
15
2
13
4
11
7
8
7
5
3
6
6
2

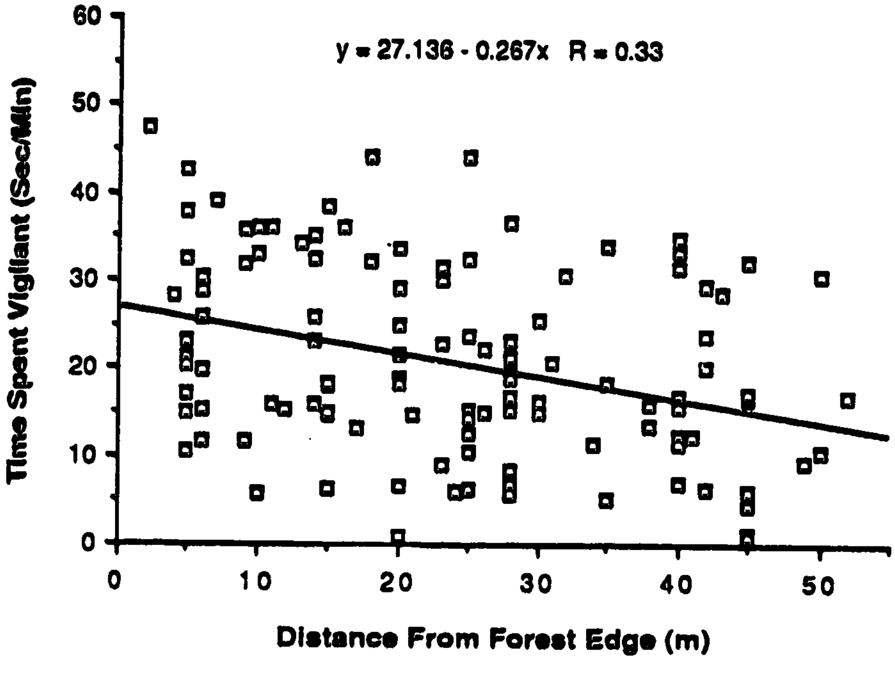
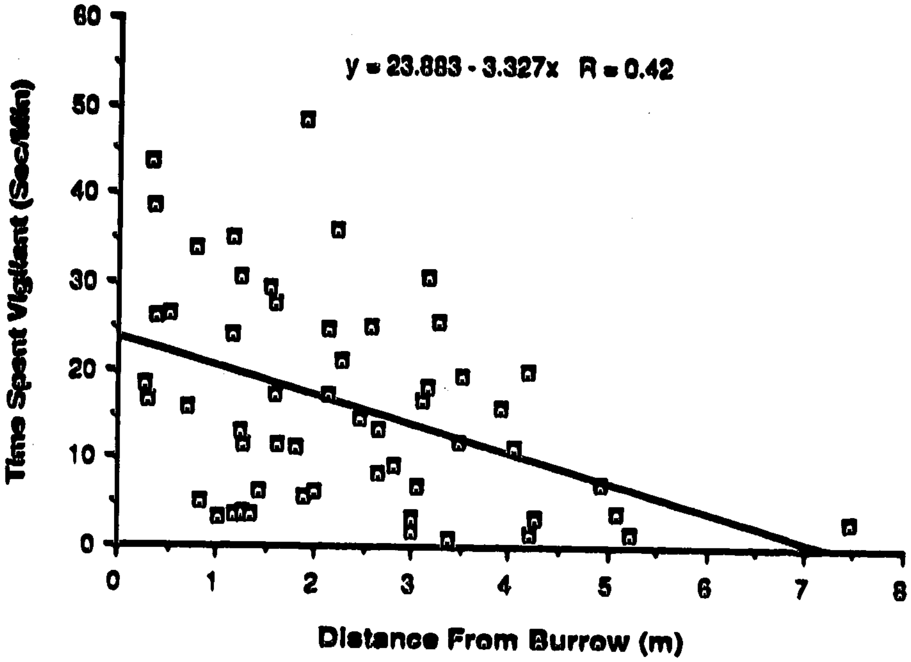

y = 27.136 - 0.267x R = 0.33
Time Spent Vigilant (Sec/Min)
Distance From Forest Edge (m)
0
10
20
30
40
50
60
0
10
20
30
40
50

Figure 3. Time spent vigilant by foraging juvenile ground squirrels at Meadow "B" in relation to the focal animal's proximity to the nearest escape burrow.

Figure 4. Time spent vigilant by foraging adult ground squirrels at Meadow "B" in relation to the focal animal's proximity to the nearest escape burrow.


y = 23.883 - 3.327x R = 0.42
Time Spent Vigilant (Sec/Min)
0
10
20
30
40
50
60
0
1
2
3
4
5
6
7
8
Distance From Burrow (m)

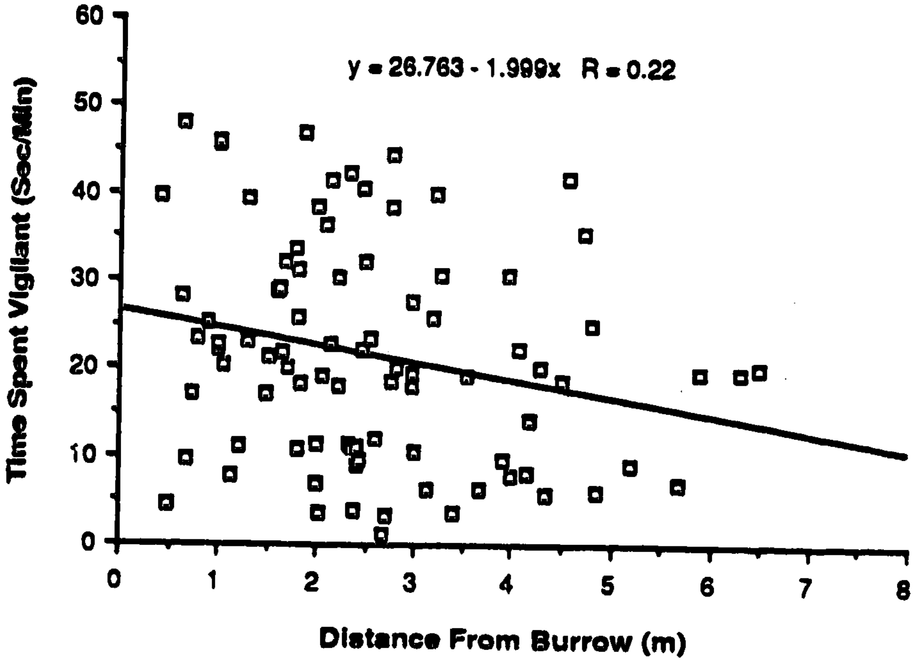
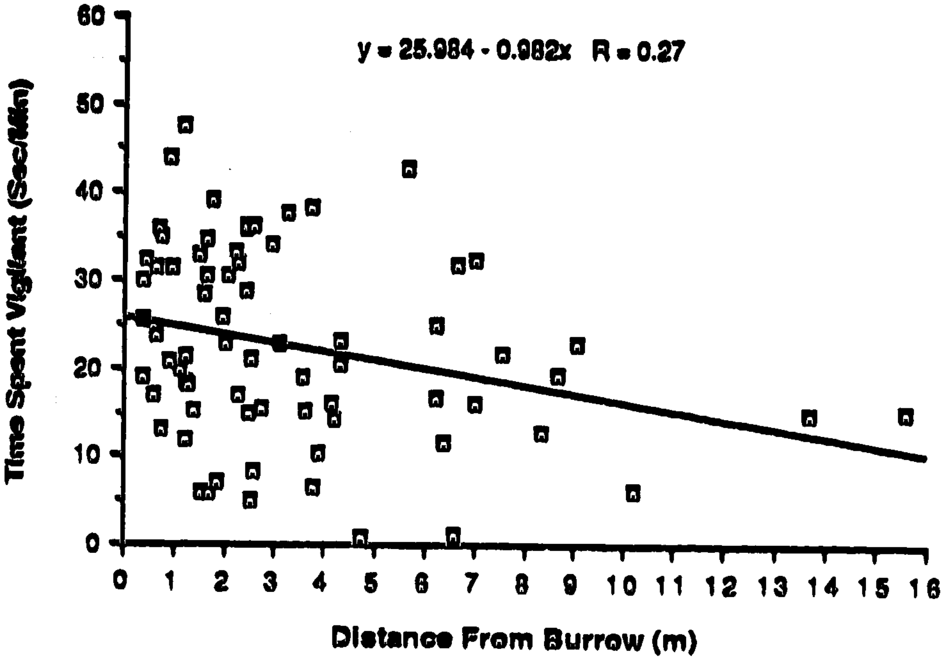

y = 26.763 - 1.999x R = 0.22
Time Spent Vigilant (Sec/Min)
0
10
20
30
40
50
60
0
1
2
3
4
5
6
7
8
Distance From Burrow (m)

Figure 5. Time spent vigilant by foraging adult ground squirrels at Dyson Creek in relation to the focal animal's proximity to the nearest escape burrow.

Figure 6. Time spent vigilant by foraging juvenile ground squirrels at Meadow "B" in relation to the focal animal's visibility with respect to terrestrial predators.


y = 25.984 - 0.982x R = 0.27
Time Spent Vigilant (Sec/Min)
60
50
40
30
20
10
0
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Distance From Burrow (m)

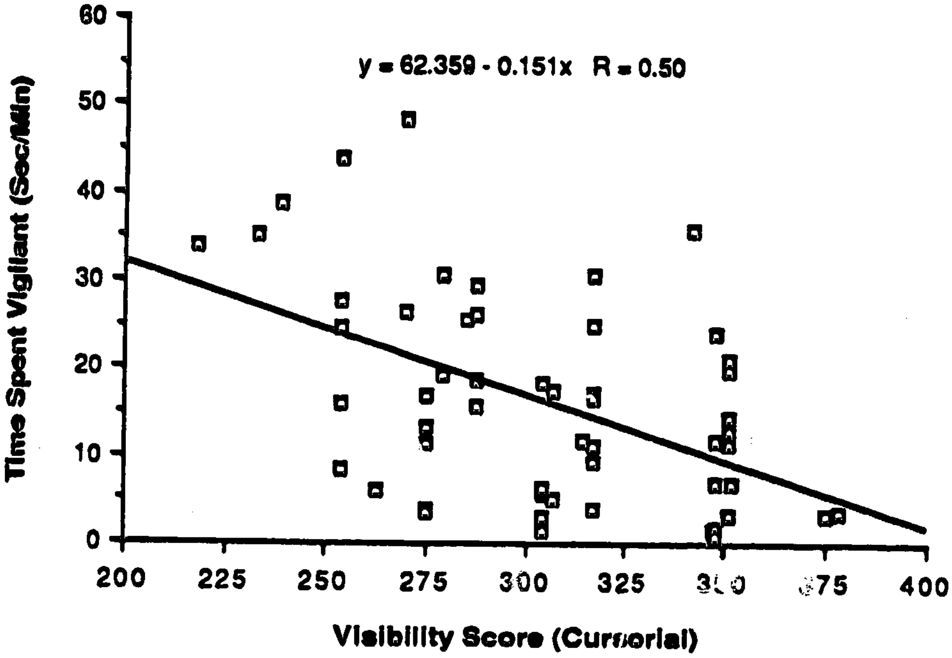
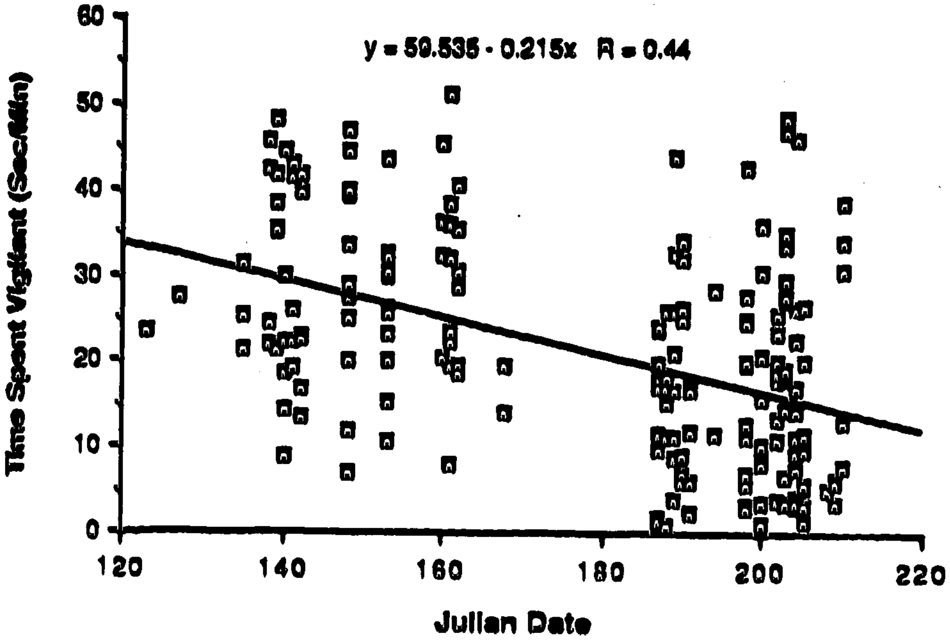

y = 62.359 - 0.151x R = 0.50
Time Spent Vigilant (Sec/Min)
60
50
40
30
20
10
0
200 225 250 275 300 325 350 375 400
Visibility Score (Cursorial)

Figure 7. Time spent vigilant by foraging ground squirrels (all age classes) at Meadow "B" in relation to the Julian calendar date. Observations were not conducted between days 170 and 185, the period of juvenile emergence from natal burrows.

Figure 8. Time spent vigilant by foraging adult ground squirrels at Meadow "B" in relation to the Julian calendar date.


y = 59.535 - 0.215x R = 0.44
Time Spent Vigilant (Sec/Min)
0
10
20
30
40
50
60
120
140
160
180
200
220
Julian Date

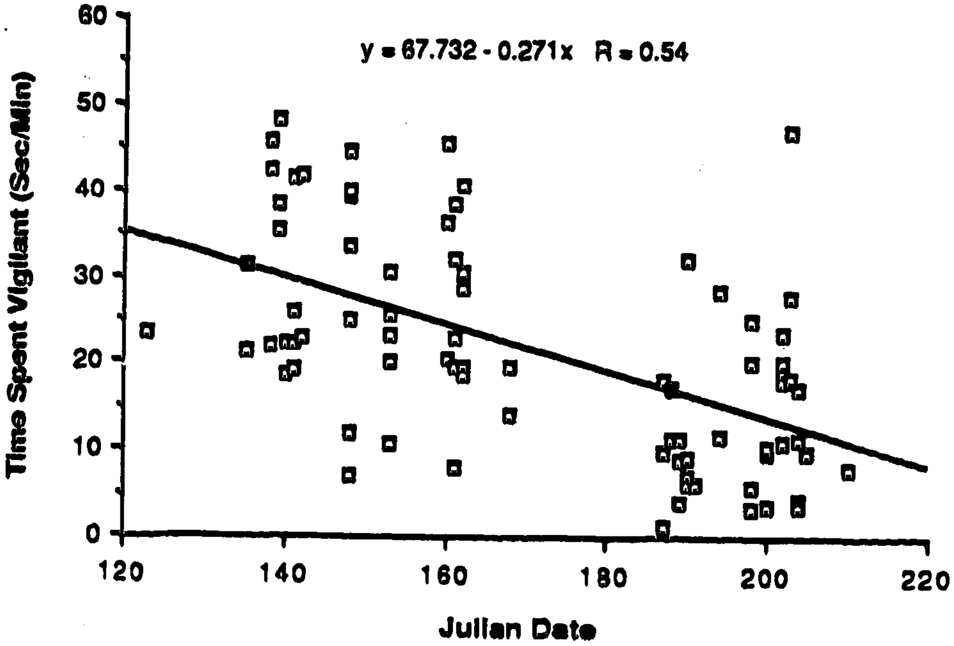
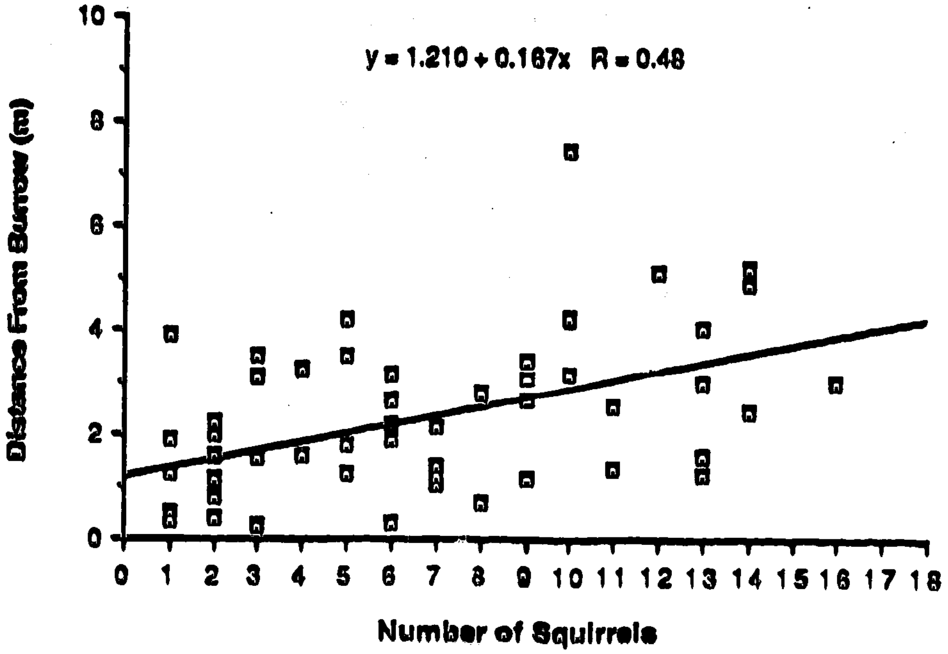

y = 67.732 - 0.271x R = 0.54
Time Spent Vigilant (Sec/Min)
0
10
20
30
40
50
60
120
140
160
180
200
220
Julian Date

Figure 9. Distance from the nearest escape burrow at which focal juvenile ground squirrels at Meadow "B" foraged in relation to the number of squirrels present and visible to focal animals (focal animal included).

Figure 10. Distance from the nearest escape burrow at which yearling ground squirrels at Dyson Creek foraged in relation to the number of squirrels present and visible to the focal animal (focal animal included).


y = 1.210 + 0.167x R = 0.48
Distance From Burrow (m)
0
2
4
6
8
10
Number of Squirrels
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18

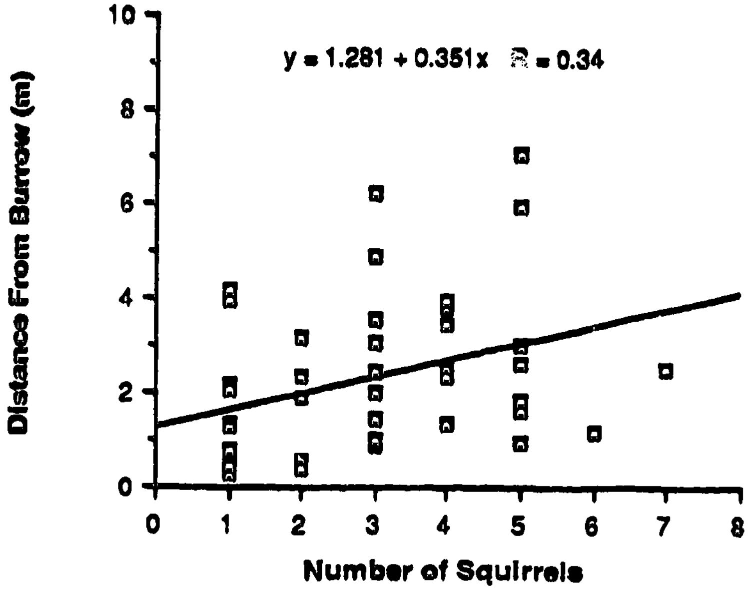
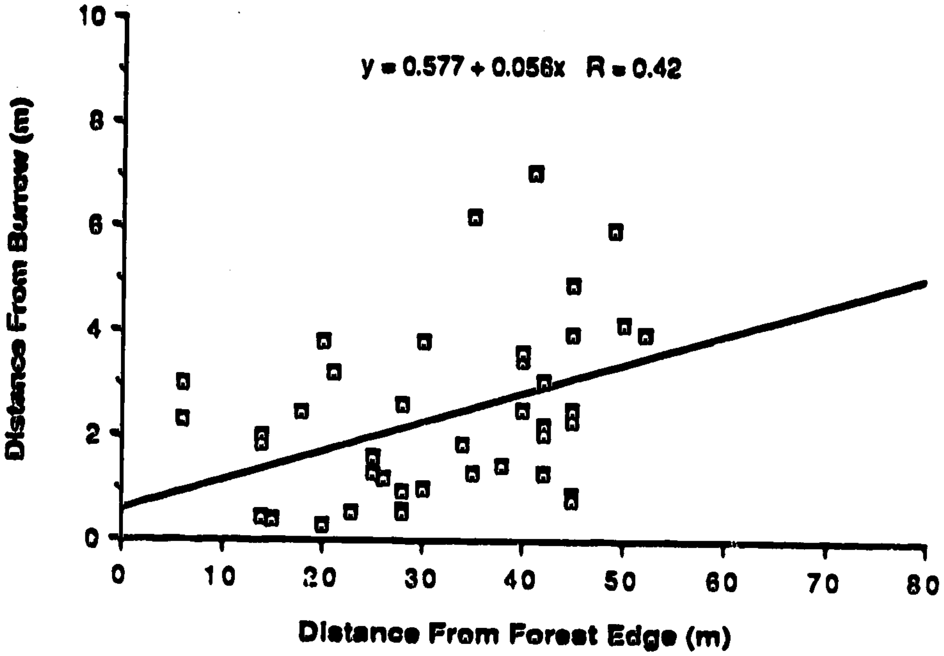

y = 1.281 + 0.351x R = 0.34
Distance From Burrow (m)
0
2
4
6
8
10
Number of Squirrels
0 1 2 3 4 5 6 7 8

Figure 11. Distance from the nearest escape burrow at which ground squirrels (all age classes combined) at Meadow "B" foraged in relation to the distance between the focal animal and the forest edge.

Figure 12. Distance from the nearest escape burrow at which yearlings at Dyson Creek foraged in relation to the distance between the focal animal and the forest edge.


y = 0.577 + 0.056x R = 0.42
Distance From Burrow (m)
0
2
4
6
8
10
0
10
20
30
40
50
60
70
80
Distance From Forest Edge (m)

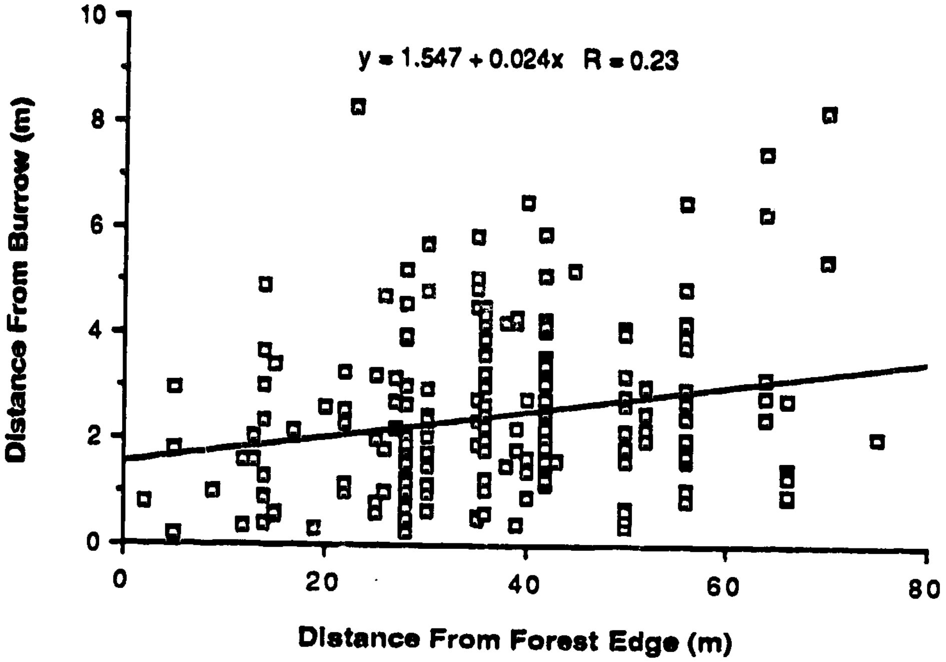
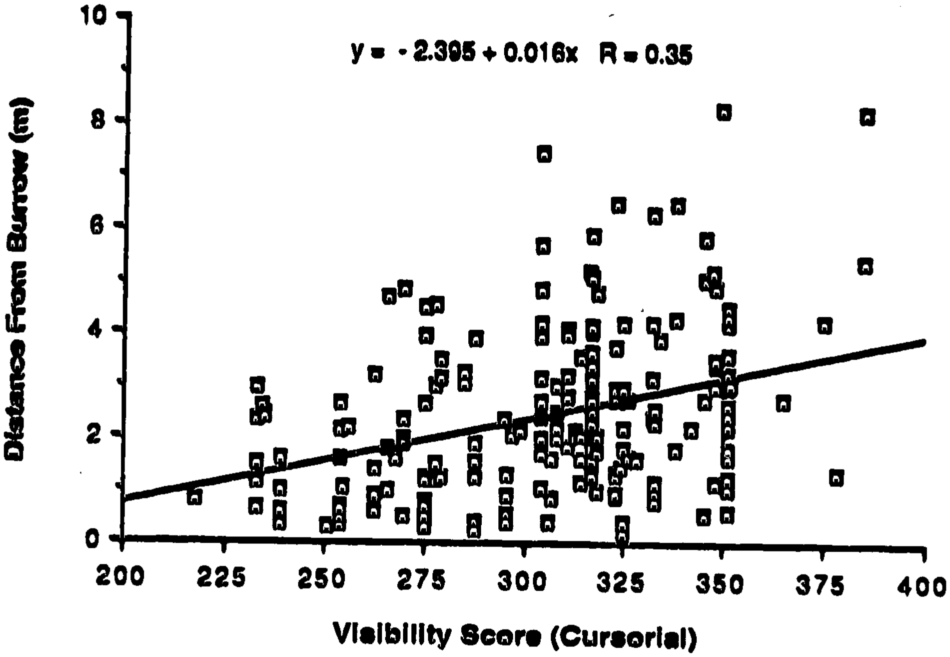
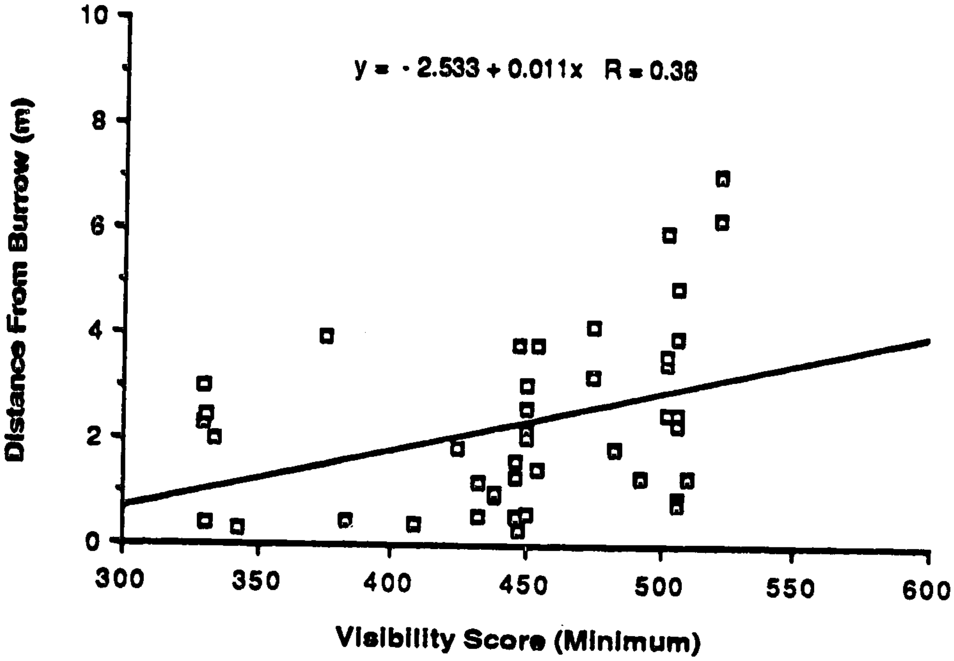

y = 1.547 + 0.024x R = 0.23
Distance From Burrow (m)
0
2
4
6
8
10
0
20
40
60
80
Distance From Forest Edge (m)

Figure 13. Distance from the nearest escape burrow at which ground squirrels (all age classes combined) at Meadow "B" foraged in relation to the focal animal's visibility with respect to terrestrial predators.

Figure 14. Distance from the nearest escape burrow at which yearling ground squirrels at Dyson Creek foraged in relation to the focal animal's visibility for predators. Visibility was taken as the lowest score for either terrestrial or aerial predators.



y = - 2.395 + 0.016x R = 0.35
Distance From Burrow (m)
0
2
4
6
8
10
200
225
250
275
300
325
350
375
400
Visibility Score (Cursorial)



y = - 2.533 + 0.011x R = 0.38
Distance From Burrow (m)
0
2
4
6
8
10
300
350
400
450
500
550
600
Visibility Score (Minimum)

Table 1a. Pearson correlations between percent of total foraging time spent vigilant by Columbian ground squirrels at Meadow "B" and six variables.

| Variable | All animals (N = 197) | Juveniles (N = 55) | Yearlings (N = 55) | Adults (N = 87) |
|---|---|---|---|---|
| Number of conspecifics | $r=-0.64$<br>$P<0.00005$ | $r=-0.59$<br>$P<0.00005$ | $r=-0.58$<br>$P<0.00005$ | $r=-0.63$<br>$P<0.00005$ |
| Distance to the forest edge | $r=-0.13$<br>$P>0.07$ | $r=-0.24$<br>$P>0.08$ | $r=-0.01$<br>$P>0.89$ | $r=-0.13$<br>$P>0.23$ |
| Distance to the nearest burrow | $r=-0.14$<br>$P=0.05$ | $r=-0.43$<br>$P=0.001$ | $r= 0.17$<br>$P>0.22$ | $r=-0.22$<br>$P<0.05$ |
| Visibility score (terrestrial) | $r=-0.18$<br>$P=0.01$ | $r=-0.50$<br>$P<0.00005$ | $r=-0.05$<br>$P>0.71$ | $r=-0.06$<br>$P>0.60$ |
| Visibility score (aerial) | $r=-0.09$<br>$P>0.22$ | $r= 0.04$<br>$P>0.78$ | $r= 0.01$<br>$P>0.96$ | $r=-0.13$<br>$P>0.21$ |
| Date | $r=-0.44$<br>$P<0.00005$ | $r=-0.02$<br>$P>0.89$ | $r=-0.28$<br>$P<0.05$ | $r=-0.55$<br>$P<0.00005$ |

Table 1b. Pearson correlations between percent of total foraging time spent vigilant by Columbian ground squirrels at Dyson Creek and six variables.

| Factor | All animals (N = 117) | Yearlings (N = 43) | Adults (N = 71) |
|---|---|---|---|
| Number of conspecifics | $r=-0.21$<br>$P=0.02$ | $r=-0.21$<br>$P>0.17$ | $r=-0.16$<br>$P>0.18$ |
| Distance to the forest edge | $r=-0.34$<br>$P<0.0003$ | $r=-0.39$<br>$P<0.011$ | $r=-0.23$<br>$P<0.05$ |
| Distance to the nearest burrow | $r=-0.21$<br>$P=0.025$ | $r=-0.24$<br>$P=0.12$ | $r=-0.27$<br>$P=0.02$ |
| Visibility score (terrestrial) | $r=-0.29$<br>$P<0.0018$ | $r=-0.46$<br>$P<0.0025$ | $r=-0.11$<br>$P>0.34$ |
| Visibility score (aerial) | $r=-0.27$<br>$P<0.003$ | $r=-0.43$<br>$P<0.0044$ | $r=-0.15$<br>$P>0.20$ |
| Date | $r=-0.05$<br>$P>0.60$ | $r=-0.06$<br>$P>0.69$ | $r=-0.09$<br>$P>0.44$ |

Table 2a. Partial correlations between percent of time spent vigilant by foraging ground squirrels (age classes combined) at Meadow "B" and six variables. $R^2 = 0.48$, $F = 29.13$, $p < 0.00005$, df = 6,190.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.53 | -8.72 | <0.00005 |
| Distance to the forest edge | r=-0.06 | -0.82 | >0.41 |
| Distance to the nearest burrow | r=-0.05 | -0.65 | >0.51 |
| Visibility score (terrestrial) | r=-0.14 | -1.88 | >0.06 |
| Visibility score (aerial) | r= 0.09 | 1.26 | >0.20 |
| Date | r=-0.30 | -4.32 | <0.00005 |

Table 2b. Partial correlations between percent of time spent vigilant by foraging juveniles at Meadow "B" and six variables. $R^2 = 0.52$, $F = 8.50$, $p < 0.00005$, df = 6, 48.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.50 | -3.98 | <0.00025 |
| Distance to the forest edge | r=-0.25 | -1.77 | >0.08 |
| Distance to the nearest burrow | r=-0.08 | -0.56 | >0.57 |
| Visibility score (terrestrial) | r=-0.28 | -2.06 | <0.046 |
| Visibility score (aerial) | r= 0.13 | 0.87 | >0.38 |
| Date | r=-0.29 | -2.07 | <0.045 |

Table 2c. Partial correlations between percent of time spent vigilant by yearlings foraging at Meadow "B" and six variables. $R^2 = 0.45$, $F = 6.48$, $p < 0.00005$, df = 6, 48.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.55 | -4.58 | <0.00005 |
| Distance to the forest edge | r= 0.09 | 0.64 | >0.52 |
| Distance to the nearest burrow | r= 0.30 | 2.17 | <0.035 |
| Visibility score (terrestrial) | r=-0.26 | -1.90 | >0.06 |
| Visibility score (aerial) | r=-0.05 | -0.34 | >0.73 |
| Date | r=-0.32 | -2.34 | <0.0236 |

Table 2d. Partial correlations between percent of time spent vigilant by foraging adults at Meadow "B" and six variables. $R^2 = 0.51$, $F = 14.02$, $p < 0.00005$, df = 6, 80.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.46 | -4.63 | <0.00005 |
| Distance to the forest edge | r=-0.04 | -0.37 | >0.71 |
| Distance to the nearest burrow | r=-0.31 | -2.92 | <0.0045 |
| Visibility score (terrestrial) | r=-0.02 | -0.18 | >0.85 |
| Visibility score (aerial) | r=-0.04 | -0.39 | >0.70 |
| Date | r=-0.31 | -2.97 | <0.0041 |

Table 3a. Partial correlations between percent of time spent vigilant while foraging (age classes combined) at Dyson Creek and six variables. $R^2 = 0.20$, $F = 4.55$, $p < 0.00045$, df = 6, 110.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.20 | -2.19 | <0.031 |
| Distance to the forest edge | r=-0.22 | -2.35 | <0.021 |
| Distance to the nearest escape burrow | r=-0.18 | -1.88 | >0.06 |
| Visibility score (terrestrial) | r= 0.01 | 0.14 | >0.88 |
| Visibility score (aerial) | r=-0.01 | -0.02 | >0.98 |
| Date | r=-0.10 | -1.05 | >0.29 |

Table 3b. Partial correlations between percent of time spent vigilant by yearlings foraging at Dyson Creek and six variables. $R^2 = 0.25$, $F = 1.98$, $p > 0.09$, df = 6, 36.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.17 | -1.04 | >0.30 |
| Distance to the forest edge | r=-0.09 | -0.51 | >0.61 |
| Distance to the nearest escape burrow | r=-0.01 | 0.06 | >0.95 |
| Visibility score (terrestrial) | r=-0.18 | -1.11 | >0.27 |
| Visibility score (aerial) | r=-0.03 | -0.17 | >0.86 |
| Date | r=-0.01 | -0.04 | >0.96 |

Table 3c. Partial correlations between percent of time spent vigilant by adults at Dyson Creek and six variables. $R^2 = 0.18$, $F = 2.39$, $p < 0.038$, df = 6, 64.

| Variable | partial correlation | partial t-value | p |
|---|---|---|---|
| Number of conspecifics | r=-0.19 | -1.53 | >0.13 |
| Distance to the forest edge | r=-0.27 | -2.29 | <0.026 |
| Distance to the nearest escape burrow | r=-0.26 | -2.13 | <0.038 |
| Visibility score (terrestrial) | r= 0.17 | 1.38 | >0.17 |
| Visibility score (aerial) | r=-0.02 | -0.18 | >0.85 |
| Date | r=-0.09 | -0.75 | >0.45 |

Table 4. The percent time spent vigilant by foraging Columbian ground squirrels of different age classes at Meadow "B" and Dyson Creek.

| | | Meadow "B" | Dyson Creek |
|---|---|---|---|
| | juveniles | 24.3 | ---- |
| | yearlings | 43.0 | 28.3 |
| | adults | 34.6 | 36.4 |
| F | | 10.16 | 5.55 |
| P | | 0.0001 | 0.02 |
| df | | 2,194 | 1,112 |

Table 5. Analysis of covariance comparing age differences in percent of time spent vigilant by foraging Columbian ground squirrels at Meadow "B" and Dyson Creek.

| | | Meadow "B" | Dyson Creek |
|---|---|---|---|
| Adjusted means* | | | |
| | juveniles | 33.7 | ---- |
| | yearlings | 35.9 | 30.5 |
| | adults | 32.6 | 34.9 |
| F | | 0.63 | 1.16 |
| P | | >0.53 | >0.28 |
| df | | 2,188 | 1,106 |

* The covariates are given in the Methods section.

Table 6a. The percent time spent vigilant by male and female Columbian ground squirrels of different age classes foraging at Meadow "B".

| | Juveniles (8,47)* | Yearlings (30,25) | Adults (66,21) |
|---|---|---|---|
| males | 24.6 | 39.3 | 33.6 |
| females | 24.4 | 47.1 | 37.6 |
| F | 0.86 | 1.85 | 0.51 |
| P | >0.97 | >0.17 | >0.47 |
| df | 1,53 | 1,53 | 1,85 |

* Numbers in brackets refer to the number of observations of males and females, respectively.

Table 6b. The percent time spent vigilant by male and female Columbian ground squirrels of different age classes foraging at Dyson Creek.

| | Yearlings (18,25)* | Adults (33,38) |
|---|---|---|
| males | 27.5 | 38.5 |
| females | 28.2 | 34.8 |
| F | 0.02 | 0.62 |
| P | >0.90 | >0.43 |
| df | 1,41 | 1,69 |

* Numbers in brackets refer to the number of observations of males and females, respectively.

Table 7a. Analysis of covariance comparing sex differences in percent of time spent vigilant by foraging Columbian ground squirrels at Meadow "B". The ANCOVA controlled for the effects of other independent variables.

| | Juveniles (8,47)* | Yearlings (30,25) | Adults (66,21) |
|---|---|---|---|
| Adjusted means** | | | |
| males | 32.1 | 42.5 | 34.1 |
| females | 23.2 | 43.2 | 35.9 |
| F | 1.41 | 0.02 | 0.20 |
| P | >0.24 | >0.87 | >0.65 |
| df | 1,47 | 1,47 | 1,79 |

* Numbers in brackets refer to the number of observations of male and females, respectively.
** The covariates are given in the Methods section.

Table 7b. Analysis of covariance comparing sex differences in percent of time spent vigilant by foraging Columbian ground squirrels at Dyson Creek. The ANCOVA controlled for the effects of other independent variables.

| | Yearlings (18,25)* | Adults (33,38) |
|---|---|---|
| Adjusted means** | | |
| males | 31.1 | 39.5 |
| females | 25.7 | 33.9 |
| F | 0.90 | 1.46 |
| P | >0.35 | >0.23 |
| df | 1,35 | 1,63 |

* Numbers in brackets refer to the number of observations of males and females, respectively.
** The covariates are given in the Methods section.

Table 8a. Pearson correlations between distance from the nearest escape burrow for ground squirrels foraging at Meadow "B" and five variables.

| Variable | All animals (N = 197) | Juveniles (N = 55) | Yearlings (N = 55) | Adults (N = 87) |
|---|---|---|---|---|
| Number of conspecifics | r= 0.13<br>P>0.06 | r= 0.49<br>P<0.0002 | r=-0.05<br>P>0.73 | r=-0.01<br>P>0.91 |
| Distance to the forest edge | r= 0.24<br>P<0.0007 | r= 0.24<br>P>0.07 | r= 0.30<br>P<0.03 | r= 0.19<br>P>0.07 |
| Visibility score (terrestrial) | r= 0.36<br>P<0.00005 | r= 0.47<br>P<0.0004 | r= 0.34<br>P<0.02 | r= 0.29<br>P<0.008 |
| Visibility score (aerial) | r=-0.02<br>P>0.77 | r=-0.08<br>P>0.58 | r= 0.34<br>P<0.013 | r=-0.14<br>P>0.18 |
| Date | r= 0.01<br>P>0.85 | r=-0.17<br>P>0.22 | r= 0.20<br>P>0.13 | r=-0.04<br>P>0.68 |

Table 8b. Pearson correlations between distance from the nearest escape burrow for ground squirrels foraging at Dyson Creek and five variables.

| Variable | All animals (N = 117) | Yearlings (N = 43) | Adults (N = 71) |
|---|---|---|---|
| Number of conspecifics | r=0.14<br>P>0.12 | r=0.39<br>P<0.02 | r=0.05<br>P>0.67 |
| Distance to the forest edge | r=0.01<br>P>0.91 | r=0.43<br>P<0.005 | r=-0.04<br>P>0.73 |
| Visibility score (terrestrial) | r=0.02<br>P>0.86 | r=0.30<br>P<0.05 | r=0.02<br>P>0.85 |
| Visibility score (aerial) | r=0.04<br>P>0.63 | r=0.38<br>P<0.013 | r=0.01<br>P>0.94 |
| Date | r=0.16<br>P>0.08 | r=-0.03<br>P>0.84 | r=0.21<br>P>0.08 |

Table 9a. Partial correlations between distance from the nearest escape burrow while foraging (all age classes combined) at Meadow "B" and five variables. $R^2 = 0.16$, $F = 7.38$, $p < 0.00005$, df = 5, 191.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r= 0.06 | 0.80 | >0.42 |
| Distance to the forest edge | r= 0.14 | 2.00 | <0.048 |
| Visibility score (terrestrial) | r= 0.30 | 4.39 | <0.00005 |
| Visibility score (aerial) | r=-0.09 | -1.25 | >0.21 |
| Date | r= 0.05 | 0.68 | >0.49 |

Table 9b. Partial correlations between distance from the nearest escape burrow for juveniles foraging at Meadow "B" and five variables. $R^2 = 0.39$, $F = 6.15$, $p < 0.00025$, df = 5, 49.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r= 0.35 | 2.59 | <0.013 |
| Distance to the forest edge | r= 0.21 | 1.54 | >0.12 |
| Visibility score (terrestrial) | r= 0.31 | 2.30 | <0.026 |
| Visibility score (aerial) | r=-0.25 | -1.81 | >0.07 |
| Date | r=-0.05 | -0.36 | >0.72 |

Table 9c. Partial correlations between distance from the nearest escape burrow for yearlings foraging at Meadow "B" and five variables. $R^2 = 0.30$, $F = 4.12$, $p < 0.0034$, df = 5, 49.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r=-0.09 | -0.62 | >0.53 |
| Distance to the forest edge | r= 0.24 | 1.73 | >0.09 |
| Visibility score (terrestrial) | r= 0.20 | 1.42 | >0.16 |
| Visibility score (aerial) | r= 0.26 | 1.92 | >0.06 |
| Date | r= 0.22 | 1.61 | >0.11 |

Table 9d. Partial correlations between distance from the nearest escape burrow for adults foraging at Meadow "B" and five variables. $R^2 = 0.13$, $F = 2.35$, $p < 0.05$, df = 5, 81.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r= 0.02 | 0.16 | >0.86 |
| Distance to the forest edge | r= 0.15 | 1.33 | >0.18 |
| Visibility score (terrestrial) | r= 0.26 | 2.43 | <0.018 |
| Visibility score (aerial) | r=-0.16 | -1.43 | >0.15 |
| Date | r=-0.02 | -0.17 | >0.86 |

Table 10a. Partial correlations between distance from the nearest escape burrow while foraging (age classes combined) at Dyson Creek and five variables. $R^2 = 0.06$, $F = 1.52$, $p > 0.18$, df = 5, 111.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r= 0.18 | 1.92 | >0.057 |
| Distance to the forest edge | r=-0.02 | -0.18 | >0.85 |
| Visibility score (terrestrial) | r=-0.03 | -0.27 | >0.79 |
| Visibility score (aerial) | r= 0.07 | 0.73 | >0.46 |
| Date | r= 0.20 | 2.18 | <0.032 |

Table 10b. Partial correlations between distance from the nearest escape burrow for yearlings foraging at Dyson Creek and five variables. $R^2 = 0.36$, $F = 4.21$, $p < 0.004$, df = 5, 37.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r= 0.45 | 3.10 | <0.0037 |
| Distance to the forest edge | r= 0.36 | 2.33 | <0.0256 |
| Visibility score (terestrial) | r=-0.13 | -0.77 | >0.44 |
| Visibility score (aerial) | r= 0.05 | 0.31 | >0.76 |
| Date | r= 0.08 | 0.50 | >0.62 |

Table 10c. Partial correlations between distance from the nearest escape burrow for adults foraging at Dyson Creek and five variables. $R^2 = 0.07$, $F = 0.95$, $p > 0.45$, df = 5, 65.

| Variable | partial correlation | partial t-value | P |
|---|---|---|---|
| Number of conspecifics | r= 0.09 | 0.76 | >0.44 |
| Distance to the forest edge | r=-0.09 | -0.71 | >0.48 |
| Visibility score (terrestrial) | r= 0.09 | 0.73 | >0.46 |
| Visibility score (aerial) | r= 0.02 | 0.13 | >0.89 |
| Date | r= 0.24 | 2.00 | <0.05 |

Table 11. The mean distance from the nearest escape burrow at which Columbian ground squirrels of different age classes foraged at Meadow "B" and Dyson Creek.

| | Meadow "B" | Dyson Creek |
|---|---|---|
| juveniles | 2.00 | ---- |
| yearlings | 2.03 | 1.95 |
| adults | 2.30 | 2.63 |
| F | 1.44 | 3.42 |
| P | 0.24 | 0.07 |
| df | 2,194 | 1,112 |

Table 12. Analysis of covariance comparing age differences in the distance (metres) from escape burrows at which Columbian ground squirrels foraged at Meadow "B" and Dyson Cree'

| | Meadow "B" | Dyson Creek |
|---|---|---|
| Adjusted means* | | |
| juveniles | 1.90 | ---- |
| yearlings | 2.03 | 1.74 |
| adults | 2.36 | 2.78 |
| F | 1.94 | 6.95 |
| P | >0.14 | <0.01 |
| df | 2,189 | 1,107 |

* The covariates are given in the Methods section.

Table 13a. The mean distance from the nearest escape burrow at which male and female Columbian ground squirrels of different age classes foraged at Meadow "B".

| | Juveniles (8,47)* | Yearlings (30,25) | Adults (66,21) |
|---|---|---|---|
| males | 2.14 | 1.88 | 2.30 |
| females | 1.99 | 2.07 | 2.41 |
| F | 0.07 | 0.21 | 0.11 |
| P | >0.78 | >0.65 | >0.73 |
| df | 1,53 | 1,53 | 1,85 |

* Numbers in brackets refer to the number of observations of males and females, respectively.

Table 13b. The mean distance from the nearest escape burrow at which male and female Columbian ground squirrels of different age classes foraged at Dyson Creek.

| | Yearlings (18,25)* | Adults (33,38) |
|---|---|---|
| males | 2.34 | 2.60 |
| females | 1.70 | 2.63 |
| F | 1.93 | 0.01 |
| P | >0.17 | >0.96 |
| df | 1,41 | 1,69 |

* Numbers in brackets refer to the number of observations of males and females, respectively.

Table 14a. Analysis of covariance comparing sex differences in the distance (metres) from the nearest escape burrow at which Columbian ground squirrels foraged at Meadow "B".

| | Juveniles (8,47)* | Yearlings (30,25) | Adults (66,21) |
|---|---|---|---|
| Adjusted means** | | | |
| males | 1.91 | 1.74 | 2.32 |
| females | 2.03 | 2.26 | 2.36 |
| F | 0.06 | 1.93 | 0.01 |
| P | >0.81 | >0.17 | >0.90 |
| df | 1,48 | 1,48 | 1,80 |

* Numbers in brackets refer to the number of observations of males and females, respectively.

** The covariates are given in the Methods section.

Table 14b. Analysis of covariance comparing sex differences in the distance (metres) from the nearest escape burrow at which Columbian ground squirrels foraged at Dyson Creek.

| | Yearlings (18,25)* | Adults (33,38) |
|---|---|---|
| Adjusted means** | | |
| males | 2.10 | 2.70 |
| females | 1.83 | 2.54 |
| F | 0.39 | 0.09 |
| P | >0.53 | >0.76 |
| df | 1,36 | 1,64 |

* Numbers in brackets refer to the number of observations of males and females, respectively.

** The covariates are given in the Methods section.

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# III. Vocal and Escape Responses of Columbian Ground Squirrels to Simulated Predator Attacks

## Introduction

A conspicuous feature of colonies of ground dwelling sciurids (marmots, prairie dogs and ground squirrels) is the propensity for individuals to vocalize in response to the presence of a predator. These vocalizations can be broadly classified according to the temporal sequence in which they are emitted within a single encounter with a predator (Owings et al. 1986). Those are, (1) nonrepetitive calls (often referred to as "alarm calls"), given as the initial vocal response to the sighting of a predator, and (2) repetitive calls ("on-guard-calls", Klump and Shalter 1984), emitted as a prolonged, rhythmic bout of vocalizations, usually subsequent to a nonrepetitive call. Early studies emphasized the structural variation of calls, particularly in regard to the environmental contexts in which they occur, and the information they may convey, e.g., predator specificity (e.g., King 1955, Balph and Balph 1966, Waring 1966, 1970; Carl 1971, Melchior 1971, Barash 1973, Turner 1973, Farentinos 1974, Fitzgerald and Lechleitner 1974, Betts 1976, Brand 1976). With the advent of the sociobiological/ behavioural-ecological approach to animal behaviour (Wilson 1975, Barash 1977), investigators shifted some of the emphasis toward testing hypotheses regarding the functional and evolutionary significance of sciurid vocal behaviour (e.g., Barash 1975, Dunford 1977, Sherman 1977, 1980a, 1985; Schwagmeyer 1980, Davis 1984, Owings et al. 1986). Interest in antipredator calling behaviour has been fostered, in large part, by the presumption that calling is risky for the caller and beneficial to perceivers of the signal; hence, calling is an altruistic behaviour (see Sherman 1977). As behaviours that increase the fitness of others at the expense of a reduction in an individual's fitness are incompatible with natural selection, many have sought to find the mechanisms by which seemingly altruistic acts may have evolved (e.g., Hamilton 1963, 1964; Maynard Smith 1965; Williams 1966, Trivers 1971, Harvey and Greenwood 1978).

Several non-mutually exclusive evolutionary hypotheses have been advanced to explain the functional and adaptive nature of antipredator vocalizations, particularly nonrepetitive calls (summarized in Sherman 1977, Harvey and Greenwood 1978, Klump and Shalter 1984). These hypotheses consider antipredator calling behaviour within two conceptual frameworks, individual selection and kin selection. Hypotheses invoking individual (phenotypically selfish) selection contend that calling functions to reduce the caller's likelihood of being captured, either immediately (e.g., Perrins 1968, Charnov and Krebs 1975, Woodland et al. 1980, Yahner 1980, Tilson and Norton 1981, La Gory 1987), or in the future (Trivers 1971, Smith 1986). The kin selection hypothesis postulates that antipredator calling behaviour is genotypically "selfish", functioning primarily to aid the escape of genetic relatives, thereby increasing the caller's inclusive fitness (Hamilton 1963, 1964; Maynard Smith 1965).

Among sciurids, studies often have shown sexual and seasonal differences in the tendency for individuals to give nonrepetitive calls in response to terrestrial predators. Adult females give antipredator calls more than adult males (*Spermophilus tereticaudus*, Dunford 1977; *S. beldingi*, Sherman 1977; *S. tridecemlineatus*, Schwagmeyer 1980), and parous females are more likely to call than nonparous females (Sherman 1977; Schwagmeyer 1980; *S. beecheyi*, Leger and Owings 1978). Furthermore, parous females call more frequently after young have emerged from natal burrows than before (Schwagmeyer 1980, Davis 1984, Owings et al. 1986). In addition, juvenile males who have not yet dispersed from their natal area call as often as juvenile females (Dunford 1977, Schwagmeyer 1980). Given that animals are more likely to call when close kin, particularly weaned juvenile offspring, are present, most have concluded that sciurid antipredator calls in response to terrestrial predators are nepotistic, implicating kin selection as the major selective force acting on this behaviour (Barash 1975, Dunford 1977, Sherman 1977, 1980a,b; Leger and Owings 1978; Smith 1978; Owings and Leger 1980; Schwagmeyer 1980; Hoogland 1981a, 1983; Davis 1984; Owings et al. 1986). By comparison, the data available for vocal responses to aerial predators are equivocal and the factors selecting for this behaviour less well understood. For instance, thirteen-lined ground squirrels rarely call (Schwagmeyer 1980), Belding's ground squirrels of both sexes and all ages call equally often (Sherman 1985), and Richardson's ground squirrel (S. richardsonii) males during lactation, and adult females with young and juvenile females after weaning, are most likely to call in the presence of an aerial predator (Davis 1984). Only the latter study provides evidence that antipredator calling in response to aerial predators may be nepotistic.

Compared to nonrepetitive calling, the function and adaptive nature of repetitive calls has received considerably less attention. Anecdotal and empirical evidence suggest that repetitive calls act as a form of "tonic" communication (Schleidt 1973), serving to promote vigilance in perceivers and/or to monitor the movements of a predator (Betts 1976, Smith et al. 1977, Owings and Hennessy 1984, Owings et al. 1986, Loughry and McDonough 1988). The signaller presumably benefits by gaining additional lookouts for detecting the predator if it returns (Loughry and McDonough 1988). There are few data available regarding the tendency for repetitive calling to vary with age, sex, kinship, parity, or type of predator.

For S. columbianus, both a male-biased dispersal of yearlings and strong natal philopatry of females promotes a social system based on female kin clusters (Michener 1983, Festa-Bianchet and King 1984, Harris and Murie 1984, Murie and Harris 1984, King and Murie 1985, King 1989). The spatial and temporal coexistence of adult matrilineal kin within Columbian ground squirrel colonies prompted King and Murie (1985) to predict a social system influenced by nepotism. They suggested that, if availability of adult female kin influence kin-differential behaviour, then female S. columbianus should favour mothers, daughters and non-littermate sisters.

Columbian ground squirrels give a number of structurally distinct nonrepetitive and repetitive vocalizations during predator encounters (Betts 1976, Harris et al. 1983, Lickley 1984), which elicit different responses from squirrels when broadcast during playback experiments (Harris et al. 1983). However, Lickley (1984) demonstrated that Columbian ground squirrel nonrepetitive calls do not differ on the basis of predator type, but may vary according to level of alarm associated with the encounter (see also Owings and Hennessy 1984, Owings et al. 1986).

In this study I simulated aerial (flying disc, see Davis 1984) and terrestrial (stuffed badger, Taxidea taxus, see Hoogland 1981b, 1983) predator attacks to elicit vocal and non-vocal responses in Columbian ground squirrels. The major aims of the study were to (1) describe the escape responses and context of antipredator calling of ground squirrels in response to simulated aerial and terrestrial predators, and (2) determine whether sex, age, parity, kinship, or the presence of close kin visible above ground influence the tendency for Columbian ground squirrels to give nonrepetitive and repetitive vocalizations and the duration of repetitive calls in response to simulated aerial and terrestrial predators. Within the context of these aims, I determine whether patterns differ for aerial and terrestrial predators, as suggested for other ground squirrels (Schwagmeyer 1980, Sherman 1985), and examine the element of risk associated with calling in response to aerial and terrestrial predators.

## Study Species

Columbian ground squirrels are medium-sized (400-900 g), group-living rodents, which inhabit montane and subalpine meadows throughout much of west-central North America (Hall and Kelson 1959). In southwestern Alberta Columbian ground squirrels breed in April and May, and juveniles emerge from their natal burrows in June and July. Both males and females typically mate with >1 individual; consequently, many litters are multiply sired (J. O. Murie, pers. comm.) and paternity may be uncertain.

Columbian ground squirrels in southwestern Alberta usually do not attain sexual maturity until 2 years of age (Murie and Harris 1982), although some females breed as yearlings (Festa-Bianchet 1981, Dobson and Murie 1987; see also Dobson and Kjelgaard 1985a).

In southwestern Alberta, Columbian ground squirrels are subject to a wide variety of predators including grizzly bear (Ursus arctos), coyote (Canis latrans), American badger (Taxidea taxus)(Dobson and Kjelgaard 1985b, Hackett 1987), weasel (Mustela spp.), and a number of avian species, particularly Northern Goshawk (Accipiter gentilis), golden eagle (Aquila chrysaetos)(Boag 1977), Red-Tailed Hawk (Buteo jamaiciensis), prairie falcon (Falco mexicanus), and Common Raven (Corvus corax).

## Study Sites

Simulated predator attack trials were conducted during 90 h between 26 May and 13 August, 1988, in two grassy meadows situated within the Sheep River Wildlife Sanctuary of southwestern Alberta, 32 km west of Turner Valley (50° 39'N, 114° 39'W). Site 1: Dyson Creek (elevation 1570 m) is a 1.06 ha meadow surrounded by aspen (Populus spp.) woodland (see Festa-Bianchet (1981) and Festa-Bianchet and Boag (1982) for a detailed description of the area). Site 2: Meadow "B" (elevation 1500 m), located 3 km north of Dyson Creek, is a 2.39 ha split-level meadow with two flat benches separated by a steep, south-facing slope, and borders the north side of the Sheep River Canyon (see fig. 1 in Wiggett et al. 1989). Elsewhere the site is surrounded by aspen and mixed coniferous forest. Ground squirrels were first introduced to the meadow in 1983 (Wiggett and Boag 1986). In 1988, squirrels occupied the southwesternmost third of the meadow. Meadow "B" is grazed by bighorn sheep (Ovis canadensis) between mid-April and late June (M. Festa-Bianchet, pers. comm.), and both areas are grazed by cattle during July and August. In order to maintain uniform visibility throughout the meadow, portions of both areas were mowed once in mid-June.

In 1988, the Dyson Creek colony consisted of 17 adult (> 2 yr old) ground squirrels (6 males and 11 females), 11 yearlings (9 males and 2 females), and 14 juveniles (10 males and 4 females). Meadow "B" consisted of 13 adults (9 males and 4 females), 12 yearlings (all females), and 45 juveniles (21 males and 24 females). As part of another aspect of my study 6 adult females at Dyson Creek were rendered nonparous by administering Mestranol, a short-term sterilant, at the time of breeding (see Methods, Chapter 4). Subsequently, 5 of 11 adult females lactated. The two yearling females at Dyson Creek did not breed. At Meadow "B" all 4 adult females and 10 of 12 yearling females bred and lactated.

## Methods

### General Procedures

All squirrels were live-trapped weekly using live traps (National and Tomahawk) baited with peanut butter, and, if previously unmarked, tagged through each ear with a numbered metal band (National Band and Tag Co., Monel No. 1). For ease of identification the fur of each squirrel was marked with an individually distinct pattern using human hair dye (Lady Clairol Nice N' Easy blue-black, No. 124). At each capture location, sex, body mass, head width, and for females, lactation status were recorded. Body mass was recorded to the nearest 5 g with a spring balance (Pesola 1500 g). Head width was measured to the nearest 0.1 mm using a modified dial caliper. Lactation status of females was determined from the degree of swelling of the nipples (Murie and Harris 1982, 1988). Kin relationships were determined by trapping each litter on emergence at or near the natal burrow associated with the mother. Age and genealogical data are available for all individuals first captured as juveniles in previous years (D. A. Boag, unpubl. data). Unmarked immigrant squirrels were assigned to an age class based on their weight, the time of year (Boag and Murie 1981), and head width (unpubl. data).

The location and entrance diameter of all burrows available to ground squirrels for escape from predators was recorded as they were opened. Each hole was labeled with a uniquely numbered aluminum tree tag (Canadian Forestry Supplies), and rechecked at least once per week. Locations were later plotted on 1/157 scale maps of the areas.

Each study area was subdivided by means of a 10 x 10 m grid with colour-coded surveyors flags on wire stakes used to mark grid coordinates. To increase the accuracy of estimates of squirrel locations small (20 cm high), uniformly colored flags were placed halfway between grid coordinates.

Observations of ground squirrel vocal and escape behaviour were made from 2-3 m high wooden platforms using 10 x 40 binoculars. Data were dictated into a taperecorder and later transcribed for analyses. Behaviours recorded here are those described by Harris et al. (1983) and Lickley (1984).

## Experimental Procedures

Two predator model stimuli (one aerial, one terrestrial) were used to elicit vocalizations and escape responses by the ground squirrels: (1) a 24 or 28 cm diameter flying disc (blue, orange or white Wham-O Frisbee), and (2) a stuffed adult male badger (*Taxidea taxus*) mounted by means of velcro adhesive on the chassis of a radio-controlled 4X4 toy truck (Radio Shack Model No. 60-4071). For each trial the stimulus was released from a portable blind located at the periphery of the colony (usually within the surrounding aspen), or in some instances, from behind natural topographic relief. The blind was always on site and was moved into position 1-3 days prior to the trial session. Both flying disc and badger trials were run from at least 5 different locations on each site.

Immediately prior to each trial the identity and location to the nearest 0.25 m of all ground squirrels above ground were recorded. Trials were initiated when no squirrels in the colony had called (either nonrepetitively or repetitively) for at least 15 min, and the focal animal(s) was facing in the direction of the blind. The latter criterion increased the probability that the subject animal would have the opportunity to respond to the stimulus rather than to the response of a conspecific.

For each subject squirrel I noted whether the squirrel gave a nonrepetitive call, when it called, and whether it ran to a burrow. The location of the burrow was recorded and compared with the subject's initial position to determine travel distance. The subject's position relative to the path taken by the flying disc or badger was plotted on a scale map of the area. The closest distance between the simulated predator and the subject was taken as the straight line drawn from the squirrel's position and the position of the model on its path at the moment the squirrel exhibited a response. The angle between that line and the flying disc's flight path was measured. I also noted whether squirrels emitted repetitive calls and the duration of calling bouts. Data on the occurrence of calling were collected on one or two (target and non-target) ground squirrels per flying disc trial. Owing to the slower speed of the badger model, as many as 4 individuals were monitored (usually 1 or 2) per trial. Data for the duration of repetitive calling bouts were gathered for all individuals that called during a trial. Bouts of repetitive calling that were interrupted due to extrinsic factors, e.g., encounters with natural predators, non-predatory animals, and humans, were not included in the analyses. An assistant estimated the height of the flying disc, the distance and direction travelled by the disc or the badger, and when possible, the response of the target squirrel. Vocal communication between an assistant and me was maintained via two-way voice-actuated headsets.

Trial sessions were distributed throughout the squirrels' daily active period (0700-2000 h, see chapter 4), but were not run in inclement weather or when winds exceeded ca. 20 km/h. In each case the focal animal(s) chosen was one that was readily observed, regardless of age or sex, as long as the individual had not previously been used in that day's trial session. Juveniles tested during the flying disc and badger trials had been above ground for at least 14 and 24 days, respectively.

### Flying disc

When the subject squirrel was facing the blind, an assistant threw a disc an average of 15.2 m (SD = 4.6, n = 70) at an average height of 1.7 m (SD = 0.7, n = 67) above the target squirrel. During each trial I observed either a "target" or another distant, "nontarget" squirrel from a 2-3 m high wooden platform. Target squirrels were classified as those subjects for which the disc passed within 5 m (horizontal plane)(median = 2 m, range = 0-5) and at an angle of <15° (median = 3°, range = 0-15°). Nontarget subjects were > 10 m (median = 17.2, range = 4.8-55.5) from the flying disc at its closest point, or at an angle of >20° (median = 40°, range= 0-147°). Seventy-five flying disc trials were conducted, all of which were used in the analyses of repetitive calling behaviour. During 5 trials the subject responded to the call of another squirrel before detecting the flying disc; therefore, analysis of nonrepetitive calling behaviour was based on 70 trials. All but 9 flying disc trials were conducted during the post-weaning period. The average number of days between trial sessions at Dyson Creek and Meadow "B" were 6.5 (range = 1-26, n = 9) days and 10.0 (range = 5-17, n = 7) days, respectively. Within trial sessions (2-6 trials/session, average = 4) the average time interval between trials was 41 min (SD = 23.9, range = 8-169). Data of nonrepetitive and repetitive vocal responses were collected for 35 target (26 individuals) and 67 nontarget subjects (42 individuals). Individuals were used a maximum of once during a given trial session. Each squirrel included in the analysis was tested as a target subject once on average (range = 1-4). Nontarget subjects were used during an average of 1 trial (range = 1-5). The analysis of duration of repetitive calling is based on 24 target (18 individuals) and 78 nontarget (51 individuals) subjects. For those analyses individuals were used once on average (ranges 1-4, and 1-5, for target and nontarget subjects, respectively).

### Badger model

The noise generated by the electric engine of the truck attracted the ground squirrels' attention; therefore, the gears were disengaged and the truck was moved manually. An assistant located within the blind pulled the truck (and badger) at a rate of ca. 25 cm/s an average of 15 m (range = 3-22, n = 54) from the blind by means of a transparent nylon fishing line attached to the front of the truck, which was looped through a pulley (affixed to a small wooden stake 20-25 m from the blind) and led back to the blind. Once a response was elicited from the subject squirrel(s) the badger model was pulled back into the blind by means of a second line attached to the back of the truck. In this way, the squirrels' exposure to the model was limited (always <2 min) and the potential for habituation presumably minimized. That experimental approach also permitted repeated trials without interruption by human observers (for an alternative approach see Hoogland 1983). My protocol simulated conditions where a predator is out of sight (not necessarily gone), rather than still visible within the colony. That is an important distinction; repetitive calling may serve different functions depending on the visual presence or absence of a predator (Owings et al. 1986). Forty-two badger and 12 control trials were conducted. During control trials, the stuffed badger was removed and the truck was run alone in the same manner as described above. All but 5 of the 54 trials were conducted after juveniles had emerged from natal burrows. The average number of days between trial sessions was 7.1 days (SD = 2.1, range = 4-10, n = 7) at Dyson Creek, and 3 days (range 1-18, n = 9) at Meadow "B". However, the actual time intervals between trials for squirrels at Meadow "B" were longer than 3 days on average because trials were run on both the upper and lower portion of the meadow; consequently, on any given day only a subset of colony members were exposed to predator models. These areas (upper and lower meadows) were alternated between trial sessions so that the average time between use of a level was 10.2 days. The mean time interval between trials (1-3 trials/session, average = 3) on multi-trial days was 47 min (SD= 15.7, range= 18-82). Data for nonrepetitive vocal responses to the badger were collected for 95 subjects (55 individuals). Each squirrel was tested in an average of one badger trial (range = 1-5). Nonrepetitive vocal responses to the control were recorded for 16 different individuals.

One-hundred and fifty-seven subjects (72 individuals) were used for the analysis of patterns of repetitive calling in response to the badger model. On average, each individual was used twice (range = 1-5). Repetitive vocal responses to a control were documented for 40 subjects (16 individuals). On average, each individual was used twice (range = 1-5). Analysis of duration of repetitive calling included 44 bouts (31 individuals) for the badger, and 4 bouts (4 individuals) for the control.

Quantitative support for the efficacy of the predator models, tests for short-term habituation, and comparisons with naturally occurring avian predator attacks are presented in Appendix 1. To summarize, ground squirrels responded to the predator models in a manner similar to their response to natural predators and there was no indication that animals became habituated to the models.

### <u>Calls</u>

Betts (1976), Koeppl et al. (1978), Harris et al. 1983 and Lickley (1984) provide sonograms or descriptions of the calls given by Columbian ground squirrels in response to predators. In the present study, nonrepetitive calls are Betts' (1976), Harris et als'. (1983) and Lickley's (1984) " (harsh) shrill chirp", and repetitive calls are Harris et als'. (1983) "hollow chirps", (Betts' 1976 "soft chirps"), and Lickley's (1984) "shrill" chirp.

### Statistical Procedures

Data were analyzed using parametric procedures if the data approximated a normal distribution and variances were homogeneous; otherwise non-parametric statistics were applied. Differences in proportions of nonrepetitive or repetitive calling were analyzed using either the G-test statistic corrected for continuity (log-likelihood test), or, when samples were <30, the Fisher exact test (Zar 1984). Comparisons of mean duration of repetitive calling bouts were analyzed using either a one-way ANOVA, Kruskal-Wallis H-test, or Mann-Whitney U-test (Zar 1984). All tests are two-tailed.

## Results

### Escape Responses and the Context of Antipredator Calling

#### Escape responses

During flying disc trials target squirrels not already at a burrow always ran, usually (94%, n = 31) for the nearest burrow entrance, and most (90%, n = 31) entered without hesitation. Of the 4 target squirrels already at a burrow, 3 went down. Nontarget squirrels typically responded by running (97%, n = 38), usually (86%, n = 37) to the nearest burrow, and immediately assuming a vertical posture. Only rarely did squirrels immediately enter burrows (10 of 67 (15%)). By contrast, in response to the badger, ground squirrels not at a burrow were less likely to run (75% ran, n = 65), usually did not run to the nearest burrow entrance (78%, n = 49), and very rarely (2%, n = 49) entered a burrow. However, of 30 ground squirrels already at a burrow, 27% went down. Ground squirrels within 20 m of the badger were significantly less likely to remain stationary (15%, n = 41) than animals more than 20 m away (42%, n = 24)(G = 4.47, p = 0.034, df = 1).

### Context of calling

When not at a burrow, nontarget ground squirrels exposed to the flying disc most often gave nonrepetitive calls while running (19%, n = 26) or after reaching the safety of a burrow (46%)(Table 1). The 4 target squirrels that called did so while running (2) or after reaching a burrow (2). By contrast, when confronted with the badger, ground squirrels were much less likely to call while (11%, n = 27) or after running (11%); rather, they usually called before running (48%) or while remaining stationary (30%)(Table 1). Of those squirrels not already at a burrow, individuals within 20 m of the badger were more likely to call while, or after, running (38%, n = 16) than were individuals >20 m away (0% of 11)(Table 2).

### Nonrepetitive Calling

Nonrepetitive calls were given during 91% of the flying disc trials and by 45% of all subject animals. Target and non-target subjects differed significantly in their tendencies to emit a nonrepetitive call (G = 24.54, df = 1,

$p \ll 0.0001$). Only 11% of 35 target squirrels called[1], while 63% of 67 nontarget squirrels called in response to the flying disc.

Nonrepetitive calls were given during 67% of the badger trials and by 37% of subject animals. The probability that ground squirrels gave nonrepetitive calls during badger trials did not vary predictably with the subject's proximity to the badger model (Fig. 1; $G = 2.23$, $df = 4$, $p = 0.68$). Ground squirrels within 20 m of the badger, and presumably the most vulnerable to "predation", were as likely to emit a nonrepetitive call (40% of 55) as those farther than 20 m away (33% of 40)($G = 0.28$, $p = 0.59$, $n = 95$).

Age and sex- The frequency of nonrepetitive calling during flying disc trials did not vary significantly across age classes (adult, yearling, juvenile)(Table 3) for either nontarget females (Table 3; $G = 1.27$, $p = 0.53$, $df = 2$, $n = 36$), or nontarget males (Table 3; $G = 2.04$, $p = 0.36$, $df = 2$, $n = 31$). In response to the badger, the tendency for squirrels to give nonrepetitive calls did not differ significantly among adult, yearling, and juvenile females (Table 3; $G = 2.26$, $p = 0.32$, $df = 2$, $n = 58$) or males

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[1] Target animals occasionally gave an almost inaudible "churr" (sensu Betts 1976) as it entered a burrow. This vocalization was probably not loud enough to be heard by conspecifics other than those within a very short distance. For this reason, and because the call did not elicit overt responses in other ground squirrels (see also Betts 1976), I do not consider it an antipredator call in the conventional sense.

(Table 3; G = 1.72, p = 0.42, df = 2, n = 37).

The occurrence of nonrepetitive calls in response to the flying disc did not differ significantly between the sexes for adults (p = 0.20), yearlings (p = 0.27), and juveniles (p = 1.0)(Table 3). That pattern held true when males were compared with parous or nonparous females only (c.f., Tables 3 and 4; adult males vs parous females: p = 0.20, adult males vs nonparous females: p = 0.29; yearling males vs parous females: p = 0.38, yearling males vs nonparous females: p = 0.50).

The frequency of nonrepetitive calling during badger trials did not differ significantly between the sexes (Table 3), for yearlings (p = 1.0) and juveniles (p = 1.0), although there was a tendency for adult females to call more often than adult males (p = 0.08). The lack of significant sex effects among adults is likely a consequence of the confounding effects of female reproductive condition (see below). Adult males called significantly less often than parous females (c.f., Tables 3 and 5; p = 0.005), but as often as nonparous females (p = 1.0). Among yearlings, the frequency of calling by males did not differ from that of either parous (c.f., Tables 3 and 5; p = 0.34) or nonparous females (p = 0.25).

Kinship and parity[2]- The frequency of nonrepetitive calling to the flying disc did not differ significantly among (nontarget) nonparous females with (NPK) or without (NPNK) close kin and parous females with (PK) or without (PNK) close kin (Fig. 2; G = 3.65, p = 0.30).

The frequency of nonrepetitive calling to the badger differed significantly among parity-kin classes (Fig. 3; G = 20.00, p = 0.00017). Nonparous females with close kin and those without did not differ in their tendency to emit nonrepetitive calls (Fig. 3; p = 1.0). Parous females with close kin and those without called with similar frequency (Fig. 3; p = 1.0). Both classes of nonparous females were significantly less likely to call than were parous females (NPK vs PNK, p = 0.015; NPK vs PK, p = 0.017; NPNK vs PNK, p = 0.003; NPNK vs PK, p = 0.003).

Presence of close kin above ground- Ground squirrels were not more likely to give nonrepetitive calls when close kin were active above ground and visible to the subject animal than when kin were not present during flying disc trials (Table 6; parous adult and yearling females: p = 1.0; juveniles: p = 1.0). The presence of close kin visible above ground at the time of a trial did not increase the probability of an individual emitting a nonrepetitive call in response to the badger model (Table 7; parous adult and

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[2] See Legend, Fig. 2 and 3 for descriptions of parity-kin classes.

yearling females: p = 0.57; juveniles: p = 1.0).

## Repetitive Calling

Repetitive calls were given during 79% (n = 75) of the flying disc trials and by 52% (n = 102) of subject animals. Mean duration of repetitive calling was 13 min (range = 1-32, n = 102). Target animals were not more likely than nontarget animals to give repetitive calls (69% vs 46%, G = 1.93, df = 1, p = 0.17). Nontarget squirrels engaged in significantly longer bouts of repetitive calling (mean = 16 min, SD = 8.0, range = 2-35, n = 78) than target squirrels (mean = 9 min, SD = 4.8, range = 1-17, n = 24)(U = 491, p = 0.004).

Repetitive calls were given during 86% of 42 badger trials and by 44% of 157 subject squirrels. Repetitive calls were, on average, 16 min (SD = 12.3) in duration (range = 1-54, n = 44). There was a trend for a decline in the probability of repetitive calls being given in badger trials with increasing distance (Fig. 1.; G = 5.34, df = 4, p = 0.22). Ground squirrels were significantly more likely to give repetitive calls if they were within 20 m of the badger (55%, n = 73), than when farther away (34%, n = 84; G = 5.74, p = 0.016). However, 9 of 40 (23%) callers within 20 m of the badger delayed repetitive calling >3 min after initial exposure to the model, whereas none of 29 callers >20 m away delayed calling (G = 7.00, df = 1, p = 0.008). The average duration of repetitive calling bouts did not differ between animals within 20 m (mean = 17 min, SD = 13.3, n = 22) and those > 20 m away (mean = 15, SD = 11.5, n = 22)(U = 249.5, p = 0.85).

Age and sex- Age did not significantly influence the occurrence of repetitive calling during flying disc trials among females (Table 8; G = 0.37, p = 0.83, df = 2) or males (G = 0.48, p = 0.79, df = 2). The duration of repetitive calling bouts to the flying disc did not vary significantly across age classes for target (Table 9; H = 0.06, p = 0.97, df = 2, n = 16) and nontarget females (H = 0.35, p = 0.84, df = 2, n = 43), or target (H = 1.22, p = 0.55, df = 2, n = 8) and nontarget males (H = 0.55, p = 0.76, df = 2, n = 35).

For both females and males, repetitive calling following badger trials did not vary among age classes (Table 8; females: G = 1.44, p = 0.49, df= 2; males: G = 2.23, p = 0.33, df = 2). The mean duration of female repetitive calling bouts during badger trials differed among age classes (Table 10; H = 6.53, p = 0.038, df =2). Adult females called for a significantly longer time than yearlings (U = 71.5, p < 0.05) and juveniles (U = U = 86, p < 0.05). The mean duration of repetitive calling bouts of males were of similar duration across age classes (Table 10; H = 1.90, p = 0.39).

Within age classes, the occurrence of repetitive calling during flying disc trials was equally probable for females and males (Table 8; adults: p = 0.47; yearling: p = 0.58;

juvenile: $p = 0.59$). The lack of sex differences for adults and yearlings persisted when males were compared with parous and nonparous females (c.f., Tables 8 and 11; adult males vs parous females: $p = 0.28$, adult males vs nonparous females: $p = 1.0$; yearling males vs parous females: $p = 0.20$, yearling males vs nonparous females: $p = 1.0$). The mean duration of repetitive calling bouts of male and female juvenile target squirrels were not significantly different (Table 9; $U = 33$, $p > 0.20$). Sample sizes for adult and yearling target squirrels were insufficient for statistical analysis. There were no sex differences in the duration of repetitive calling bouts of nontarget adults (Table 9; $U = 54.5$, $p > 0.20$), yearlings ($U = 26.5$, $p > 0.20$) and juveniles ($U = 144$, $p > 0.20$).

There was a tendency for adult females to give repetitive calls more often than adult males following encounters with the badger ($p = 0.083$). More specifically, parous females ($p = 0.006$), but not nonparous females ($p = 1.0$), called significantly more often than males (c.f., Tables 8 and 12). Such a trend was not evident among yearlings (males vs all females (Table 8; $p = 0.43$; c.f., Tables 8 and 12, males vs parous females: $p = 1.0$; males vs nonparous females: $p = 0.13$) or juveniles (Table 8; $p = 0.91$). The duration of repetitive calling did not differ between the sexes for adults (Table 10; $U = 14$, $p > 0.20$), yearlings ($U = 15$, $p > 0.20$), and juveniles ($U = 74$, $p > 0.10$, $n = 9.12$).

Kinship and parity- Parous females with offspring only and those with offspring and close kin were not more likely to give repetitive calls to the flying disc than nonparous females with or without close kin (Fig. 2; G = 5.13, p = 0.16). Sample sizes for the duration of repetitive calls among parity-kin classes were insufficient for analysis.

Closely paralleling the pattern observed for nonrepetitive calling, the frequency of repetitive calling varied significantly among parity-kin classes (Fig 3; G = 15.13, p = 0.0017). Nonparous females with close kin and those without close kin did not differ in their propensity to give repetitive calls to the badger model (Fig. 3., p = 1.0). Parous females with close kin and those without did not differ in their propensity to give repetitive calls (p = 0.72). However, parous females with offspring and close kin present, or those with offspring only, called significantly more often than nonparous females (NPK vs PNK, p = 0.027; NPK vs PK, p = 0.022; NPNK vs PNK, p = 0.007; NPNK vs PK, p = 0.011). Sample sizes for the duration of repetitive calls among parity-kin classes were insufficient for analysis.

Presence of close kin above ground- Ground squirrels were not more likely to give repetitive calls when close kin were active above ground and visible to the subject animal during flying disc trials (Table 13; parous adult and yearling females: p = 1.0; juveniles: p = 0.33). The presence of close kin visible above ground at the time of a trial did not influence the probability of an individual emitting a repetitive call in response to the badger model (Table 14; parous adult and yearling females: p = 1.0; juveniles: p = 0.18).

## Discussion

### Escape Responses and the Context of Antipredator Calling

#### Escape responses

Columbian ground squirrels in the direct line of the flying disc responded by virtually always running to (94%), and entering (90%), the nearest burrow. Lickley (1984) reported that 59% ran and 43% of Columbian ground squirrels entered the nearest burrow during encounters with a trained hawk. However, the hawk did not attack, and Lickley did not distinguish between squirrels that responded to the hawk and those that may have responded to the calls of other squirrels. Betts (1976) noted that Columbian ground squirrels usually entered a burrow in response to an attacking hawk. Using an experimental procedure similar to mine, Davis (1984) found that Richardson's ground squirrels ran to a burrow on 80% of flying disc trials. Similarly, Belding's ground squirrels usually ran to the nearest burrow or other refuge in response to avian predators (Sherman

1985). Of those running to a burrow, most (86%) went down (Sherman 1985). During experimental encounters with a trained red-tailed hawk Belding's ground squirrels always ran to or down the nearest burrow (Turner 1973). Clearly, the general escape response of ground squirrels during simulated or natural encounters with aerial predators is to run to, and usually into, the nearest burrow entrance. That ground squirrels virtually always ran to the nearest open burrow suggests that these animals maintain an acute sense of their spatial position relative to escape burrows. Such a response suggests that attacks by aerial predators represent conditions of immediate danger to ground squirrels (c.f., response to badger below).

When exposed to the badger model ground squirrels not at a burrow often did not run, and of those that did, most did not seek or enter the nearest burrow, rather they ran to a vantage point farther away from the approaching badger model. However, squirrels within 20 m of the badger were more likely to run than those farther away. When distant from the badger, squirrels are in less imminent danger and may avoid attracting attention to themselves by remaining stationary, whereas those in close proximity may benefit most by fleeing. The apparent avoidance of burrows seems adaptive given the badgers ability to capture animals below, as well as above, ground (Balph 1961, Anderson and Johns 1977, Schwab 1978). During trials with a trained dog, Belding's ground squirrels virtually always ran to a multi-entranced burrow regardless of whether it was the closest (Turner 1973). For Columbian ground squirrels confronted by the badger, the decision to avoid a given burrow also may depend on the number of entrances that the burrow has. Although there are no directly comparable data for the escape responses of other ground squirrel species to badgers, Sherman (1977) reported that Belding's ground squirrels ran to a rock or sat in place in response to terrestrial predators. Thus ground squirrels behaved in a manner that enhanced their view of the terrestrial predator (Sherman 1985).

The findings of the present study compare favorably with those of Lickley (1984); in his study, Columbian ground squirrels were more likely both to run and to enter burrows, in response to encounters with an aerial predator (trained hawk) than to a terrestrial predator (dog)(Lickley 1984). California and Richardson's ground squirrels were more likely to run immediately in response to aerial than terrestrial predators (Owings et al. 1977, Davis 1984), and Belding's ground squirrels were much less likely to run to a burrow when encountering mammalian predators than avian predators (Sherman 1977, 1985). Those predator-specific differences seem appropriate given the apparent greater urgency required in a confrontation with an aerial predator relative to a terrestrial one.

### Context of calling

Columbian ground squirrels usually gave nonrepetitive calls to the flying disc after reaching an escape burrow. That implies the prior existence of danger, and suggests that ground squirrels may have acted to reduce personal risk by reaching safety before calling. Since callers usually waited to reach safety before calling, it is unlikely that Columbian ground squirrels gain immediate survival benefits by calling (c.f., Sherman 1985). Davis (1984) found that Richardson's ground squirrels were most likely to call after reaching a burrow (50%) when distant to a flying disc, and Barash (1975) indicated that marmots (Marmota spp.) invariably run to a burrow entrance before calling. Unlike California and Belding's ground squirrels, which are most likely to call when close to the aerial predator (Leger et al. 1980, Sherman 1985), Columbian ground squirrels rarely called when in direct line of the flying disc's flight.

Columbian ground squirrels usually gave nonrepetitive calls while stationary or before running when confronted by the badger. However, animals within 20 m of the badger were more likely to call while, or after running, than those farther than 20 m away. California ground squirrels usually assume an alert posture and call before or while running when confronted by a terrestrial predator (Owings et al. 1977, Owings et al. 1986, Leger et al. 1980). Belding's ground squirrels generally respond to terrestrial predators by calling after running or while remaining stationary (Sherman 1977, Sherman 1985).

## Antipredator Calling Behaviour

Columbian ground squirrels frequently responded to simulated aerial and terrestrial predator attacks by giving nonrepetitive and repetitive vocalizations. There were, however, predator- and reproductive status-related differences in the tendency for ground squirrels to emit antipredator calls.

### Nonrepetitive Calling

As with the response of Belding's ground squirrels and hoary marmots to natural and experimental encounters with aerial predators (Turner 1973; Noyes and Holmes 1979; Sherman 1985), the flying disc almost always elicited nonrepetitive calling in Columbian ground squirrels. However, the tendency for ground squirrels to call was dependent upon the animal's proximity to the flying disc. Ground squirrels were much more likely to give nonrepetitive calls when they were distant to the flying disc and at a safe vantage point (i.e., burrow entrance) than when they were close to, and in the direct line of, the flying disc. The lack of a vocal response by target animals in "extreme danger" may be a consequence of the very short detection distances (and detection times) they experience during encounters with avian predators that surprise their prey (e.g., goshawk). With the predator so close, they may either not have the time, or it is not advantageous, to emit a call prior to escaping down a burrow. If, however, under natural conditions attacking hawks select animals that are unaware (c.f., Barash 1975, Sherman 1985), "target" squirrels may rarely, if ever, have an opportunity to call.

Lickley (1984) noted that Columbian ground squirrels called during 66% of trials using a trained dog. That value, and mine of 67% for trials using the badger model, are comparable to the 71% reported for Uinta ground squirrels (S. armatus) in response to ground predators (dogs, weasels, badgers)(Balph and Balph 1966). In Robinson's (1980) study at least one Belding's ground squirrel called in encounters with large terrestrial predators (dog, coyote, mink, badger). Both Belding's ground squirrels and California ground squirrels always called in trials using a trained dog (Turner 1973, Owings and Virginia 1978, Leger et al. 1980, Owings and Leger 1980). Thus, antipredator calling in response to natural terrestrial predators, the badger model, and other simulated terrestrial predators occurs frequently among ground squirrels. However, in the present study, only 37% of focal animals called upon exposure to the badger model. Similarly, for Belding's ground squirrels, Sherman (1977, 1985) reported that 38% of focal animals called during encounters with terrestrial predators. Hoogland (1981a) found that 38.3 % of male and female adult and yearling black-tailed prairie dogs emitted a nonrepetitive call during encounters with a badger model. The lower frequency of calling by focal individuals relative to the overall frequency for the colony (i.e., per trial) likely reflects the pronounced reproductive-status differences observed in the present study and that of Sherman (1977)(see below).

Age and Sex- Neither age or sex, per se, appeared to influence the propensity with which Columbian ground squirrels gave nonrepetitive calls to the flying disc or badger model. Sherman (1985) did not find significant age or sex differences in the tendency for Belding's ground squirrels to give nonrepetitive calls during encounters with wild and semi-tame hawks.

For several of the ground-dwelling sciurid species studied, females are more likely than males to emit nonrepetitive calls in response to a terrestrial predator (e.g., Dunford 1977, Sherman 1977, Schwagmeyer 1980). In response to the badger adult male Columbian ground squirrels were unlikely to give either nonrepetitive nor repetitive calls. This may relate, in part, to the potential for males of this species to be unassured of paternity (J. O. Murie, pers. comm.). Similarly, male Belding's ground squirrels call much less frequently than females (Sherman 1977), and are subject to uncertain paternity (Hanken and Sherman 1981). However, the tendency for male Belding's to move into areas away from females (and young) after the breeding period (Sherman 1985) may also contribute to the low frequency of calling by males in that species. Dunford (1977) invoked such an explanation for the lower frequency of calling by males relative to female round-tailed ground squirrels. That is not, however, a viable proximate mechanism for the pattern observed in my study because males in southwestern Alberta remain in close proximity of females (and young) throughout the active season. Conversely, male California ground squirrels (Owings and Leger 1980), Richardson's ground squirrels, and black-tailed prairie dogs (Hoogland 1981a, 1983) are at least as likely as females to call in the presence of terrestrial predators.

Kinship and Parity- If individuals call to warn all close kin (mothers, daughters, siblings and juvenile offspring), then calling should be more frequent among those with close kin than among those without. If calling functions primarily to warn juvenile kin only, then parous females should call more frequently than nonparous females. The prediction that nonrepetitive calls are given by those with close kin present, regardless of their reproductive status, is not supported for Columbian ground squirrels responding to an aerial predator model. The tendency for nontarget yearling and adult female ground squirrels to give nonrepetitive calls was not contingent upon parity nor the presence of other classes of close kin. These findings are in keeping with hypotheses advocating individual selection and it appears that kin selection is not involved in maintaining calling behaviour in this context. The tendency to call in the presence of an aerial predator is also not influenced by kinship in Belding's ground squirrels (Sherman 1985). Sherman (1985) has argued that because callers are usually "target" squirrels, and are more successful than noncallers at eluding predators, calling serves to enhance the callers immediate survival. The absence of calling by "target" Columbian ground squirrels argues against such a function for nonrepetitive calling in this species. By comparison, Schwagmeyer (1980) reported that thirteen-lined ground squirrels did not call to nearby hawks. She did not, however, indicate whether hawks were attacking, and did not quantify the distances between the hawk and ground squirrels. Davis (1984) noted that Richardson's ground squirrels were most likely to call in response to a flying disc when they had offspring or siblings living nearby. He suggested that antipredator calling in that species is maintained by kin selection.

The data of the present study suggest that the tendency to emit nonrepetitive vocalizations to terrestrial predators is strongly influenced by the presence of juvenile offspring among adult and yearling female Columbian ground squirrels. Therefore, I suggest that nonrepetitive calling functions primarily to warn vulnerable juvenile relatives of danger and, hence, is an example of nepotism. The lack of a demonstrable difference in the calling behaviour of nonparous females with and without collateral kin suggests that selection for antipredator calling to terrestrial predators has been through direct, rather than indirect fitness, and calling by parous females has evolved in the context of parental investment (Shields 1980, Armitage 1988). The relatively high frequency with which females with juvenile offspring called relative to nonparous females is not surprising given that badgers are known to concentrate their hunting activity in ground squirrel colonies at the time juveniles are due to emerge from their natal burrow and prey disproportionately on that age class (Knopf and Balph 1969, J. O. Murie pers. comm.). Thus, juveniles are probably more vulnerable to predation by badgers than older animals, and juveniles (and by extension, their mothers) would receive the greatest benefit from a warning call. It is important, however, to recognize that, unlike mustelids, canids and felids are a threat to both young and adults (Owings and Hennessy 1984). Therefore, patterns of calling among various age, sex, parity and kin classes may differ from the present study depending on the type of terrestrial predator. Controlled experiments using other terrestrial predators (e.g., a trained dog) are required to determine whether Columbian ground squirrels respond differently to different terrestrial predators according to the type of threat they pose. Schwagmeyer (1980) found that parous thirteen-lined ground squirrels called more frequently to approaches by canids and humans, particularly after juveniles emerged, than nonparous females and males. California ground squirrels increased the rate of nonrepetitive calling to a dog after juvenile emergence, prompting Owings et al. (1986) to conclude that antipredator calling in response to terrestrial predators functions to warn vulnerable offspring. Davis (1984) found that parous and nonparous female Richardson's ground squirrels did not differ in their propensity to give nonrepetitive calls in response to terrestrial predators. In Hoogland's (1981a) study male and female black-tailed prairie dogs (both adults and yearlings) with kin present in the coterie did not differ in the frequency of calling; however, adult and yearling males with relatives present were significantly more likely to call than those without such relatives. A similar but non-significant trend existed between adult and yearling females with kin present vs those without kin. Also, yearling males with close relatives present called more frequently than those without (Hoogland 1983). Thus he concluded that calling is nepotistic and is, at least in part, a consequence of kin selection. Both Belding's and round-tailed ground squirrels appeared to call in order to warn adult relatives because they called at a time of the year when only adults were above ground (Dunford 1977, Sherman 1977, but see Shields 1980).

Presence of close kin above ground- For the Columbian ground squirrels studied here, the presence of kin within an individual's immediate social environment (i.e., visible above ground) at the moment of predator detection did not appear to influence the tendency for squirrels to give nonrepetitive or repetitive calls in response to either an aerial or terrestrial predator model. Sherman (1977) found that reproductive females called to terrestrial predators regardless of whether their adult relatives were above ground. He suggested that females may gain more by responding quickly to predators than by trying to determine whether kin are in immediate jeopardy.

### Repetitive Calling

Columbian ground squirrels gave repetitive calls during 79% of flying disc trials and 86% of badger trials. In Lickley's (1984) study repetitive calls were given during 90% of trials using a trained hawk, and during 60% of trials with a trained dog.

Age and Sex- Age did not significantly influence the occurrence of repetitive calling during flying disc or badger trials among females or males. Within age classes, the occurrence of repetitive calling during flying disc trials was equally probable for females and males. There was a tendency for adult females to give repetitive calls more often than adult males following encounters with the badger. More specifically, parous females, but not nonparous females, called significantly more often than males. Such a trend was not evident among yearlings.

Kinship and Parity- The effects of kinship and parity on repetitive calling behaviour have not previously been examined for any sciurid species. In the present study parous females were more likely than nonparous females to emit repetitive calls in response to a terrestrial predator. Individuals that perceive themselves or their juvenile offspring to be particularly vulnerable to a second badger attack, would gain the most by attempting to maintain vigilance among conspecifics.

In regard to the functional significance of repetitive calling, Lickley (1984) made an important distinction between the situation when the predator is visible and when the predator is not visible. He suggested that while the predator is in sight repetitive calling serves to inform conspecifics about the presence of the predator (see also Owings and Hennessy 1984). An alternative, but not mutually exclusive, hypothesis is that repetitive calling may function to discourage further attacks by informing the predator that at least one squirrel is vigilant (Owings and Hennessy 1984). This may be particularly effective against predators that rely on surprise attacks to capture their prey, e.g., goshawks.

Repetitive calls given once the predator is no longer visible, probably function to maintain or increase vigilance among conspecifics. Increased vigilance among conspecifics could function as an early warning during subsequent attacks (Betts 1976, Lickley 1984, Owings and Hennessy 1984, Owings et al. 1986, Loughry and McDonough 1988). Anecdotal evidence suggests that both aerial and terrestrial predators will attempt another attack after apparently leaving the area (Barash 1973; Lickley 1984; Owings et al. 1986; W. J. King, pers. comm.; pers. obs.).

### Is Calling "Risky" For Columbian Ground Squirrels?

The condition under which antipredator vocalizations are given is presumably influenced by the balance between the risks and benefits associated with calling. Indeed, some of the difficulty in explaining the evolution of such a seemingly altruistic behaviour as antipredator calling stems from the uncertainty of whether callers experience a risk. However, for most sciurids, the potential costs associated with calling (or not calling) have not been quantified (but see Sherman 1977, 1985). In my study, the infrequency of predator attacks and kills (unpubl. data), and the difficulty of identifying the caller, made it impossible to determine whether callers are more vulnerable to predation than noncallers. However, data on the squirrel's position relative to the simulated predator and escape burrows while calling permits an indirect evaluation of the relative risk experienced by calling individuals.

Columbian ground squirrels usually did not give a nonrepetitive call unless distant from the flying disc and not until after reaching the safety of a burrow entrance. That suggests that in this species calling to an aerial predator entails relatively little risk. Similarly, there is no evidence to suggest that callers are in greater danger of being preyed upon by avian predators than noncallers in Richardson's ground squirrels (Davis 1984) and hoary marmots (Noyes and Holmes 1979). If there is little cost, then nonrepetitive calling in response to an aerial predator should not be considered altruistic (see similar arguments for hoary marmots, Noyes and Holmes 1979). In the only study to adequately quantify the costs associated with calling in the presence of an aerial predator, Sherman (1985) showed that Belding's ground squirrels that called were captured less frequently than non-callers and he reasoned that calling was an act of "self-preservation".

The nonrepetitive vocal responses of Columbian ground squirrels to the badger model do not clearly support the assumption that calling increases a caller's vulnerability to a terrestrial predator. Squirrels in close proximity to the badger were as likely to call as more distant animals. However, because all but parous females called infrequently, calling may indeed be risky, and thus selected against. For parous females the risk to personal safety associated with calling may be outweighed by the benefits of warning and aiding the escape of vulnerable juvenile offspring. A few studies have concluded that callers do not suffer increased mortality when exposed to terrestrial predators (e.g., Barash 1975, Dunford 1977). In Barash's (1975) study predators killed marmots that did not call. He reasoned that callers were already aware of a predator and were relatively safe from predation themselves. To date, only Sherman (1977) has demonstrated that antipredator calling to terrestrial predators by a sciurid may entail significant risk to the caller. Belding's ground squirrels that called were stalked or chased and captured more often than non-callers (Sherman 1977, 1985).

## Conclusions

Most studies of antipredator calling by ground-dwelling sciurids have concluded that kin selection has played an important role in the evolution and maintenance of this behaviour in response to terrestrial predators (e.g., Dunford 1977, Sherman 1977, Schwagmeyer 1980, Davis 1984). However, for a few ground squirrel species calling in response to terrestrial predators is limited largely to parous females and their young (Schwagmeyer 1980, Owings et al. 1986). Armitage (1988) argued that the behaviour of ground-dwelling squirrels is directed toward maximizing their direct fitness, rather than aiding the reproduction of kin. The antipredator calling behaviour of adult and yearling female Columbian ground squirrels to a badger model suggests that parous females are attempting to maximize their direct, rather than indirect fitness, and calling in this context should be considered a component of parental care.

A kin selection argument (c.f., Davis 1984) appears insufficient to explain the observed pattern of antipredator calling to an aerial predator model by Columbian ground squirrels. In the present study, the tendency for ground squirrels to emit nonrepetitive and repetitive calls was generally equitable among age, sex, parity, and kin classes. Sherman (1985) concluded that Belding's ground squirrels use calls in response to aerial predators "selfishly" to elicit running among other squirrels, and thereby minimizing their own conspicuousness while running. Immediate self-preservation is unlikely the selective force acting on callers, since Columbian ground squirrels usually did not call until they had already reached the safety of a burrow. Given the apparent low risk to callers, calling to aerial predators may have evolved via reciprocal "altruism" or cooperation (Trivers 1971, Axelrod and Hamilton 1981). Reciprocity may be favored if the cost to the caller is small and the benefit to the recipient is large (Trivers 1971). Further, reciprocal altruism will be favored when animals interact frequently and over extended periods, if animals can recognize individuals, and if callers can withhold benefits from non-reciprocators (Trivers 1971, Axelrod and Hamilton 1981). The applicability of Trivers'

(1971) hypothesis to explain antipredator calling by Columbian ground squirrels may be reduced, however, because of the caller's limited ability to restrict benefits to potential future altruists. All individuals within a certain range can hear the call such that non-reciprocators and altruists cannot be discriminated. Antipredator calling may, of course, be multiply-targeted, whereby calls are directed at conspecifics and the predator (Owings and Hennessy 1984). Calls directed at the predator may serve as both a "pursuit deterrent" and as a means of reducing the likelihood of later attacks by the same predator. The benefit to an individual of reducing a predator's immediate or future hunting success may be greater than any initial cost in antipredator calling.

Figure 1. Proportion (%) of ground squirrels that gave antipredator calls in response to the badger in relation to the distance between the badger and the subject squirrel. Numbers above bars refer to the number of focal animals.

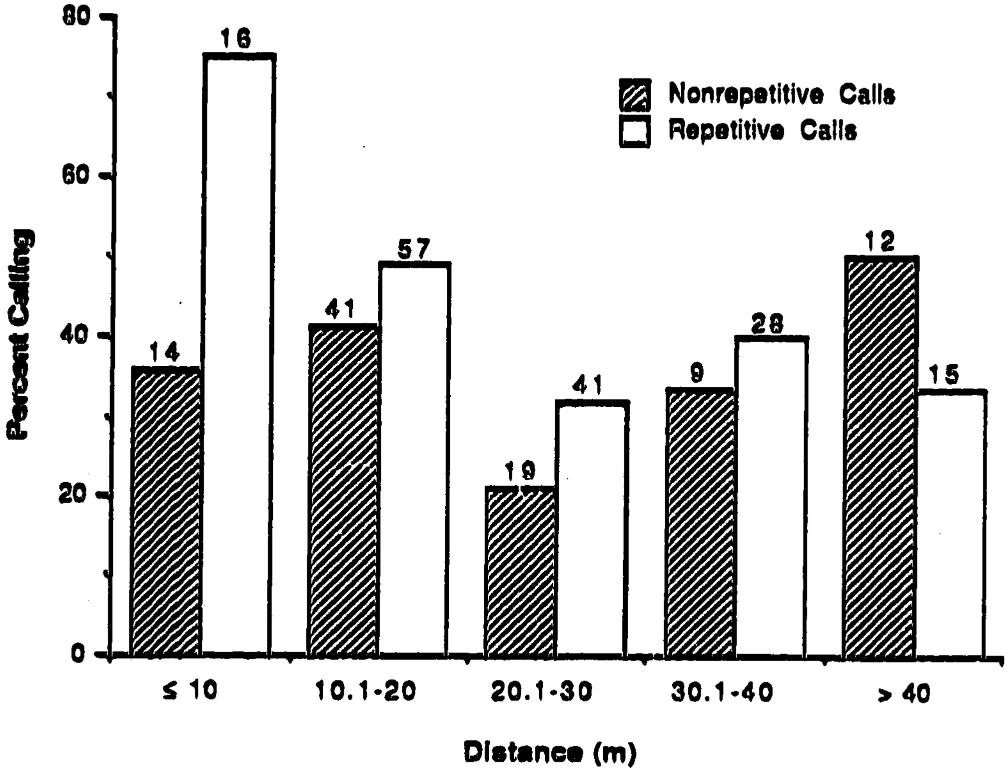

80
60
40
20
0
Percent Calling
16
14
41
57
19
41
9
28
12
15
▨ Nonrepetitive Calls
☐ Repetitive Calls
≤ 10
10.1-20
20.1-30
30.1-40
> 40
Distance (m)

Figure 2. Frequency (%) of antipredator calling to the flying disc by female ground squirrels with or without juvenile offspring and/or other close kin living in the colony (see Legend below). Data for nonrepetitive calling includes nontarget squirrels only. Numbers above bars refer to the number of subject animals observed.

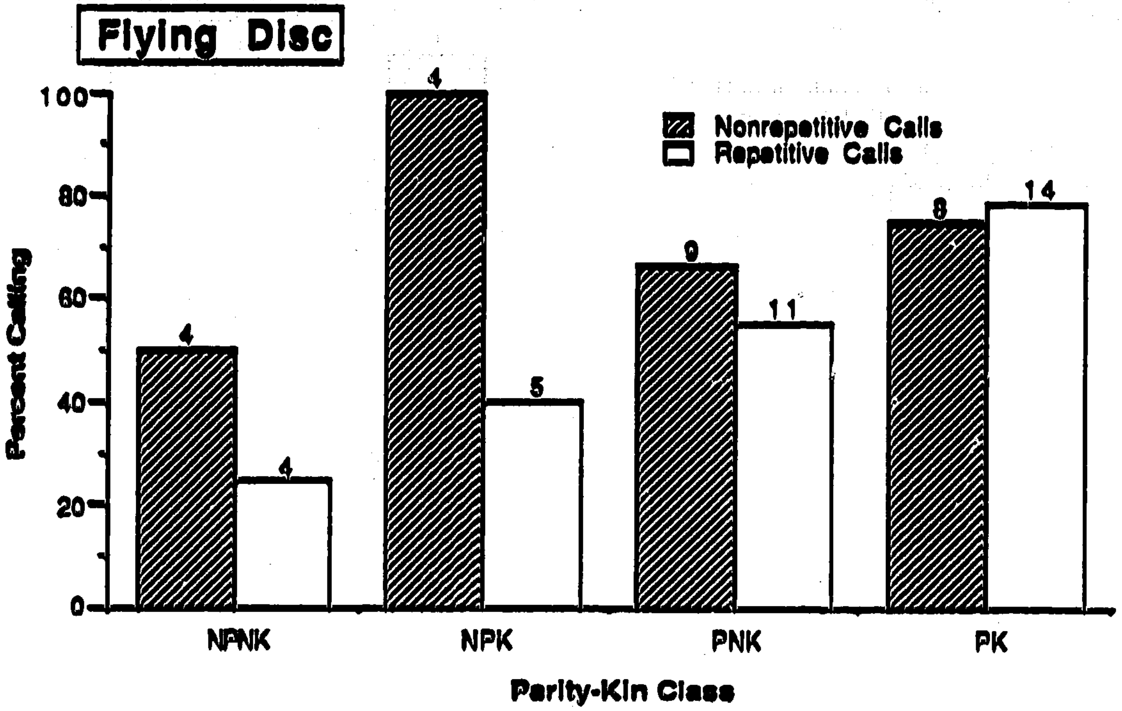
Legend: NPNK = Nonparous yearling and adult females without close kin (e.g., mothers, daughters, littermate and nonlittermate siblings, excluding juveniles).

NPK = Nonparous yearling and adult females with close kin.

PNK = Parous yearling and adult females without close kin.

PK = Parous yearling and adult females with close kin.

Figure 3. Frequency (%) of antipredator calling to the badger by female ground squirrels with or without juvenile offspring and/or other close kin living in the colony (see Legend above). Numbers above bars refer to the number of subject animals observed.


Flying Disc
100
80
60
40
20
0
Percent Calling
▨ Nonrepetitive Calls
☐ Repetitive Calls
4
4
4
5
9
11
8
14
NPNK
NPK
PNK
PK
Parity-Kin Class

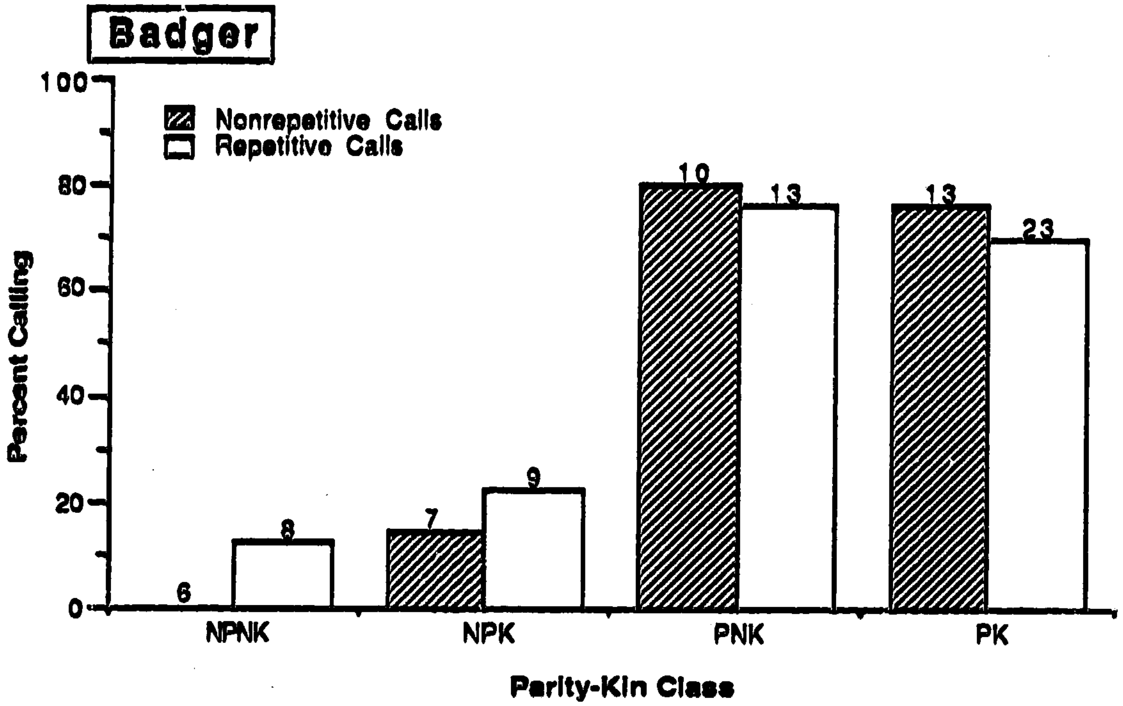

Badger
100
80
60
40
20
0
Percent Calling
▨ Nonrepetitive Calls
☐ Repetitive Calls
6
8
7
9
10
13
13
23
NPNK
NPK
PNK
PK
Parity-Kin Class

Table 1. Context in which initial vocal responses by Columbian ground squirrels to simulated aerial (frisbee, non-target squirrels) and terrestrial (badger) predators occurred.

| | Context | | | | |
|---|---|---|---|---|---|
| | while stationary away from burrow | before running | while running | after running | already at a burrow |
| **Stimulus** | | | | | |
| Flying disc | 0 | 9 | 5 | 12 | 16 |
| Badger | 8 | 13 | 3 | 3 | 8 |

G = 20.19, p = 0.0005, df = 4

Table 2. Context in which initial vocal responses were emitted by ground squirrels <20 m and >20 m from the badger model.

| Proximity to badger | Called before running, or called and remained stationary | Called while, or after, running |
|---|---|---|
| <20 m | 10 | 6 |
| >20 m | 11 | 0 |

Fisher exact test, p = 0.053

Table 3. Frequency (%) of nonrepetitive calling by age/sex class for Columbian ground squirrels during the post-weaning period in response to simulated aerial (flying disc)(non-target subjects only) and terrestrial (badger) predator attacks. Numbers in parentheses refer to number of subject animals. N = number of individual squirrels.

| Age/Sex Class | N | % Calling to flying disc | N | % calling to badger |
|---|---|---|---|---|
| Adult female | 11 | 58.8 (17) | 10 | 56.2 (16) |
| Adult male | 5 | 25.0 (8) | 8 | 12.5 (8) |
| Yearling female | 6 | 100.0 (8) | 12 | 50.0 (20) |
| Yearling male | 2 | 66.7 (3) | 4 | 50.0 (6) |
| Juvenile female | 6 | 63.6 (11) | 17 | 27.3 (22) |
| Juvenile male | 12 | 65.0 (20) | 21 | 26.1 (23) |

Table 4. Frequency (%) of nonrepetitive calling by nontarget parous and nonparous adult and yearling females in response to the flying disc. Numbers in parentheses refer to the number of subject squirrels.

| Age Class | Reproductive Status | |
|---|---|---|
| | Parous | Nonparous |
| Adult | 58 (12) | 60 (5) |
| Yearling | 100 (5) | 100 (3) |

Table 5. Frequency (%) of nonrepetitive calling by parous and nonparous adult and yearling females in response to the badger model. Numbers in parentheses refer to the number of subject squirrels.

| | Reproductive Status | |
|---|---|---|
| Age Class | Parous | Nonparous |
| Adult | 82 (11) | 0 (5) |
| Yearling | 75 (12) | 13 (8) |

Table 6. Comparison of the frequency (%) of nonrepetitive calling by nontarget juveniles, and parous adult and yearling females combined, with and without close kin (see Legend, Fig. 2) visible above ground during flying disc trials. Numbers in parentheses refer to the number of subject animals.

| | Kin Present | No kin present |
|---|---|---|
| Age Class | | |
| Parous adult and yearling females | 67 (12) | 80 (5) |
| Juveniles | 65 (23) | 63 (8) |

Table 7. Comparison of the frequency (%) of nonrepetitive calling by juveniles, and parous adult and yearling females combined, with and without close kin (see Legend, Fig.2) visible above ground during badger trials. Numbers in parentheses refer to the number of subject animals.

| Age Class | Kin Present | No kin present |
|---|---|---|
| Parous adult and yearling females | 82 (17) | 67 (6) |
| Juveniles | 28 (25) | 25 (20) |

Table 8. Frequency (%) of repetitive calling by age/sex class for Columbian ground squirrels during the post-weaning period in response to simulated aerial (flying disc) and terrestrial (badger) predator attacks. Analysis of flying disc trials includes both target and non-target subjects. Numbers in parentheses refer to number of subject animals. N = number of individual squirrels.

| Age/sex Class | N | % Calling to flying disc | N | % calling to badger |
|---|---|---|---|---|
| Adult female | 13 | 52.4 (21) | 8 | 58.3 (24) |
| Adult male | 7 | 33.3 (12) | 7 | 25.0 (12) |
| Yearling female | 8 | 69.2 (13) | 10 | 51.7 (29) |
| Yearling male | 3 | 50.0 (4) | 4 | 71.4 (7) |
| Juvenile female | 9 | 56.5 (23) | 12 | 38.6 (44) |
| Juvenile male | 13 | 48.3 (29) | 14 | 37.5 (40) |

Table 9. Mean duration (min ± 1 SD) of repetitive calling bouts to the flying disc by target and nontarget squirrels in relation to age/sex class. Numbers in parentheses refer to the number of calling bouts.

| | Position relative to the flying disc | |
|---|---|---|
| Age/sex class | Target | Nontarget |
| Adult female | 7 ± 4.2 (2) | 15 ± 8.7 (19) |
| Yearling female | 9 ± 7.3 (4) | 15 ± 5.9 (14) |
| Juvenile female | 8 ± 3.8 (10) | 16 ± 4.7 (10) |
| Adult Male | 14 ± 3.5 (2) | 16 ± 6.4 (5) |
| Yearling Male | 9 (1) | 11 ± 0.6 (3) |
| Juvenile male | 11 ± 5.3 (5) | 16 ± 9.9 (27) |

Table 10. Mean duration (min ± 1 SD) of repetitive calling bouts to the badger model in relation to age/sex class. Numbers in parentheses refer to the number of calling bouts.

| | Age Class | | |
|---|---|---|---|
| Sex Class | Adult | Yearling | Juvenile |
| Female | 29 ± 16.5<br>(9) | 12 ± 6.4<br>(10) | 15 ± 10.6<br>(12) |
| Male | 18 ± 13.4<br>(2) | 7 ± 2.8<br>(2) | 9 ± 5.3<br>(9) |

Table 11. Frequency (%) of repetitive calling by parous and nonparous adult and yearling females in response to the flying disc. Numbers in parentheses refer to the number of subject squirrels.

| | Reproductive Status | |
|---|---|---|
| Age Class | Parous | Nonparous |
| Adult | 56 (16) | 40 (5) |
| Yearling | 89 (9) | 25 (4) |

Table 12. Frequency (%) of repetitive calling by parous and nonparous adult and yearling females in response to the badger model. Numbers in parentheses refer to the number of subject squirrels.

| | Reproductive Status | |
|---|---|---|
| Age Class | Parous | Nonparous |
| Adult | 81 (16) | 13 (8) |
| Yearling | 65 (20) | 22 (9) |

Table 13. Comparison of the frequency (%) of repetitive calling by nontarget juveniles, and parous adult and yearling females combined, with and without close kin (see Legend, Fig. 2) visible above ground during flying disc trials. Numbers in parentheses refer to the number of subject animals.

| Age Class | Kin Present | No kin present |
|---|---|---|
| Parous adult and yearling females | 67 (18) | 71 (7) |
| Juveniles | 48 (40) | 67 (12) |

Table 14. Comparison of the frequency (%) of repetitive calling by juveniles, and parous adult and yearling females combined, with and without close kin (see Legend, Fig. 2) visible above ground during badger trials. Numbers in parentheses refer to the number of subject animals.

| Age Class | Kin Present | No kin present |
|---|---|---|
| Parous adult and yearling females | 74 (27) | 67 (9) |
| Juveniles | 31 (51) | 48 (33) |

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# IV. Effects of Reproductive Status on Activity and Foraging Behaviour of Adult Female Columbian Ground Squirrels

## Introduction

In order to maximize their inclusive fitness animals should behave in a manner that favors the success of current reproductive effort while maximizing their probability of surviving to the next breeding season. For many animals reproductive success and survivorship are inextricably linked to the trade-off between the conflicting demands of foraging efficiency and predator avoidance. Empirical evidence indicates that the trade-off between foraging and anti-predator behaviour is sensitive to changes in the relative importance of food demand and predation risk (e.g., Grubb and Greenwald 1982, Dill and Fraser 1984, Morgan 1988). Moreover, some animals appear capable of attaining an "optimal" balance that represents the best compromise between the conflicting selective pressures of feeding and predator avoidance (e.g., Sih 1980, Lima 1985, Lima and Valone 1986). A change in the relative costs and benefits of foraging and antipredator behaviour often results in a concomitant shift in behavioural priorities. For instance, animals may take greater risks in order to increase food intake when energy demand is high (e.g., Caraco et al. 1980, Grubb and Greenwald 1982, Metcalfe and Furness 1984, Schneider 1984, Hogstad 1988, Lima and Valone 1986, Lima 1988, Morgan 1988). For female mammals, reproduction is metabolically expensive, often placing increased nutritional demands on females, particularly during lactation (Migula 1969, Millar 1975, 1977, 1978, 1979; Hanwell and Peaker 1977, Kiell and Millar 1980, Lochmiller et al. 1982, Oftedal 1984). In addition, during lactation the necessity of nursing and keeping young warm may impose time constraints on the foraging activity of females. Thus, during periods when energetic need is high and foraging time is limited, parous females may alter their foraging tactics, possibly at the expense of increased predator risk (e.g., Barash 1980).

In ground-dwelling sciurids, females have sole responsibility for rearing young and energy demand increases from gestation through lactation (Kenagy 1987, Kenagy et al. 1989a,b; Melcher et al. 1989, Michener 1989). Differences in the allocation of time by parous and nonparous females might be expected as a consequence of the disparity in nutritional (and time) demands (e.g., Barash 1980). In particular, the need for high food intake may affect the cost a foraging parous female will accept to attain the required nutrients invested in reproduction.

Since Columbian ground squirrels (Spermophilus columbianus) appear to make trade-offs between predator avoidance and foraging when risk of predation increases (chapter two), it is possible that the balance of this trade-off may be affected by energetic demands imposed on reproductive females. In addition to the high energy demands of gestation and lactation incurred by parous females, Columbian ground squirrels experience a comparatively short active season in which to accumulate the fat reserves necessary for overwinter survival (Michener 1974, Michener 1978; Murie and Boag 1984, Young 1988). Further, for many species of ground-dwelling squirrels most of those fat reserves are deposited after the female has weaned her offspring (Murie 1973, Morton 1975, Andersen et al. 1976, Armitage et al. 1976, Michener 1978, Rickart 1982, Phillips 1984, Choromanski-Norris et al. 1986), and this may be true of Columbian ground squirrels as well.

Among the ground-dwelling sciurids, the effect of reproduction on foraging and antipredator behaviour has only been examined rigorously for hoary marmots (Marmota caligata)(Barash 1980). No studies have examined the effects of reproduction on the activity patterns of females concurrently with analysis of patterns of body mass gain. Information regarding the latter may help to clarify any relationship between the energetic demands of reproduction and observed behaviour patterns. In the present study my primary aim was to investigate the effect of reproduction on the activity patterns, particularly foraging and antipredator behaviour, of adult female Columbian ground squirrels. More specifically, are differences in energy demand between parous and nonparous females reflected in differences in behaviour? Secondly, do any behavioural differences imply exposure to increased predation risk by parous females?

I hypothesized that parous, compared to nonparous, females will accept greater risks, particularly during lactation, in order to obtain the required energy intake. To examine this hypothesis, I tested the following predictions.

1) Parous females will spend a greater proportion of their total daily active period above ground foraging than nonparous females.

2) Parous females will forage earlier in the day and later in the evening than nonparous females, in order to increase their daily food consumption.

3) If increased time spent foraging head down increases the rate of food intake (see arguments in chapter 2), parous females will devote less time to vigilance while foraging than nonparous females.

4) If the availability of preferred, high quality forage increases with increasing distance from burrows (e.g., Andrusiak and Harestad 1989), parous females should forage farther from escape burrows than nonparous females.

To help clarify the role of reproduction as a factor mediating the behaviour of adult females, the effects of parity on body mass gain and the duration of the active season are described and discussed in the context of observed seasonal patterns of activity.

## Study Animal

Columbian ground squirrels are medium-sized (400-900 g), diurnal, group-living rodents, which inhabit montane and subalpine meadows throughout much of west-central North America (Hall and Kelson 1959). They have a relatively short (3-4 month) active season in which to breed, produce young, and accumulate fat reserves before entering hibernation in late summer (Boag and Murie 1981, Young 1988). In southwestern Alberta sexually mature, typically >1 yr old, Columbian ground squirrels emerge from hibernation in April and May, and breed shortly thereafter. Males and females typically mate with >1 individual (J.O. Murie, pers. comm.). The gestation period lasts 24 d (Shaw 1925, Murie and Harris 1982) and litters emerge from natal burrows 24-32 days after birth (Murie and Harris 1982)(during June and July in southwestern Alberta). Typically, each female produces one litter of 1-6 young (Wroot et al. 1987). Columbian ground squirrels in southwestern Alberta usually do not attain sexual maturity until 2 years of age (Murie and Harris 1982), although some females breed as yearlings (Festa-Bianchet 1981, Dobson and Murie 1987; see also Dobson and Kjelgaard 1985a).

Columbian ground squirrels in southwestern Alberta are subject to a wide variety of terrestrial predators, including grizzly bear (Ursus arctos), coyote (Canis latrans), American badger (Taxidea taxus)(Dobson and Kjelgaard 1985b, Hackett 1987), weasel (Mustela spp.), and a number of avian species, particularly northern goshawk (Accipiter gentilis), golden eagle (Aquila chrysaetos)(Boag 1977), red-tailed hawk (Buteo jamaicienssis), prairie falcon (Falco mexicanus) and common raven (Corvus corax).

## Study Area

Columbian ground squirrels were observed at Dyson Creek, a 1.06 ha grassy meadow almost entirely surrounded by aspen (Populus spp.) woodland, situated within the Sheep River Wildlife Sanctuary, 32 km west of Turner Valley, Alberta (50° 39′ N, 114° 39′ W; elevation 1570 m). A creek divides the study area (Fig 1. in Festa-Bianchet and Boag 1982). The site is more fully described in Festa-Bianchet (1981) and Festa-Bianchet and Boag (1982). Cattle graze the area from late June through August; however, in order to maintain uniform visibility throughout the study area, portions of the meadow were mowed once in mid-June.

In spring, 1988, the Dyson Creek colony consisted of 17 adult (> 2 yr old)(6 males and 11 females), and 13 yearling (8 males and 5 females) ground squirrels.

## Methods

### General procedures

All adult female ground squirrels were trapped at least once every two days during the breeding season, and weekly thereafter, using live traps (National and Tomahawk) baited with peanut butter. For ease of identification the fur of each squirrel was marked with an individually distinct pattern using human hair dye (Lady Clairol Nice N' Easy blue-black, No. 124). Location, body mass, head width, and reproductive status was recorded at each capture. Body mass was recorded to the nearest 5-g with a spring balance (Pesola 1500 g). Head width was measured to the nearest 0.1 mm using a modified dial caliper. Reproductive status and time of breeding of females were determined from the degree of swelling of the vulva and vaginal smears during the breeding season, and from swelling of the nipples during lactation (Murie and Harris 1982, 1988). In a given year most adult female Columbian ground squirrels give birth (62-92%, Murie and Harris 1982, Dobson et al. 1986, Dobson and Murie 1987). To ensure an adequate sample of nonparous females I treated a portion of the adult female population with a short-term chemosterilant, ethynylestradiol 3-methyl ether (Mestranol), to block pregnancy (Goulet and Sadleir 1974, Hackett 1987). Beginning with the second adult female to come into oestrus, and alternating females thereafter, individuals were force-fed, using a plastic syringe, a solution consisting of 1 mg of Mestranol suspended in 1 ml of peanut oil on the day of, and the day following breeding (Goulet and Sadleir 1974, Hackett 1987). A total of six females received Mestranol, five of which subsequently did not gestate. Of the five females not given Mestranol (hereafter, nonparous females), four produced litters, and one bred but apparently did not lactate. As a result, the sample of adult females consisted of five parous females (ages = 2, 2, 6, 6, 6 yr) with litter sizes of 3, 3, 3, 4, 5, and six nonparous females (ages = 2, 2, 2, 3, 4, 5 yr).

In spring, beginning before any females had emerged from hibernation, the study area was trapped or observed daily; therefore, the date of emergence from hibernation and date of breeding was known for all adult females. The median date of breeding was not significantly different between parous females (22 April, range = 16 April-12 May) and nonparous females (27 April, range = 22 April-10 May)(Median test, p=0.242). In late July and August the colony was observed or trapped at least once during any three day period. Consequently, the date of entry into hibernation was known for several females. Otherwise, the date of fall immergence was taken as the midpoint of the interval of the last sighting for the year and the first day of subsequent observation or trapping when the individual was no longer seen for the remainder of the season (Michener 1978).

Kin relationships were determined by trapping each litter on emergence at or near the natal burrow associated with the mother. Age and genealogical data were available for all adult females, first captured as juveniles in previous years (D. A. Boag, unpubl. data).

The location and entrance diameter of all known burrows available to ground squirrels for escape from predators was recorded as they were opened. Each hole was labeled with a uniquely numbered aluminum tree tag (Canadian Forestry Supplies) anchored with a nail, and rechecked at least once per week. Locations were later plotted on 1/157 scale maps of the areas.

The study area was subdivided by means of a 10 x 10 m grid with colour-coded surveyor's flags on wire stakes used to mark grid coordinates. To increase the accuracy of estimates of squirrel locations, small (20 cm high) uniformly colored flags were placed halfway between grid coordinates.

### Behavioural observations

Ground squirrel activity was recorded using scan and focal-animal sampling techniques (Altmann 1974). Observations were made from two 2-3 m high wooden stands, one located at the southwest edge, the other near the centre of the colony (see Fig. 1 in Festa-Bianchet and Boag 1982), using 10 x 40 or 10 x 50 binoculars. During the breeding period a single observer monitored ground squirrel activities from the centre platform, recording the identity, location to the nearest 0.25 m, and activity of each animal at hourly intervals. Between scan samples, focal animals were observed for 5-min (or until lost from sight). Focal animals were chosen according to a randomly generated list of all individuals present on the study area. Following the breeding period, two observers collected data on the activities of adult females only; one observer on the southwest platform monitored the three adult females inhabiting the 0.3 ha area south of the creek, while the other observer recorded the behaviour of eight adult females residing on the larger portion of the meadow north of the creek (Fig. 1 in Festa-Bianchet and Boag 1982). Behavioural sampling procedures post-breeding involved scan-sampling at 15-min intervals. Since the entire study area could be observed easily, females not recorded during a scan or focal sample were assumed to be below ground. The relatively small size of the meadow, small number of females monitored, knowledge of each individual's main area of activity and location of the nest burrows of parous females, coupled with frequent and intensive scanning, permitted almost continuous tracking of each female's movements. Infrequently, adult females moved into the woodland surrounding the meadow rendering them unobservable. At such times individuals were recorded as being out of sight and were not included in any of the analyses. Data were dictated into a tape recorder and later transcribed for analyses.

Observations were made from 14 April, at or soon after females had emerged from hibernation, to 4 August, when all but one (parous) adult female had immerged to hibernate, for 117 h on 28 days. Observation periods, usually 4-5 h in length, were evenly distributed between morning (0700-1100h), afternoon (1100-1500h), and evening (1500-2000h). Morning watches were initiated prior to ground squirrel emergence, and evening watches were continued until the last animal ceased above-ground activity, except on 2 days when observations were interrupted by horseback riders who set up camp on the meadow. The earliest and latest appearance of animals above ground were 0709h and 2009h, respectively. Therefore, analyses of time allocation were based on data collected between 0700h and 2000h.

For some analyses the active season of each adult female was divided into nine periods relative to the day of breeding: (1) pre-breeding (from emergence to day of breeding), (2) early and (3) late gestation (corresponding to the first and second halves of the 24 d gestation period, respectively), (4) early and (5) late lactation (corresponding to the first and second halves of the 30 d lactation period, respectively), (6)-(9) post-weaning periods 1 through 4, each 14 d in length. For some analyses the data were pooled within periods 2 and 3 (gestation), periods 4 and 5 (lactation), periods 6 and 7 ("early" post-weaning), and periods 8 and 9 ("late" post-weaning), in order to attain more robust sample sizes.

The behavioural categories recorded during this study included; (1) below ground, (2) foraging: time spent with head down searching for, and ingesting vegetation, and time spent masticating food in a vigilant posture, usually with head up (see Methods, chapter 2), (3) "idle" time spent resting and grooming at the entrance of a burrow, and (4) vigilance: time spent either with head up, in a sitting position, or vertical while away from a burrow (see diagrams of Harris et al. 1983 and Lickley 1984).

For scan sample data, the percentage of time devoted by each female to a given category of behaviour was calculated by summing the number of scan samples in which a given behaviour was recorded and dividing by the total number of scans for each phase of the active season. The values for each individual were pooled within each reproductive class to obtain an average percentage frequency for each behaviour. A minimum of eight scans for a given female during any one reproductive period was required for an individual to be included in the analysis. For the analysis of focal sampling data, observations of individuals were pooled within gestation, lactation and post-weaning periods to produce a composite record for each reproductive class. Time spent vigilant was calculated as the percentage of total focal animal minutes spent in a vigilant posture away from a burrow during each period of the reproductive cycle. The behaviours recorded are more fully described by Steiner (1970a, 1970b), Betts (1976) and Harris et al. (1983).

As squirrels were trapped and weighed weekly, for maximum resolution, body mass data were analyzed by week post-breeding.

### Statistical analyses

If applicable, the data were analyzed using parametric procedures (Sokal and Rohlf 1981, Zar 1984). Where the assumptions of normality and homogeneity of variances were not met, non-parametric statistics were applied. Within each reproductive class (i.e., parous or nonparous) comparisons of data for each period of the reproductive season were evaluated by a repeated measures analysis of variance, or the nonparametric equivalent, Friedman's $X^2$ test. Differences between parous and nonparous females within a given phase of the reproductive season were evaluated with Student's t-test or a Mann-Whitney U-test. All tests are two-tailed and differences were considered statistically significant if the probability of committing a type I error was $< 0.05$.

## Results

### Patterns of Body Mass Gain and Timing of Fall Immergence

#### Body mass changes

On the day of breeding, the average body mass of parous females was higher than that of nonparous females (Fig. 1), but the difference was not significant ($t = 1.95$, $p = 0.08$). During gestation, parous and nonparous females appeared to gain body mass at similar rates (Fig. 1).

Although parous females had a lower mean body mass the week following parturition (week 4, Fig. 1), their postpartum body mass was, on average, 19% higher than their body mass at the time of breeding (week 0, Fig. 1). The difference was significant ($t = 5.09$, $p = 0.007$). Thus, in addition to weight gain attributable to embryo development, parous females gained personal body weight during gestation.

During lactation, in late May and early June (weeks 4-7 post-breeding), the body mass of parous females stabilized, whereas that of nonparous females continued to increase (Fig. 1). Evidently, the lack of an increase in body mass by parous females during lactation was [illegible], at least in part, to their energetic investment in young. By the time litters were weaned (week 8) nonparous females had significantly greater body mass than parous females ($t = 3.29$, $p = 0.009$). A significant difference in mean body mass between the two reproductive classes persisted through weeks 9 ($p = 0.0006$) and 10 ($p = 0.007$). However, during the 3-4 weeks post-weaning (weeks 8-11) parous females appeared to gain body mass at a greater rate than nonparous females (Fig. 1); consequently, during weeks 11 ($p = 0.09$) and 12 ($p = 0.08$) the mean body mass of parous and nonparous females were not significantly different. It must be kept in mind, however, that by week 11, one, and by week 12, 3 nonparous females had already entered into hibernation. Using the final body mass recorded for each female, the pre-hibernation mean body mass of parous and nonparous females were essentially the same (last column, Table 1, $t = 0.25$, $p = 0.81$). Parous females were able to accumulate sufficient fat stores during gestation and post-weaning periods to compensate for the energetic cost of lactation. In keeping with these results, overwinter survival rates were similar for both groups, with 4 of 5 parous females and 5 of 6 nonparous females emerging in spring 1989 (D. A. Boag and D. W. R. Wiggett, unpubl. data).

### Length of active season

The mean duration of the active season from emergence to immergence, for parous and nonparous adult females was 105 days (SD = 6, range = 94-110) and 91 days (SD = 5, range = 83-98), respectively. Thus, parous females immerged into hibernation significantly later ($t = 3.99$, $p = 0.003$), 14 days on average, than nonparous females, presumably because of the added energy costs of gestation and lactation. Despite the importance of fat reserves to overwinter survival, nonparous females entered hibernation early rather than continue to accumulate additional fat deposits. Is it possible that nonparous females could have entered hibernation even earlier, without compromising their pre-hibernation body condition? There was a trend for mean body mass of both parous and nonparous females to increase during the 3 weeks prior to entry into hibernation (Table 1); however, an analysis of variance by repeated measures revealed that the increase was highly significant for parous females ($F = 28.32$, $p < 0.001$), but nonsignificant for nonparous females ($F = 2.92$, $p > 0.50$). It appears then, that nonparous females may have been capable of entering hibernation earlier than they did, or could have increased their fat stores more during the few weeks prior to hibernation. Instead, nonparous females appeared to decrease their rate of weight gain and delay their entry into hibernation. Ground squirrels that attain sufficiently large fat reserves for overwinter survival may be restricted from entering hibernation too much earlier than normal because they run the risk of depleting their fat stores before conditions are suitable for above-ground activity in spring (Trombulak 1989, c.f., Morton and Sherman 1978). Conversely, the accumulation of fat beyond a level that gives a ground squirrel a reasonable chance of surviving overwinter may be selected against if additional fat reduces locomotory ability (c.f., Trombulak 1989) and increases vulnerability to predators.

There was no strong indication that either parous or nonparous females lost weight immediately prior to entry into hibernation, as has been reported for other ground squirrels (Michener 1978, Phillips 1984). For 4 of 5 parous females and 5 of 6 nonparous females, the final recorded body mass was also the highest.

## Daily Time Budgets

### Time spent below ground

Depending on the phase of their reproductive cycle, parous females spent, on average, between 41% and 66% of their daytime activity below ground (Table 2). The trend for variation between phases of the reproductive cycle of parous females was almost significant (Friedman's $X^2 = 12.93$, $p = 0.07$). Parous females devoted somewhat more time to above-ground activities during and following the late lactation period, than earlier in the reproductive season (Table 2). An increase in time spent above ground during late lactation may be, in part, a consequence of an increase in daylength at that time (early June). However, there was no indication that nonparous females were similarly affected (Table 2). The amount of time nonparous females spent below ground throughout the active season was less variable than that of parous females (Friedman's $X^2 = 6.45$, $p = 0.38$). There were no significant differences in the amount of daily activity time spent below ground by parous and nonparous females during pre-breeding ($t = 0.93$, $p = 0.38$) and early gestation ($t = 1.17$, $p = 0.27$). During late gestation, parous females spent significantly more time below ground than nonparous females (Table 2; $t = 2.30$, $p = 0.047$). An increase in time spent below ground by parous females at that time may reflect time spent investigating, selecting and preparing a nest burrow prior to the birth of young. During early lactation, parous and nonparous females spent similar proportions of time below ground (Table 2, $t = 0.02$, $p = 0.99$); however, parous females spent significantly more time above ground than nonparous females during late lactation ($U = 27.5$, $p = 0.035$) and early post-weaning ($t = 5.21$, $p = 0.0006$), but not thereafter ($t = 1.55$, $p = 0.16$). An *a posteriori* combined comparison indicated that, overall, parous females spent significantly more time above ground than nonparous females ($X^2 = 31.14$, $p < 0.01$). Taken in sum, the significant differences between parous and nonparous females suggest that daylength is unlikely to be a primary cause of the increased time spent above ground by parous females just prior to and following the weaning of litters.

### Time spent foraging

The proportion of total daily activity time devoted to foraging by parous females differed among phases of the active season, and was highest during late lactation (Table 3). However, differences across phases of the reproductive season fell shy of statistical significance (Friedman's $X^2 = 13.95$, $p = 0.052$). The amount of time spent foraging by nonparous females varied significantly during the active season (Table 3; Friedman's $X^2 = 16.14$, $p = 0.013$). A post hoc pairwise comparison did not reveal significant differences between phases of the active season, although the data suggest than the amount of time spent foraging by nonparous females decreased in late May and June (Table 3; L1, L2, PW1), before increasing prior to entry into hibernation (Table 3; PW2). Time spent foraging did not differ significantly between reproductive classes during pre-breeding ($t = 0.99$, $p = 0.35$), or early ($t = 1.99$, $p = 0.08$) and late gestation ($t = 0.88$, $p = 0.40$). Parous females spent significantly more tin foraging than nonparous females during early ($U = 30$, $p = 0.005$) and late ($t = 4.89$, $p = 0.0009$) lactation, and during the first two weeks after litters were weaned (PW1)($U = 27$, $p = 0.05$), but not thereafter ($t = 0.19$, $p = 0.86$). An _a posteriori_ comparison revealed that overall there was a highly significant difference between parous and nonparous females in the proportion of total daily activity spent foraging ($X^2 = 40.20$, $p < 0.001$). Those results suggest that parous females may respond to the increased energetic demand of reproduction by devoting as much time as possible, within the constraints of their digestive capacity, to foraging throughout the active season. By contrast, nonparous females appear to reduce foraging in mid-season, perhaps to avoid reaching hibernation condition too early.

## Time spent "idle" at burrows

Both parous and nonparous females, on average, spent <20% of the active day in body maintenance and "resting" at burrow entrances (Table 4). There was a slight, but nonsignificant trend for the time parous females spent "idle" to vary according to phases of the reproductive season (Friedman's $X^2 = 12.15$, $p = 0.096$). By contrast, the percentage of time spent "idle" by nonparous females varied little during the active season (Table 4; Friedman's $X^2 = 3.29$, $p = 0.77$). There were no significant differences between parous and nonparous females in the proportion of daily activity time spent "idle" during any of the phases of the reproductive season (all p's > 0.10 for 7 tests)(but see below).

## Activity Budgets While Above Ground

In order to investigate further the effects of reproductive status on the activity patterns of parous females, the proportion of time spent above-ground devoted to foraging and being "idle" at burrow entrances by parous and nonparous females was compared. To reduce the variability resulting from small sample sizes data were pooled within gestation, lactation, "early" post-weaning (first month after litters were weaned), and "late" post-weaning (3-4 weeks prior to entry into hibernation) periods.

The proportion of above-ground time spent foraging did not vary significantly among phases of the reproductive season (Table 5) for either parous females (Friedman's $X^2 = 3.24$, $p = 0.36$) or nonparous females (Friedman's $X^2 = 4.33$, $p = 0.12$). The mean proportion of above-ground activity spent foraging did not differ significantly between parous and nonparous females during gestation ($t = 1.75$, $p = 0.11$) or during the first month post-weaning (PW1, Table 5)($t = 0.11$, $p = 0.92$); however, parous females devoted significantly more of their time above ground to foraging during lactation compared to nonparous females at that time (late May to mid-June)($t = 5.00$, $p = 0.0007$). That difference was due, in part, to an increase in time spent "idle" while above ground by nonparous females (Table 6). Although the average amount of above-ground time spent "idle" at burrow entrances did not differ significantly across phases of the reproductive season for either parous (Friedman's $X^2 = 4.32$, $p = 0.210$) or nonparous females (Friedman's $X^2 = 2.33$, $p = 0.31$), nonparous females spent significantly more above-ground time "idle" during the "lactation" period than parous females ($t = 3.37$, $p = 0.008$). _A posteriori_ comparisons revealed that, over the active season, parous females spent significantly more of above-ground time foraging than nonparous females ($X^2 = 18.94$, $p < 0.005$), but the difference between the two reproductive classes in time spent "idle" at burrows was not significant ($X^2 = 11.20$, $p > 0.05$). Again, those results suggest that parous females devoted near the maximum amount of time to foraging, within the constraints of their digestive system, throughout the active season, whereas nonparous females reduced time spent foraging and increased time spent "idle" during mid-season.

## Time of Day

The proportion of time spent above ground in early morning (0700-0900h) varied significantly across phases of the reproductive season for parous females (Table 7; $G = 11.83$, $p = 0.019$), but not nonparous females ($G = 3.42$, $p = 0.33$). A post hoc pairwise comparison revealed that time spent above ground by parous females in early morning differed significantly only between pre-breeding and early post-weaning periods ($p < 0.05$). Parous and nonparous females spent similar proportions of time above ground in early morning during all phases of the active season (Table 7; Log-likelihood G-test, all $p > 0.20$). The proportion of time spent above ground in late evening (1900-2000h) varied significantly across phases of the reproductive season for parous females (Table 8; $G = 16.97$, $p = 0.002$) and nonparous females ($G = 9.59$, $p = 0.02$). Parous females were active above ground in late evening significantly more than nonparous females during lactation (Table 8; $G = 4.65$, $p = 0.031$, $df = 1$), but not during other phases of the active season (Table 8; PW1, $p = 0.49$). Thus, parous females may compensate for the increased demands of lactation by extending their above-ground activity later in the day.

### Vigilance

The amount of time adult females devoted to vigilance (when not at a burrow) varied little across phases of the reproductive season for parous (Table 9; $X^2 = 0.41$, $p > 0.20$) and nonparous females ($X^2 = 0.04$, $p > 0.20$). There were no significant differences between parous and nonparous females within phases of the active season (Table 9; all $p > 0.20$).

### Foraging Distance

There was considerable intra- and inter-individual variation in the average distance that females foraged from escape burrows (Table 10). Although the average foraging distance of three of five parous females increased from gestation to the first month post-weaning, this trend was not significant for parous females as a whole (Friedman's $X^2 = 3.60$, $p = 0.16$, $n = 5$ females). The lack of a significant difference across reproductive periods persists when data for the post-weaning-2 period were incorporated in the analysis ($X^2 = 5.40$, $p = 0.14$, $n = 4$ females). Among nonparous females there was no consistent trend in foraging distance during the active season ($X^2 = 0.33$, $p = 0.85$, $n = 6$ females). The average foraging distances of parous and nonparous females did not differ significantly during gestation ($U = 17$, $p > 0.20$), lactation ($U = 18$, $p > 0.20$), or post-weaning ($U = 22$, $p > 0.20$). However, because of the considerable inter-individual variability, the entire data set (not simply the average values for individuals) was subjected to an analysis of covariance, with each individual included as the covariate. Again, no significant differences emerged between reproductive classes for gestation ($F = 0.44$, $p = 0.51$, df = 1, 100), lactation ($F = 2.44$, $p = 0.12$, df = 1, 156), and post-weaning periods (RANCOVA, Variance ratio = 1.50, $p = 0.22$, df = 1, 89).

## Discussion

### Body Mass Changes and Timing of Fall Immergence

#### Body mass changes

Parous female Columbian ground squirrels gained personal body weight during gestation as evidenced by greater female weight post-partum than at breeding. Michener (1989), Choromanski-Norris et al. (1986) and Kenagy et al. (1989b) observed a similar phenomenon in *S. richardsoni*, *S. franklinii*, and *S. saturatus*. Mean body mass of parous females remained fairly stable during lactation before increasing after litters emerged from natal burrows. Similarly, the weight of adult female *S. beldingi*, *S. armatus*, *S. elegans*, *S. franklinii* and *S. saturatus* decreased or stabilized during lactation before increasing after litters emerged from natal burrows (Morton 1975, Knopf and Balph 1977, Choromanski-Norris et al. 1986, Fagerstone 1988, Kenagy et al. 1989b).

That female ground squirrels gain personal body mass during gestation, but not during lactation is indicative of the greater energetic cost of lactation for these mammals (Kenagy et al. 1989a,b; Melcher et al. 1989, Michener 1989). As Michener (1989) suggests for S. richardsoni, investment in offspring by parous Columbian ground squirrels may be energy-limiting during lactation, but not gestation.

In the present study reproduction did not result in lower prehibernation body mass for parous females relative to nonparous females. Parous and nonparous adult females entered into hibernation at similar body masses. That result provides a possible proximate explanation for the lack of disparity in overwinter survival rates and subsequent fecundity between parous and nonparous females in Murie and Dobson's (1987) analysis of the Dyson Creek colony.

## Length of the Active Season

For female Columbian ground squirrels reproduction resulted in delayed immergence into hibernation. Parous adult females had significantly longer active seasons, by 14 days on average, compared to nonparous females. With no reproductive demands, nonparous females apparently were able to divert a large portion of their energy intake earlier in the season into fat stores for hibernation. Similarly, Goulet and Sadleir (1974) found that nonparous (Mestranol treated) females immerged into hibernation an average of 15 days earlier than parous females (untreated). A relatively prolonged period of above-ground activity among parous females relative to nonparous females has been reported for Olympic marmots, _Marmota olympus_ (Barash 1973), hoary marmots, _M. caligata_ (Barash 1976), yellow-bellied marmots, _M. flaviventris_ (Kilgore and Armitage 1978, Melcher et al. 1989), Richardson's ground squirrels, _Spermophilus richardsoni_ (Michener 1977, 1978, 1979), and Franklin's ground squirrels, _Spermophilus franklinii_ (Choromanski-Norris et al. 1986). Those differences are presumably related to the difficulty experienced by parous females in directing metabolized energy to fat reserves during lactation.

By entering hibernation earlier, nonparous females apparently did not attempt to improve their body condition further by feeding longer in the season, but rather sought to reduce the amount of time spent active. That is expected if the benefits of entering hibernation outweigh those of remaining active. The advantages of early hibernation may be enhanced if the additional survival benefits of increased fat reserves are outweighed by an increase in vulnerability to predators due to reduced locomotory ability (Trombulak 1989).

The prolonged active season of parous females, coupled with the similarity in prehibernation body masses of parous and nonparous females, indicates that immergence into hibernation may be influenced as much by an individual's physical condition as by seasonal events (Michener 1978, 1979), and are in keeping with the suggestion that the amount of fat accumulated for hibernation is regulated by a system of changing set points (Mrosovsky and Fisher 1970, Barnes and Mrosovsky 1974, Mrosovsky 1976, Dark et al. 1986).

Phillips (1984) reported that golden-mantled ground squirrels exhibited a plateau phase of little or no increase in weight just before entry into hibernation. A similar phenomenon is suggested by Morton's (1975) data for Belding's ground squirrels. Results of the present study suggest that that may have been true of nonparous, but probably not parous, females (Table 1). At Dyson Creek, the mean body mass on nonparous females did not increase significantly during the 3-week period prior to entry into hibernation.

### Time Budgets

The allocation of time by adult female Columbian ground squirrels varied depending on their reproductive status and the phase of the reproductive cycle. Over the active season, parous females spent significantly more time above ground than did nonparous females. That difference was most pronounced during late lactation and the first 3-4 weeks post-weaning, when parous females spent a significantly greater proportion of their total daily activity time foraging than did nonparous females. The increase in time devoted to foraging during late lactation and the failure of parous females to gain body mass at that time implies strongly that lactation represents a substantial energetic cost to parous females. After weaning litters parous females continued to devote relatively more time to foraging and, without the burden of nursing young, increased their body mass at a rate higher than nonparous females. By spending substantially more time above ground and foraging throughout the active season, parous females were able to attain a prehibernation body mass similar to that of nonparous females. However, differences between parous and nonparous females in time spent foraging was due largely to a mid-season reduction in foraging by nonparous females. Time spent foraging was consistently high among parous females throughout the active season, suggesting perhaps that they were foraging at near maximum capacity. The general decrease in foraging and increase in time spent "idle" by nonparous females during mid-season, and reduced rate of body mass gain later in summer, suggests that nonparous females may have delayed fattening and entering into hibernation.

### Time of Day

During lactation, but not during other phases of the active season, parous females spent more time active above ground late in the day than nonparous females. Similarly, Barash (1980) found that parous female hoary marmots foraged later in the day than nonparous females during lactation. Presumably, that allows parous females to increase their daily food intake at a time when nutritional demands are greatest. By increasing time spent above ground later in the day, parous females lengthen their daily active period and presumably increase the amount of time exposed to predators. The potential risks associated with foraging in the evening may be exacerbated because generally fewer ground squirrels are active above ground and available to detect predators at that time.

### Vigilance

The amount of time devoted to vigilance by adult female Columbian ground squirrels did not vary appreciably with either reproductive status or across phases of the reproductive season. Thus, the prediction that parous females would compromise time spent vigilant in order to increase their feeding rate is not supported. Barash (1973) reported that parous adult female Olympic marmots were more vigilant than nonparous females, particularly at the time of juvenile emergence from natal burrows, while parous Belding's ground squirrels are most vigilant during lactation (Holekamp and Nunnes 1989). Increased vigilance by parous females of those species during and shortly after lactation suggests that increased vigilance may, in part, serve to protect young that are particularly vulnerable to predators and infanticidal conspecifics.

### Foraging Distance

There was no strong indication that parous female Columbian ground squirrels foraged farther from burrows than nonparous females, nor did foraging distance vary significantly among phases of the reproductive season. During lactation, but not later, parous female hoary marmots fed significantly farther from burrows than nonparous females (Barash 1980). Interspecific differences may be, in part, a consequence of differences in the ecological environments in which marmots and Columbian ground squirrels forage. In 1988, weekly burrow densities at Dyson Creek ranged from 2.6-3.8 burrows/10 $m^2$ (unpubl. data), and individual average foraging distances were generally <4 m (Table 10). By comparison, in Barash's study, marmots foraged, on average, 5-11 m from burrows. Thus, unlike hoary marmots, which may have to forage farther from burrows to obtain high quality or abundant food, Columbian ground squirrels at Dyson Creek may not have to do so, owing, in part, to the high density of burrows in the meadow. Also, the meadow may have a heterogeneous distribution of quality forage which is not related to the distribution of burrows. The random pattern of elimination (i.e., urination and defecation) by grazing cattle may contribute to the heterogeneity of forage quality at Dyson Creek (D. A. Boag, pers. comm.)

## Conclusions

The central premise of this study was that the energetic demands of reproduction, coupled with the relatively short active season available to Columbian ground squirrels for accumulating sufficient fat reserves for overwinter survival, would predispose parous females to accept a greater risk of predation in order to meet energy requirements. The observed significant differences in the pattern of body mass gain, timing of fall immergence, and activity and foraging behaviour patterns between parous and nonparous adult females support the assumption that reproduction places substantial energetic demands upon female Columbian ground squirrels. Relative to nonparous females, parous females had a longer active season, spent more time above ground, and increased their total foraging effort by devoting proportionately more of their above-ground time to foraging and, during lactation, increasing the amount of time spent above ground later in the day. In sum, these results suggest that parous females experienced greater exposure to potential predators than did nonparous females, by sheer virtue of being active above ground for a greater absolute period of time. However, the question remains: did parous females take additional risks when energy demand was high?

Parous females did not forage further from escape burrows than nonparous females during any phase of the reproductive season. Assuming that risk of predation increases with increasing distance from burrows, that result suggests that parous females were unwilling to accept an increase in their risk to predation in order to gain the possible foraging advantages of foraging farther from burrows. It is more likely, however, given the high density of escape burrows on the meadow, that females at Dyson Creek seldom have to venture far from burrows to find suitable forage.

Time devoted to vigilance did not differ appreciably between parous and nonparous females, or across phases of the reproductive season. Assuming reduced vigilance entails a greater risk of predation, it does not appear that parous female Columbian ground squirrels traded-off increased predation risk for increased foraging benefits. Thus, there was no indication that parous females altered their foraging tactics or ran more "short-term" risks in order to meet their increased energy demands of foraging.

The lack of any strong indication that parous females increased their "short-term" risk to predation under conditions of greatest energy demand suggests that, in the short term at least, the benefits of increased foraging does not outweigh the risk of predation at any given time. Rather than increase their vulnerability to predation during a given foraging bout, parous females compensated for the energetic costs of reproduction primarily by foraging at a high rate throughout the season, and by remaining active later in summer. Evidently, any increase in the risk of predation for females that are active longer in the season is likely outweighed by the costs of not accumulating sufficient fat for overwinter survival.

Figure 1. Mean body masses of parous and nonparous adult female Columbian ground squirrels in relation to week post-breeding. Bars indicate ± 1 SD. Week 0 = day of breeding. Sample sizes for parous females for weeks 0-12 = 5, week 13 = 4, and week 14 = 1. Sample sizes for nonparous females for weeks 0-10 = 6, week 11 = 5, and week 12 = 2.

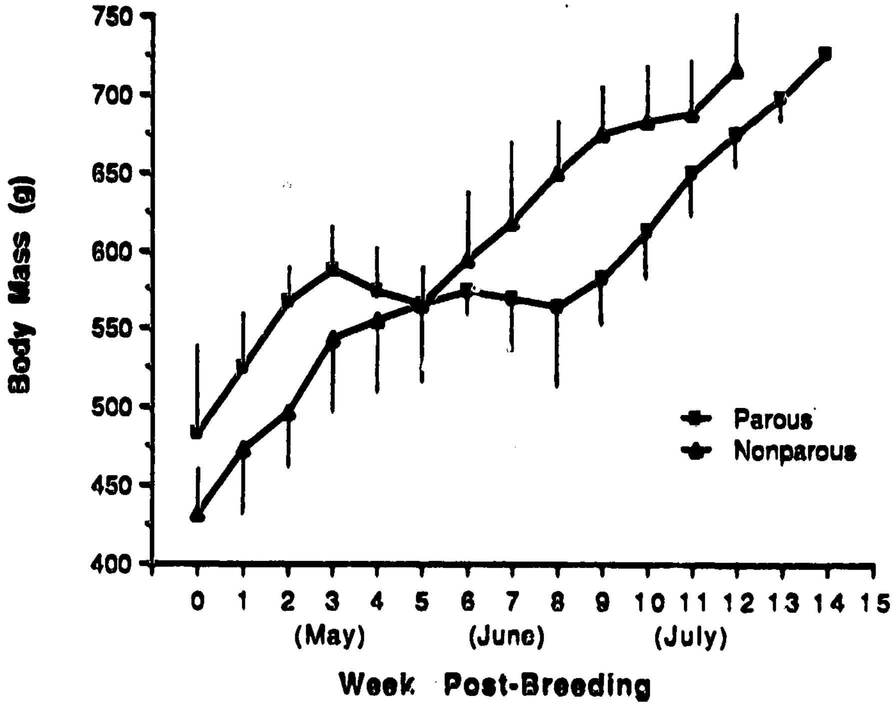
750
700
650
600
550
500
450
400
Body Mass (g)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
(May)
(June)
(July)
Week Post-Breeding
Parous
Nonparous

Table 1. Mean body mass (g) (± 1 SD) of parous and nonparous adult female Columbian ground squirrels for the three weeks prior to entry into hibernation.

| Reproductive class | Weeks Prior to Entry into Hibernation | | |
|---|---|---|---|
| | 3 | 2 | 1 |
| Parous | 649 ± 25.2 | 681 ± 20.8 | 699 ± 21.9 |
| Nonparous | 667 ± 30.4 | 685 ± 29.3 | 704 ± 40.0 |

Table 2. Mean percentage (± 1 SD) of daily activity spent below ground by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Analysis based on scan-sampling data.

| Reproductive class | Period* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | PB | G1 | G2 | L1 | L2 | PW1 | PW2 | PW3 |
| Parous females | 58<br>(13) | 53<br>(12) | 66<br>(11) | 57<br>(14) | 43<br>(1) | 44<br>(6) | 41<br>(15) | 42<br>(10) |
| Nonparous | 66<br>(15) | 61<br>(12) | 50<br>(12) | 57<br>(7) | 63<br>(14) | 66<br>(8) | 55<br>(13) | — |

* Legend for reproductive periods: PB = pre-breeding, G1 and G2 = first and second halves of gestation, L1 and L2 = first and second halves of lactation, PW1 and PW2 = first and second two week periods after litter emergence; PW3 = 3-4 week period prior to entry into hibernation.

Table 3. Mean percentage (± 1 SD) of daily activity (including time below ground) spent foraging by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Analysis based on scan-sampling data.

| Reproductive class | Period* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | PB | G1 | G2 | L1 | L2 | PW1 | PW2 | PW3 |
| Parous females | 17<br>(9) | 31<br>(7) | 19<br>(9) | 24<br>(10) | 34<br>(10) | 17<br>(7) | 23<br>(19) | 27<br>(8) |
| Nonparous | 12<br>(9) | 20<br>(11) | 23<br>(6) | 11<br>(3) | 11<br>(5) | 7<br>(3) | 25<br>(11) | — |

* Legend for reproductive periods as in Table 2.

Table 4. Mean percentage (± 1 SD) of daily activity (including time below ground) spent "idle" at burrows by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Analysis based on scan-sampling data.

| Reproductive class | Period* | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | PB | G1 | G2 | L1 | L2 | PW1 | PW2 | PW3 |
| Parous females | 14<br>(13) | 6<br>(4) | 8<br>(3) | 7<br>(3) | 12<br>(4) | 20<br>(10) | 17<br>(11) | 12<br>(9) |
| Nonparous | 14<br>(10) | 7<br>(5) | 13<br>(9) | 16<br>(8) | 13<br>(6) | 12<br>(7) | 11<br>(9) | — |

* Legend for reproductive periods as in Table 2.

Table 5. Mean percentage (± 1 SD) of time above-ground spent foraging by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Analysis based on scan-sampling data.

| | Period* | | | |
|---|---|---|---|---|
| Reproductive class | Gestation | Lactation | Post-weaning-1 | Post-weaning-2 |
| Parous females | 61 ± 10 | 58 ± 13 | 34 ± 14 | 47 ± 12 |
| Nonparous females | 48 ± 15 | 29 ± 7 | 34 ± 7 | ——— |

Table 6. Mean percentage (± 1 SD) of time above-ground spent "idle" at burrows by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Analysis based on scan-sampling data.

| | Period* | | | |
|---|---|---|---|---|
| Reproductive class | Gestation | Lactation | Post-weaning-1 | Post-weaning-2 |
| Parous females | 19 ± 4 | 21 ± 7 | 33 ± 16 | 20 ± 14 |
| Nonparous females | 23 ± 13 | 40 ± 10 | 31 ± 13 | ——— |

Table 7. Percentage of time spent above ground in early morning (0700-0900h) by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Numbers in parentheses refer to the total number of observations for all individuals combined within each reproductive class. Analysis based on scan-sampling data.

| | Period* | | | | |
|---|---|---|---|---|---|
| Reproductive class | Pre-breeding | Gestation | Lactation | PW1 | PW2 |
| Parous females | 6<br>(18) | 18<br>(49) | 25<br>(69) | 39<br>(62) | 22<br>(23) |
| Nonparous females | 12<br>(24) | 18<br>(55) | 24<br>(83) | 28<br>(60) | --- |

* Legend: PW1 and PW2 = first and second months after litter emergence.

Table 8. Percentage of time spent above ground in late evening (1900-2000h) by parous and nonparous adult female Columbian ground squirrels relative to the reproduction-based periods of the active season. Numbers in parentheses refer to the total number of observations for all individuals combined within each reproductive class. Analysis based on scan-sampling data.

| | Period* | | | | |
|---|---|---|---|---|---|
| Reproductive class | Pre-breeding | Gestation | Lactation | PW1 | PW2 |
| Parous females | 0<br>(5) | 0<br>(21) | 44<br>(16) | 14<br>(21) | 33<br>(6) |
| Nonparous females | 0<br>(9) | 0<br>(19) | 11<br>(28) | 23<br>(26) | --- |

* Legend: PW1 and PW2 = first and second months after litter emergence.

Table 9. Comparison of parous and nonparous females in the proportion (%) of time spent vigilant while above-ground (time spent "idle" at burrow entrances excluded). Numbers within parentheses refer to the total number of 1-min focal observations.

| | Period* | | | | |
|---|---|---|---|---|---|
| Reproductive class | Pre-breeding | Gestation | Lactation | FW1 | FW2 |
| Parous females | 32.5<br>(6) | 44.9<br>(13) | 49.5<br>(40) | 46.5<br>(28) | 41.5<br>(15) |
| Nonparous females | 45.3<br>(9) | 41.8<br>(16) | 45.6<br>(36) | 44.2<br>(17) | — |

* Reproductive periods as in Table 7.

Table 10. Average distance (metres) from the nearest escape burrow at which individual parous and nonparous adult female Columbian ground squirrels foraged during each reproduction-based period of the active season. Numbers in parentheses refer to the number of observations for each female. Analysis based on scan-sampling data.

| Female | Period* | | | |
|---|---|---|---|---|
| | Gestation | Lactation | Post-weaning-1 | Post-weaning-2 |
| Parous female # | | | | |
| 7771 | 2.31 (10) | 2.67 (18) | 3.09 (9) | 2.22 (5) |
| 7763 | 1.50 (11) | 1.66 (30) | 2.28 (13) | 0.96 (5) |
| 8202 | 2.60 (15) | 4.28 (17) | 2.59 (14) | 3.37 (7) |
| 8257 | 1.10 (11) | 4.51 (18) | 9.33 (5) | 4.32 (9) |
| 8260 | 4.59 (6) | 2.22 (21) | 4.94 (14) | ——— |
| Mean | 2.42 | 3.07 | 4.45 | 2.72 |
| Nonparous female # | | | | |
| 7417 | 1.73 (11) | 2.73 (6) | 2.11 (6) | ——— |
| 7745 | 3.10 (8) | 1.87 (10) | 2.84 (4) | ——— |
| 7761 | 2.28 (4) | 1.86 (9) | 1.45 (5) | ——— |
| 7779 | 4.16 (7) | 3.09 (12) | 4.80 (7) | ——— |
| 7788 | 1.98 (11) | 2.27 (7) | 2.23 (6) | ——— |
| 8344 | 2.54 (9) | 2.58 (11) | 3.30 (8) | ——— |
| Mean | 2.63 | 2.40 | 2.79 | |

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# V. General Discussion

Predation has frequently been advanced as a major factor promoting group-living in animals. Although the importance of predation in the evolution of animal gregariousness is not open to hypothesis testing, some inference regarding the role of predation as a factor maintaining antipredator behaviour in social mammals can be made by observing their behavioural responses to predator attacks and changes in the relative risk of predation. In this study I examined several aspects of the antipredator behaviour repertoire of a diurnal, group-living rodent, the Columbian ground squirrel, at two sites in southwestern Alberta. More specifically, I examined the effects of several variables on ground squirrel vigilance while foraging, and their antipredator calling and escape responses to simulated aerial and terrestrial predator attacks. In addition, I examined the effects of reproductive status on the activity and foraging behaviour of adult females to determine whether the energetic and time constraints of reproduction resulted in a greater risk of predation for adult female Columbian ground squirrels.

Observations of the vigilance behaviour of foraging Columbian ground squirrels indicate that individuals are responsive to features of their social and ecological environment that likely reflect changes in the risk of predation. The general behavioural response to a (presumed) increase in predation risk was an increase in the amount of time spent vigilant while foraging. Ground squirrels spent less time vigilant and more time foraging with the head down when feeding among conspecifics than when alone. That suggests that increased feeding efficiency without a compromise in predation risk is likely an advantage of group-living for Columbian ground squirrels. However, the suite of variables that were significant predictors of time spent vigilant differed somewhat between study sites and among age classes. At one site, Dyson Creek, ground squirrel vigilance appeared sensitive to changes in the proximity to the surrounding forest. Ground squirrels at Meadow "B", an area featuring a relatively "open" habitat, were less sensitive to their proximity to the closest forest when establishing their level of vigilance.

Unexpectedly, time devoted to vigilance by foraging ground squirrels generally decreased, rather than increased, with an increase in the distance from the nearest escape burrow. Thus, as Lima (1987) cautioned, levels of vigilance may not necessarily vary in accordance with changes in risk of predation. A decrease in vigilance with increasing distance from escape burrows may reflect a foraging strategy whereby squirrels increase their feeding rate and minimize the absolute amount of time exposed to predators, while away from burrows.

Ground squirrels at Meadow "B", but not Dyson Creek, increased the amount of time spent vigilant when foraging in areas where visibility for detecting predators was lower. That response may reflect increased predation risk in areas of reduced visibility, where predator detection distances and time to escape are shortened.

There were no consistent age or sex class differences in time spent vigilant. Assuming that greater vigilance is associated with increased predation risk, the findings of my study argue against age-specific differences in vulnerability to predators. However, juveniles were most responsive to changes in their (presumed) risk of predation, both in terms of their level of vigilance and the distance from burrows at which they foraged. Thus, younger ground squirrels may indeed be more vulnerable to predators than older squirrels, but simply compensate for greater vulnerability by modifying their foraging and vigilance behaviour in accordance with changes in their risk of predation.

At Meadow "B", where observations continued until just prior to hibernation, there was a general decline in vigilance, but not foraging distance, as the active season progressed. Such a seasonal trend is expected if the availability of preferred forage decreases throughout the season, and ground squirrels must devote proportionately more time to searching for food with the head down, in order to maintain an adequate rate of food intake. Devoting a greater amount of time to foraging as the season progresses may be especially advantageous if there are constraints on the amount of time available for the accumulation of fat prior to entry into hibernation.

Simulated aerial (flying disc) and terrestrial (stuffed badger) predator attacks revealed predator specific differences in the vocal and escape responses of Columbian ground squirrels. Ground squirrels in direct line of the flying disc (i.e., under "attack"), ran to, and into, the nearest escape burrow, and rarely gave a nonrepetitive call. Whereas squirrels distant from the flying disc often called, usually while running or after reaching the nearest burrow. The frequency of nonrepetitive calling in response to the flying disc did not vary significantly across age, sex, parity, or kin classes. Those results suggest that nonrepetitive calling to aerial predators is not costly to callers, and is unlikely to be maintained through either kin selection (c.f., Davis 1984) or immediate self-preservation benefits (c.f., Sherman 1985). Rather, Columbian ground squirrels may call to aid the escape of conspecifics, who will reciprocate in the future (Trivers 1971), and/or to decrease the hunting success of the predator (Perrins 1968).

By contrast, ground squirrels were less likely to run or call in response to the badger, rarely ran to the nearest burrow, and were more likely to call before running or while remaining stationary. However, ground squirrels in close proximity to the badger were less likely to remain stationary than those farther away. That suggests that badgers are a greater immediate threat to individuals in close proximity than to those farther away. Nonrepetitive calling in response to the badger did not differ between the sexes or among age classes; however, parity had a pronounced effect on the propensity with which yearling and adult females called. Parous females were much more likely to give nonrepetitive calls in response to the badger than were nonparous females. The presence of close kin (other than juvenile offspring) in the colony did not influence the tendency for females to give nonrepetitive calls in response to the badger. Those results suggest that nonrepetitive calling in response to the badger is a component of parental care and functions primarily to warn vulnerable juvenile offspring.

The predator-specific differences in repetitive calling paralleled those observed for nonrepetitive calling. The frequency of repetitive calling in response to the flying disc did not vary significantly across age, sex, parity or kin classes. By comparison, parous females were more likely than nonparous females to give repetitive calls in response to the badger. That suggests that parous females and their juvenile offspring may gain a greater benefit than nonparous females from maintaining greater colony vigilance (c.f., Loughry and McDonough 1988) during encounters with badgers. The similarity in parity differences for nonrepetitive and repetitive calling in response to the badger suggests that both types of antipredator calling in response to a terrestrial predator may be under hormonal control (see also Shields 1980).

Parity had a dramatic effect on the seasonal activity patterns of adult female Columbian ground squirrels. Relative to nonparous females, parous females had a longer active season, spent more time above ground, and more time foraging, particularly during late lactation and early post-weaning. Thus, in absolute terms, parous females spent proportionately more time exposed to predators than nonparous females. However, parity differences in activity patterns were due largely to reduced activity by nonparous females rather than seasonal increases by parous females. That suggests that parous females may have been foraging to near maximum capacity (within the constraints of their digestive system), whereas nonparous females may have reduced foraging and delayed accumulating sufficient fat stores for hibernation. There was no indication that parous females foraged farther from escape burrows or reduced their level of vigilance while foraging in order to increase their rate of food intake. The mortality-related costs of reduced vigilance may outweigh those associated with increased long-term exposure to predators.

To conclude, the results of my study indicate that the threat of predation is an important, but not the only, factor influencing the foraging and vigilance decisions of Columbian ground squirrels. Similar to other ground squirrel species, Columbian ground squirrels vocalize in response to predators. The antipredator calling behaviour of this species appears well developed; the tendency for squirrels to call is influenced by the type of predatory threat (i.e., aerial vs terrestrial), the squirrel's proximity to the predator, and, in the case of terrestrial predators, a female's reproductive status. The energetic demands of reproduction likely results in a greater exposure to predation for females.

Finally, I suggest that predation has played an important role in shaping the behaviour patterns of Columbian ground squirrels and likely has contributed to the evolution and maintenance of group-living in this species.

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# Appendix 1 : Tests for Habituation Effects, Efficacy of the Badger Model, and Comparisons with Naturally Occurring Predator Attacks

## Preamble

I believe the manner and speed of approach of the predator models used in this study (see chapter 3) to elicit vocal and escape responses in ground squirrels were representative of the essential sign stimuli associated with live predators. The flying disc was silent, could be thrown low, straight, and fast, all regular elements of the attack of goshawks and red-tailed hawks on the study areas (pers. obs.). The badger was mounted on the truck in a lifelike position, with tail raised, and front paws extended in front of the wheels of the truck. A human observer viewing the badger from ground squirrel height (20 cm) could not readily discern the front wheels from the badger (although they could be observed from the side and rear). Further, the movement of the badger model could be controlled easily using the line-pulley system.

Qualitatively, the ground squirrels responded to the models as they did to natural aerial (primarily goshawk) and terrestrial (dog, coyote) predators. Also, the nonrepetitive and repetitive calls given in response to the predator models were not distinguishable from those recorded by Lickley (1984) given in response to trained hawks or dogs. However, I sought to obtain quantitative support for the efficacy of the models and to test for the effects of repeated short-term exposure on the occurrence of nonrepetitive and repetitive calling and the duration of bouts of repetitive calling.

### Flying Disc and Aerial Predators

Too few target animals gave nonrepetitive calls to analyze for possible habituation to the flying disc among that class of subject animals (see Results, chapter 3); however, within trial sessions, the number of flying disc trials (1-5) during which a target subject was present did not influence significantly the probability that squirrels gave repetitive calls (Table 1; $G = 5.29$, $p = 0.26$, $df = 4$, $n = 35$), nor the mean duration of calling bouts (Table 2; Kruskal-Wallis $H = 5.78$, $p = 0.22$, $df = 4$, $n = 24$. Repeated exposure (1-4 trials) of nontarget subjects to the flying disc did not significantly influence the tendency to give nonrepetitive (Table 3; $G = 2.42$, $p = 0.49$, $df = 3$) or repetitive calls (Table 1; $G = 0.19$, $p = 0.98$, $df = 3$), nor the duration of calling bouts (Table 2; Kruskal-Wallis $H = 5.51$, $p = 0.14$, $df = 3$).

The proportion of trials during which repetitive calls were given in response to the flying disc (79% of 75) was not significantly different than the proportion given during naturally occurring avian predator attacks (89% of 19)(goshawk, red-tailed hawk, raven)(G = 0.59, p = 0.44, df = 2). By comparison, ground squirrels gave repetitive calls to only 2 of 12 (16.6%) non-threatening species (e.g., American robin, *Turdus migratorius*; common flicker, *Colaptes auratus*; blue-winged teal, *Anas discors*; solitary sandpiper, *Tringa solitaria*). The mean duration of repetitive calling bouts following flying disc trials (average = 13 min, range = 2-35, n = 47) did not differ significantly from the mean duration for natural avian predator attacks (average = 13 min, range = 3-22, n = 15)(U = 276.5, p > 0.21).

### *Badger Model and Control*

The number of times (1-3) an individual ground squirrel was exposed to the badger during a trial session did not significantly influence the probability of emitting either nonrepetitive (Table 3; G = 0.51, p = 0.77, df = 2, n = 95), or repetitive calls (Table 1; G = 0.11, p = 0.95, df = 2, n = 157), nor the duration of bouts of repetitive calling (Table 2; Kruskal-Wallis H = 1.16, p = 0.56, df = 2, n = 44).

The proportion of trials during which at least one squirrel gave a nonrepetitive call did not differ between the badger model and the control (Table 5; G = 1.48, p = 0.22, n = 54). The proportion of subject animals that gave nonrepetitive calls did not differ between the badger model and the control (Table 4; $G = 1.35$, $p = 0.25$, $n = 111$). However, ground squirrels were significantly more likely to give repetitive calls in response to the badger than to the control, whether analyzed for subject animals as a group (Table 4; $X^2 = 13.66$, $p = 0.0002$, $df = 1$, $n = 197$), or by the proportion of trials (Table 5; Fisher exact test, $p = 0.004$, $df = 1$, $n = 54$). Moreover, ground squirrels never approached within 5 m of the badger model ($n = 95$), although 3 of 16 (19%) individuals approached the control. The difference was statistically significant ($G = 7.47$, $p = 0.006$). The mean duration of repetitive calling bouts was not significantly different between badger trials (mean = 16 ± 12.3, $n = 44$) and control trials (mean = 10 ± 5.5)($U = 110.5$, $p > 0.20$), although the variance is high and the number of calls to the control is small.

## Conclusions

By all measures, there was no clear evidence that the propensity with which Columbian ground squirrels emitted antipredator calls in response to the predator models varied predictably with the number of times an individual was exposed to the model during trial sessions. That suggests there was little effect of any short-term habituation to the predator models. Therefore, data of nonrepetitive and repetitive calling are pooled across all trials.

Ground squirrels were as likely to give repetitive calls to the flying disc as they were to natural avian predators.

Ground squirrels were as likely to give nonrepetitive calls in response to the control as they were to the badger model. Although that result does not provide support for the use of the badger model as an appropriate predator stimulus, it is not altogether unexpected, given the artificial nature of the control. From the squirrels' perspective, under natural conditions, it may be adaptive to respond immediately to any slow moving object on the ground. Indeed, that squirrels frequently called to the control suggests those simple features may represent the essential sign stimuli necessary to elicit nonrepetitive calls to "badger-sized" predators. However, squirrels were significantly less likely to give repetitive calls in response to the control than to the badger model, suggesting that specific features of the object may be important in eliciting that type of call.

To conclude, I reaffirm my belief that the predator models used in this study were appropriate for examining the vocal and escape responses of Columbian ground squirrels to aerial and terrestrial predators, and I assume the levels of alarm and reaction of ground squirrels to the models are representative of those associated with natural predator attacks.

## Literature Cited

Lickley, D. F. 1984. Alarm vocalizations of Columbian ground squirrels (*Spermophilus columbianus*). Unpublished MSc Thesis. Univ. of Alberta, Edmonton.

Table 1. Frequency (%) of repetitive calling to the flying disc by target and nontarget animals, and to the badger model by subject animals, in relation to the number of previous trials during which individuals were exposed to the stimulus during a given trial session. Numbers in parentheses refer to the number of squirrels observed.

| | Number of trials previously exposed | | | | |
|---|---|---|---|---|---|
| Stimulus | 0 | 1 | 2 | 3 | 4 |
| Flying disc (target animals) | 75 (16) | 29 (7) | 100 (5) | 25 (5) | 100 (2) |
| Flying disc (nontarget animals) | 45 (29) | 44 (18) | 45 (11) | 56 (9) | ——— |
| Badger model (all subjects) | 45 (95) | 42 (50) | 42 (12) | ——— | ——— |

Table 2. Duration (min ± 1 SD) of repetitive calling to the flying disc by target and nontarget animals, and to the badger model by subject animals, in relation to the number of previous trials during which individuals were exposed to the stimulus during a given trial session. Numbers in parentheses refer to the number of squirrels observed.

| | Number of trials previously exposed | | | | |
|---|---|---|---|---|---|
| Stimulus | 0 | 1 | 2 | 3 | 4 |
| Flying disc (target animals) | 7 ± 5.5<br>(8) | 14 ± 4.2<br>(3) | 10 ± 4.5<br>(8) | 9 ± 4.0<br>(3) | 6 ± 0.0<br>(2) |
| Flying disc (nontarget animals) | 17 ± 7.4<br>(36) | 15 ± 9.5<br>(20) | 12 ± 6.0<br>(17) | 18 ± 9.8<br>(5) | ——— |
| Badger model (all subjects) | 14 ± 11.5<br>(31) | 18 ± 13.9<br>(11) | 25 ± 19.1<br>(2) | ——— | ——— |

Table 3. Frequency (%) of nonrepetitive calling to the flying disc by nontarget animals, and to the badger model by subject animals, in relation to the number of previous trials during which individuals were exposed to the stimulus during a given trial session. Numbers in parentheses refer to the number of squirrels observed.

| | Number of trials previously exposed | | | |
|---|---|---|---|---|
| Stimulus | 0 | 1 | 2 | 3 |
| Flying disc (nontarget animals) | 71 (28) | 72 (18) | 50 (12) | 33 (9) |
| Badger model (all subjects) | 40 (60) | 32 (31) | 25 (4) | ------ |

Table 4. Proportion (%) of ground squirrels that gave nonrepetitive or repetitive calls during badger and control trials. Numbers in parentheses refer to the number of squirrels observed.

| | Stimulus | |
|---|---|---|
| Call type | Badger model | Control |
| Nonrepetitive | 37 (95) | 19 (16) |
| Repetitive | 44 (157) | 13 (40) |

Table 5. Proportion (%) of badger and control trials during which at least one squirrel gave a nonrepetitive or repetitive call. Numbers in parentheses refer to the number of trials.

| | Stimulus | |
|---|---|---|
| Call type | Badger model | Control |
| Nonrepetitive | 67 (42) | 42 (12) |
| Repetitive | 86 (42) | 42 (12) |