

**BREEDING DISPERSAL, MALE MATING TACTICS, AND POPULATION  
DYNAMICS OF ARCTIC GROUND SQUIRRELS**

by

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## Abstract

Arctic ground squirrels are the northernmost hibernating mammal and they live in an extremely harsh and unpredictable environment with a short growing season. This environment has the potential to exert strong selection pressure on life-history traits and behaviour. I studied arctic ground squirrels living at high elevation in alpine tundra in Southwest Yukon in order to answer 5 main questions: (1) How do changes in elevation and associated habitat affect demography of arctic ground squirrels? (2) What is the fate of adult males that disappear at very high rates from local populations? (3) What factors are correlated with an individual's probability of death and dispersal?, (4) What factors are correlated with a male's reproductive tactic and success?, and (5) Why do adult males disperse?

Female arctic ground squirrels living at high elevation in the alpine had higher reproductive output and survival during the active season, but lower survival over winter, than their counterparts living at lower elevation in the boreal forest. A demographic model indicated that the forest was sink habitat ( $\lambda < 1$ ) but that the alpine habitat maintained a ground squirrel population in the absence of immigration ( $\lambda \geq 1$ ).

Adult males had two peak periods of disappearance during the active season – late in the mating season, caused by mortality, and around the time of juvenile emergence, caused by dispersal. Age was an important predictor of both mating season and winter survival, with older ( $\geq 2$  years old) males having a lower survival rate than yearlings.

Age may also have played a key role in the mating and dispersal tactics of adult males. Older males invested more energy into reproduction than yearlings, and the reasons why yearlings and older males disperse differed. Older males may have dispersed to avoid mating with their daughters, to increase their access to mates, or to increase their access to unrelated mates, but yearlings appeared to disperse for other reasons.

I combined the results of my study and previous studies in a conceptual model relating mating tactics, natal and breeding dispersal, and survival in male arctic ground squirrels. This model provides testable hypotheses about casual relationships among variables.

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## **Chapter 1. General Introduction**

Animals at every stage of their life cycle must decide whether to stay in their present location or move to another, possibly more profitable area, and whether to allocate more or fewer resources to reproduction. How do they decide this? In this thesis, I use variation among individual adult male arctic ground squirrels (*Spermophilus parryii*) to identify the internal and external factors associated with different dispersal and mating tactics. I also use this variation to evaluate the survival and reproductive consequences of different mating and dispersal tactics.

Variation in behaviour among individuals can be approached from a variety of perspectives in ecological studies. In many population studies, relative to other sources of variation, individual variation is assumed to have little impact on population dynamics and so it is assumed that all individuals within a sex and age cohort respond equally to changes in environmental conditions. In contrast, some behavioural studies set out to explain why variation among individuals exists, but do not consider the survival and reproductive consequences of different behaviours or their cumulative impacts on population dynamics. To extend our understanding of dispersal and mating tactics, we need to unite these two perspectives. Such unification has provided insights in the past. For example, predator-sensitive foraging may explain the synergistic effect of food and predators on prey reproduction (Karels *et al.* 2000, Zanette *et al.* 2003) and spacing behaviour (e.g. territoriality and dispersal) can be the mechanism by which density dependence operates to regulate populations (Sinclair 1989, Krebs 1992). In this thesis, I use all three of the approaches I have mentioned and discuss the implications of individual behaviour to survival and reproduction and consider how behaviours may change in response to changes in density or survival.

### **Research objectives, rationale, and thesis layout**

This study focuses on five main questions: (1) How do changes in elevation and habitat affect arctic ground squirrel demography? (2) What is the fate of adult males that disappear at very high rates from local populations? (3) What factors are correlated with a male's probability of death and dispersal?, (4) What factors are correlated with a male's reproductive tactic and success?, and (5) Why do adult males disperse? I provide the

rationale for focussing on these particular questions below, along with reference to the chapters in which each question is addressed in more detail. Specific objectives, predictions, background information, and a larger theoretical context are provided in the introductions of individual chapters.

#### Why study arctic ground squirrels? A brief overview of ground squirrel life history

Arctic ground squirrels are one of 21 *Spermophilus* species in North and Central America and 33 species found worldwide (Nowak 1998). Ground squirrels are all semi-fossorial herbivores with a mean adult mass ranging from 85g to 1000g, depending on the species (Nowak 1998). Except for the most southern species, ground squirrels are obligate hibernators and have a time-constrained active period in which they must reproduce and obtain sufficient resources to survive the next hibernation period (Michener 1984, Nowak 1998). Females mate during a very short oestrous period shortly after emerging from hibernation and generally produce only one litter of young per year (Dobson 1984, Michener 1984). Altricial young are born about 4 weeks after parental mating, and develop in underground natal nests for an additional 3 – 4 weeks before coming above ground and being weaned (Ferron 1984). Juvenile males usually disperse whereas juvenile females remain philopatric (Holekamp 1984a). This results in a spatial clustering of female kin (McLean 1984). There is high mortality among juvenile male *Spermophilus* during dispersal (Holekamp 1984a) and this creates a female-biased adult sex ratio (Dobson 1984). Depending on the species, individuals are sexually mature as either yearlings or two-year olds (Michener 1984).

Ground squirrels have been the subject of a wide variety of biological studies. They are diurnally active, highly trappable, easy to mark, and large enough to be individually identified in the field and therefore have been used in many behavioural studies. Behavioral studies on ground squirrels have investigated such topics as mating tactics (Dobson 1984, Schwagmeyer and Packer 1987, Sherman 1989, Lacey *et al.* 1997), natal dispersal (Holekamp 1984b), intraspecific interactions (McLean 1984, Schwagmeyer and Packer 1987), and kin recognition (Holmes and Sherman 1982, Mateo and Johnston 2000). Observational and experimental population studies of *Spermophilus* have also been possible because of their life history (Michener and Michener 1977, Boag

and Murie 1981, Boonstra *et al.* 2001a, Dobson and Oli 2001, Oli *et al.* 2001, Hoffmann *et al.* 2003). In particular, female philopatry, predictable timing of reproduction and dispersal, and the association of individuals with permanent burrows have facilitated these studies. Despite the shared aspects of general life-history, species differ subtly in some behavioural and life history traits and these differences are associated with differences in geographical distribution (Michener 1984). Thus, interspecific comparisons of ground squirrels have examined the role of environmental factors in the evolution of sociality (Armitage 1981, Michener 1984), communication complexity (Blumstein and Armitage 1997), and mating systems (Dobson 1984, Schwagmeyer 1990). Finally, because they are obligate hibernators, *Spermophilus* are frequently used in physiological studies of hibernation (Barnes 1987, 1989, Geiser and Kenagy 1993, Buck and Barnes 1999a).

Arctic ground squirrels (*Spermophilus parryii*, subspecies *kennicottii*, *parryii*, and *plesius*) are the largest of the North American ground squirrels and have the most northern distribution (Alaska, Yukon, Northwest Territories, Nunavut, and north-western British Columbia; Banfield 1974). In most of their range, they inhabit arctic and alpine tundra, but in the portion of their distribution south of the tree line, they also live in the boreal forest (Nadler and Hoffmann 1977). Unlike other extant North American species that originated in North America, arctic ground squirrels reinvaded North America from northern Europe during the mid-Pleistocene where they had differentiated from their original North American ancestors that had invaded Europe during the Miocene (Black 1972). Thus, *S. parryii* is more closely related to species in northern Europe than to species in North America (Black 1972, Nadler and Hoffmann 1977).

Arctic ground squirrels are unique among North American *Spermophilus* in several ways. In most species of ground squirrels, adult males enter hibernation before adult females, but in arctic ground squirrels, adult males start hibernating approximately 3 to 4 weeks after adult females (Michener 1984, Buck and Barnes 1999a). Once hibernating, core body temperatures of arctic ground squirrels can drop to  $-2.9^{\circ}\text{C}$  (Barnes 1989), lower than the minimum reported for other *Spermophilus* and other hibernating mammals (Barnes 1989, Geiser and Kenagy 1993). When emerging from hibernation in the spring, the date of emergence for arctic ground squirrels shows less

yearly variation than other species of *Spermophilus*, indicating that arctic ground squirrels may have a more time constrained active season (Michener 1984, Buck and Barnes 1999a). Finally, although multiple paternity of litters is very common for most ground squirrel species (Hanken and Sherman 1981, Sherman 1989, Schwagmeyer and Foltz 1990, Boellstorff *et al.* 1994), it is rare in arctic ground squirrels. Many female arctic ground squirrels mate with only one male and multiple paternity within a litter of young is rare even when multiple mating occurs (Lacey *et al.* 1997).

As a group, ground squirrels offer a unique opportunity to ecologists. The general similarities among species in their life history allow many of the results of studies conducted on one species to be transferred to others. Thus, reasonable assumptions based on knowledge from other ground squirrel species can be made in the absence of data on a particular species. Equally as useful, subtle differences in life history among species allow general hypotheses regarding the influence of environment and sociality on life history and behaviour to be tested. Arctic ground squirrels live at the northern extreme of this environmental gradient, and ecological studies on this particular species in their typical habitat are helpful in the testing of these general hypotheses.

#### Effect of elevation and habitat on ground squirrel demography

Our current understanding of arctic ground squirrel ecology and population dynamics is limited to studies conducted in only a few sites and habitats. Field studies have been conducted on northern populations (*S. p. kennicottii* and *S. p. parryii*) living in arctic tundra (Carl 1971, Buck and Barnes 1999a) or on southern populations (*S. p. plesius*) living in low-elevation boreal forests and grassy meadows (McLean 1982, Lacey 1991, Boonstra *et al.* 2001a).

Population dynamics differ between the northern and southern populations studied. In some areas of arctic tundra, populations are stable, possibly because suitable locations for hibernacula are limiting (Carl 1971). In the boreal forest, squirrel population densities fluctuate in response to changes in predator abundance associated with the 10-year snowshoe hare cycle. In this habitat, food availability interacts with predation to limit ground squirrel density (Boonstra *et al.* 2001a). The population dynamics of southern arctic ground squirrels living in alpine (as opposed to arctic) tundra

is unknown because only one 2 ½-year study has been conducted in this habitat (Green 1977). If habitat is critical in influencing population dynamics, then the southern subspecies of squirrels (*S. p. plesius*) living in alpine tundra may exhibit dynamics more similar to their northerly counterparts (*S. p. kennicottii*) than to nearby populations of *S. p. plesius* living in the boreal forest.

In the current study, I directly compare the population demography of *S. p. plesius* living at high and low elevations. Two main factors, habitat and weather, vary with elevation and have the potential to affect demography. Habitats may differ in food availability, predation pressure, and burrow availability and thus squirrels living in distinct habitats may have different demographic rates. With respect to weather, environmental conditions at high elevation are assumed to be less predictable and more severe than at lower elevations and the growing season is shorter at high elevation. These local conditions may select for slightly different life histories at low and high elevation (Zammuto and Millar 1985).

To determine if arctic ground squirrel demography does differ at different elevations, in CHAPTER 2 I compare the data from two long-term studies, one conducted at a low-elevation boreal forest site and the other at a high-elevation alpine site. I incorporate survival and reproductive data for each site in a demographic model to compare the sensitivities of the population growth rate in the two habitats to various demographic parameters. I also use the survival and reproductive data to test the hypothesis that life history trade-offs exist along elevation gradients.

#### Fate of adult males that disappear

Regardless of the study location, local disappearance of adult male arctic ground squirrels is very high. Annually, 70 – 90% of adult males disappear from areas where they previously lived (Carl 1971, Lacey 1991), compared with only about 50% of adult females (Carl 1971, Byrom and Krebs 1999). Live-trapping studies have indicated that both dispersal and death contribute to this disappearance (Green 1977) and that disappearance occurs more often during the mating season and just after juvenile emergence than at other times (Green 1977, McLean 1983, Boonstra *et al.* 2001b). Trapping studies, however, cannot conclusively establish the fate of all animals that have

disappeared, the location of deaths, causes of death, or the survival or reproductive consequences of dispersal.

In the first section of CHAPTER 3, I present details on the timing of male disappearance the population and the fate of radio-collared males that disappear from their home range. For males that disperse, I analyze dispersal distances, and for those that die, I determine the cause of death.

#### Factors correlated with death and dispersal

In the second section of CHAPTER 3, I examine several attributes of individuals to identify those that are correlated with death and dispersal of adult males.

Although a mortality rate describes the number of individuals in the population that will die over a period of time, it cannot predict which individuals die. This is because the probability of a particular individual dying at any point in time is a function of two factors – (1) the mortality rate and (2) the susceptibility of the individual to the mortality pressure. The mortality rate depends on the mortality pressure (e.g. risk of predation and disease, availability of required resources) and may therefore vary annually and seasonally. All animals in a local area, however, simultaneously experience similar levels of pressure, so which animals die will largely depend on each individual's susceptibilities to the pressure and chance events.

A variety of factors may increase an individual's susceptibility to mortality either by increasing the probability of encountering the mortality agent or by decreasing the probability of overcoming the mortality agent once encountered. For example, increases in movement rate may increase the chances an animal will encounter predators or diseases (Sievert and Keith 1985). Similarly, dominant animals may be less likely to experience resource shortages than subordinates (Sinclair 1986). Even if encountered, a mortality agent may or may not kill the animal. Predators may preferentially kill animals of a particular body size (McDonald 2002), and predators may be more able to successfully attack and kill animals that are very old, very young, or in poor body condition (Wirsing *et al.* 2002). Likewise, animals in poor body condition or experiencing chronic stress may be more likely to die from diseases or infections (Scott 1987).

The probability of an individual dispersing also varies through time and among individuals because not all individuals are exposed or respond equally to cues to disperse (Ims and Hjermann 2001). Dispersal may be triggered by internal or external cues or a combination of both. Internal cues may be physiological cues, such as testosterone exposure, body condition, and body mass (Nunes and Holekamp 1996, Dufty and Belthoff 2001) or knowledge based cues such as past reproductive success or public information such as reproductive success of conspecifics (Haas 1998, Danchin *et al.* 2001). External cues include social conditions, such as aggressive or lack of amicable interactions with conspecifics (Bekoff 1977, Cockburn *et al.* 1985, Wolff 1993), population density (Nunes *et al.* 1997), or environmental conditions, including resource availability (Waser 1985). The conventional wisdom for higher vertebrates is that (1) males are more likely to disperse in mammals and females are more likely to disperse in birds, and (2) in both taxa, individuals are more likely to disperse before they are reproductively mature than after they have started breeding. Dispersal is thus expected to be sex and age biased (Greenwood 1980).

#### Factors correlated with male reproductive tactics and success

What mating tactics should a male ground squirrel adopt? A variety of possibilities exist. At one extreme, a male may defend females or a space in which they reside. Alternatively, he may follow a more nomadic tactic, searching for receptive females and mating with them once found. After mating, the male must make more decisions – should he try to prevent females from mating with other males or should he leave the female in search of new mates? The costs (energetic resources) and benefits (reproductive fitness) associated with a given tactic vary with the male's external environment and individual qualities (Brockmann 2001). For example, the cost-benefit ratio for males defending a space containing females is greater if females are uniformly, as opposed to patchily, distributed (Dobson 1984). Alternatively, the costs of defending an area may be less for large males than small males if large size increases the probability of winning these encounters (Watton and Keenleyside 1974). The mating tactics of males also depend upon the resources they are able to devote to reproduction, which may be influenced by body condition and age.

Before any hypotheses to explain why males use different mating tactics can be suggested, tactics must be described, and internal and external conditions associated with those tactics must be identified. In CHAPTER 4, I describe variation in mating tactics used by male arctic ground squirrels and examine several attributes of males to determine which are correlated with the mating tactic employed. In particular, I focus on the influence of age on mating tactics.

#### Ultimately, why do males disperse?

Although a large number of potential cues may initiate dispersal, evolutionary reasons why animals may disperse are summarized by four hypotheses. Dispersal may help individuals reduce close inbreeding (Shields 1987, Johnson and Gaines 1990), increase their access to mates (Greenwood 1980, Dobson 1982), increase their access to resources (Greenwood 1980, Dobson 1982), or allow current offspring to remain and breed on the natal territory (Lambin 1997, Berteaux and Boutin 2000). These four hypotheses are not mutually exclusive (Dobson and Jones 1985) so that for any given species, two, three, or even all four hypotheses may apply.

In CHAPTER 5, I use variation in individual dispersal histories of adult males to identify proximate cues that males use to initiate dispersal and I evaluate three hypotheses used to explain why some individuals disperse; (1) to avoid breeding with close relatives, (2) to increase access to mates, and (3) to increase access to unrelated females. I also present data on the consequences of dispersal in terms of a male's proximity to females.

#### Putting it all together

In the final chapter, I summarize the major findings of this study, and present a conceptual model relating mating tactics, natal and breeding dispersal, and survival in male arctic ground squirrels (CHAPTER 6). The model combines the results of previous studies and suggestions by other arctic ground squirrel researchers with the findings of my study, and it provides a hypothesis about causal relationships among variables with testable predictions.



As with most research projects, in addition to answering many questions, my study raises many questions. In the final section, I highlight those questions and suggest areas of research that I feel will most benefit both ground squirrel research and ecological theory.

## **Chapter 2: A demographic and morphological comparison of arctic ground squirrels living at high and low elevations in southwestern Yukon**

### **Introduction**

Whereas some vertebrate species are restricted in distribution to valley bottoms or mountaintops, other, often closely related, species are able to exploit habitats at a range of elevations. These "elevation generalists" often show plasticity of life-history traits at a relatively small spatial scale as environmental conditions vary along the elevation gradient. In general, populations of vertebrates living at low elevations have higher reproductive output per season, earlier age of first reproduction, and may have lower adult survival than populations of the same species living at high elevations (reviews in Sandercock and Martin *manuscript in preparation*, Badyaev and Ghalambor 2001). Such intraspecific differences in reproduction and survival along elevation gradients may result from genotypic differences among populations (Zammuto and Millar 1985, Bronson 1979), but evidence indicates that they more often arise from phenotypic plasticity (Sorci *et al.* 1996, Bronson 1979, Dobson and Murie 1987). Body size may also vary along environmental gradients. Bergmann's rule predicts that, within a species, races living in colder environments should be larger than those living in warmer environments (Begon *et al.* 1990), possibly because a decreased surface area to mass ratio reduces rate of heat loss.

Because intraspecific variation in life-history characteristics can occur along elevation gradients, populations living at either end of the gradient may have very different demographic rates. Demographic comparisons of these populations provide insights into factors limiting populations in different environments and may also reveal the relative impact of regional versus local environmental factors in population dynamics. Geographically close populations experience the same regional factors (e.g. El Niño effects, long winters) that may synchronize population trends, whereas large differences in local conditions serve to differentiate them. Although regional population synchrony has received much theoretical consideration (Rohani *et al.* 1997, Haydon and Greenwood 2000), understanding the demographic mechanisms by which synchronization occurs

requires empirical demographic studies at a local and regional scale (Björnstad *et al.* 1999).

My objectives were to compare the demography and morphology of an elevation generalist, the arctic ground squirrel (*Spermophilus parryii*), at two elevations. The low elevation boreal forest site (900 m) and high elevation alpine site (1700 - 2200 m) were located approximately 30 km apart in southwestern Yukon. I measured the association of elevation and related environment and habitat on population density, population trends, adult morphology (size and mass), female survival, and reproduction. I incorporated survival and reproductive rates for each population into a simple demographic model to compare the sensitivity and elasticity of population growth rate at each site to various demographic parameters. I tested the following predictions, which were based on the general trends observed in other species: (1) ground squirrels living at high elevation are larger than those living at lower elevation, (2) females living at higher elevation delay the age at which they first breed, (3) adult females living at higher elevation have higher adult survival, and (4) per capita seasonal reproductive output of females is lower at higher elevations.

## **Methods**

### The study species

Arctic ground squirrels are burrowing, herbivorous small mammals (ca. 500 g) found throughout northern North America and eastern Siberia (Banfield 1974). In most of their range, they inhabit arctic and alpine tundra, but in the southern portion of their distribution they also live in the boreal forest (Nadler and Hoffmann 1977).

Arctic ground squirrels hibernate for approximately 8 months of the year (September to May; Banfield 1974). Females produce only one litter of young a year, mating as soon as they emerge from hibernation in early May (Lacey *et al.* 1997). Altricial young are born approximately 25 days after conception, develop in underground nests for an additional 28 days, and are weaned within a week of emerging from their natal nests (Carl 1971, Green 1977, Lacey *et al.* 1997). Dispersal in this species is sex-biased; juvenile males disperse before their first winter (Byrom and Krebs 1999) and

most reproductively mature males disperse between breeding seasons (Lacey 1991). Both males and females are reproductively mature as yearlings (Carl 1971).

#### Description of study site

I studied two populations of ground squirrels living 30 km apart. Due to differences in elevation between the sites (900 m versus 1700 - 2200 m), the sites differed in a number of abiotic factors (Table 2.1). The low elevation site was located in a boreal forest habitat dominated by white spruce forests whereas the high elevation alpine site consisted of boulderfields interspersed with alpine meadows (Table 2.1). The dominant herbivores and ground squirrel predators also differed between sites (Table 2.1).

Both the low elevation boreal forest and the higher elevation alpine site are part of two long-term ecosystem projects, the Kluane Boreal Forest Ecosystem Project and Monitoring Program (Krebs *et al.* 2001, C. Krebs and R. Boonstra, *unpublished data*), and the Kluane Alpine Ecosystem Project (D. Hik, *unpublished data*). Data were available from 1990 to 2002 at the low elevation site and were collected between 1998 and 2002 at the high elevation site. All data were not available for all years, so the number of years of data included in each analysis varied (Appendix 1). At the low-elevation boreal forest, ground squirrels were studied on two to four (10 ha) study grids spaced 1.5 to 15 km apart (see Hubbs and Boonstra 1997 and Boonstra *et al.* 2001 for grid spatial arrangements). At the high-elevation alpine study site, ground squirrels were studied on two (12 ha) study grids 400 m apart (except grid size in 1998 was 3 ha).

#### Population trends

In late July 1998 – 2002, population censuses were conducted on two grids at each site. Each mark-recapture census consisted of two to six consecutive days of trapping. On trapping days, Tomahawk live traps were baited with peanut butter and checked three times during a three to four hour period. In 1998, traps at the alpine site were set at burrows, whereas in all other years, traps were set at permanent grid stakes systematically located within the trapping area (50 m intervals in the alpine, 42 m intervals in the boreal forest). Animals were tagged with uniquely numbered Monel eartags on first capture, and on this and subsequent captures, identity, age (adult or

**Table 2.1** Comparison of the low-elevation boreal forest study area and the higher elevation alpine study area in southwestern Yukon. Temperature inversions, which are common in the winter, explain why the mean January temperature at the forest site is lower than at the alpine site. Data for the forest site are from Hik *et al.* (2001) and Krebs *et al.* (2001) and data from the alpine site are from Hik *et al.* (2001), McIntire and Hik (2002), and D. Hik and E. Gillis *unpublished data*.

	Forest Site	Alpine Site
Location	60° 57' N, 138° 12' W	61° 20' N, 138° 25' W
Elevation <sup>a</sup>	900 m	1700 – 2200 m
Mean January temperature	-22 °C	-13 °C (at 1700 m)
Mean July temperature	11 °C	7 °C (at 1700 m)
Mean annual precipitation	286 mm	250 mm
Snow free period	early May to October	mid-June to late August
Dominant vegetation	white spruce forests (43%) willow shrub thickets (45%) grass meadows (8%) aspen poplar stands (5%)	unvegetated boulderfields (36%) vascular plants, dominated by <i>Salix</i> , <i>Carex</i> , <i>Dryas</i> , <i>Cassiope</i> (27%) moss, lichens, bare ground (37%)
Dominant herbivores	snowshoe hare ( <i>Lepus americanus</i> ) red squirrel ( <i>Tamiasciurus hudsonicus</i> ) arctic ground squirrel mice and voles ( <i>Peromyscus</i> , <i>Clethrionomys</i> , and <i>Microtus</i> spp.) moose ( <i>Alces alces</i> )	hoary marmot ( <i>Marmota caligata</i> ) arctic ground squirrels collared pika ( <i>Ochotona collaris</i> ) voles and lemmings ( <i>Lemmus</i> , <i>Clethrionomys</i> , and <i>Microtus</i> spp.)
Dominant ground squirrel predators	coyote ( <i>Canis latrans</i> ) lynx ( <i>Lynx canadensis</i> ) great horned owl ( <i>Bubo virginianus</i> ) goshawk ( <i>Accipiter gentilis</i> )	red fox ( <i>Vulpes vulpes</i> ) golden eagle ( <i>Aquila chrysaetos</i> ) grizzly bear ( <i>Ursus arctos</i> )

<sup>a</sup> Tree line is at approximately 1200 m.

juvenile), sex, reproductive condition, weight ( $\pm 5$  g), and zygomatic arch breadth (the width of the skull at the widest point  $\pm 0.5$  mm) were recorded. The yearly censuses at the boreal forest site were a continuation of a monitoring program that began in 1990, with the data for 1990 – 1997 previously published (Boonstra *et al.* 2001, Karels 2000).

All population estimates were converted to densities by dividing the estimate by the effective trapping area (Appendix 2). The effective trapping area included an “edge effect” area to account for the area occupied by animals who were caught on the grid but whose entire home range was not encompassed by the grid (Bondrup-Neilsen 1983). The edge-effect distance (the average distance moved by individuals caught more than once during the census) was added to all sides of the actual trapping grid to determine the effective trapping area.

### Morphology

During each summer census, zygomatic arch breadth (an indicator of skeletal size) and mass were measured once for each individual. Morphological traits of juveniles were not compared between the two sites because in late summer because juvenile mass and structural size are strongly influenced by age and the age of juveniles during the census differed among years due to small yearly changes in the timing of juvenile emergence and census period.

### Survival

Female arctic ground squirrels are philopatric whereas both adult and juvenile males disperse (Lacey 1991, Byrom and Krebs 1999). Because disappearance due to dispersal and death cannot be distinguished through the live trapping methods I employed, survival was estimated for females only. Minimum annual survival of juvenile and adult females was estimated from late summer to late summer as the proportion of residents captured during one census that were captured during the following year’s census. I defined residents as individuals captured more than once during the census. Female arctic ground squirrels are highly trappable (mean minimum trappability = 81%; Hubbs and Boonstra 1997) and minimal survival based on trapping recaptures underestimates active season survival by an average of 10% relative to

estimates obtained from radio telemetry (this study compared with data in Karels 2000 and Byrom *et al.* 2000).

In addition to the summer census, a spring census was conducted each year in the boreal forest, and at the alpine site in 2000-2002. Annual survival for these years was subdivided into active season (summer) and winter survival. Active season survival was the proportion of females first caught before May 31 that were recaptured after July 15 of the same year (July 1 for 2002). Winter survival estimates for the boreal forest populations were obtained from the literature for 1990-1998 (Karels *et al.* 2000, Karels 2000). For all other years and for the alpine population, winter survival was calculated in the same manner as the 1990-1998 estimates, as the proportion of females caught during the last week of July or August that were caught in a subsequent year. Because age has no effect on winter survival in the boreal forest, data from adults and juveniles were combined to calculate winter survival (Karels *et al.* 2000). For the alpine population, adult and juvenile winter survival were calculated separately.

### Reproduction

In some years, ground squirrels were trapped throughout the active season to monitor reproductive success (Appendix 1). A female was classified as lactating (i.e. had given birth) milk could be manually expressed. Between onset of lactation and juvenile emergence, lactating females were radio-collared with 1.5-g transmitters (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada) and their nest burrows were located. These nest burrows were monitored, and once juveniles emerged, minimum litter size was determined through observation and live trapping. Weaning success was defined as the percentage of lactating females that had one or more juveniles emerge from nests. Reproductive output (number of juveniles/female/year) was calculated by multiplying yearly lactation rate, weaning success, and mean litter size. To compare reproductive output between populations for concurrent years, I used a surrogate of reproductive output; the ratio of juveniles to adult females caught in the summer census.

I determined the lactation rate of yearlings at the two sites by classifying all known yearlings caught during the two-week period when most females were lactating (June 1-14 at the forest site, June 8-22 at the alpine site) as either lactating or not

lactating. The % yearling females lactating represented the minimum breeding rate for yearling females.

### Demographic model

For each site, I incorporated the measured demographic parameters into a simple model that predicted the number of females in one spring ( $n_{(t+1)}$ ) from the number of females alive the previous spring ( $n_t$ ). I assumed an equal sex ratio at birth (Green 1977) and that females had to live half of the active season (8 weeks) in order to successfully wean young, so:

$$n_{(t+1)} = (n_t \times LA_{act} \times LA_{ow}) + (n_t \times LA_{act}^{1/2} \times m/2 \times LJ_{act} \times LJ_{ow}) \quad (1)$$

where:  $LA_{act}$  = adult female active season survival

$LA_{ow}$  = adult female winter survival

$m$  = reproductive output (young weaned per female)

$LJ_{act}$  = juvenile female active season survival

$LJ_{ow}$  = juvenile female winter survival

The per capita growth rate of the female population ( $\lambda$ ) was:

$$\lambda = n_{(t+1)} / n_t \quad (2)$$

At high density, arctic ground squirrels show strong density dependence in reproduction and winter survival (Karels and Boonstra 2000). However, over the range of densities in this study, I found no indication that either of these parameters was affected by density, and the inclusion of density dependence in the model did not increase my ability to predict spring density for the previous spring's density. Therefore, I chose not to incorporate density dependence into my final model.

Female arctic ground squirrels are highly trappable (mean minimum trappability = 81%; Hubbs and Boonstra 1997), and minimum survival estimates based on trapping are, on average, 10% less than survival estimates from concurrent telemetry studies during the active season (this study compared with Hubbs and Boonstra 1997 and Byrom *et al.* 2000 (assuming a 16 week active period)). I therefore multiplied mean minimum survival estimates by 1.1 to parameterize the model.

I did not measure juvenile active season survival in this study. However, a previous 3-year study at the lower elevation site reported 28-day survival rates for



juvenile females that were, on average, 87% of adult 28-day survival rates (Byrom *et al.* 2000). I therefore assumed juvenile 28-day survival to be 87% of adult 28-day survival. Assuming adult females were active for 16 weeks and juvenile females were active for 10 weeks prior to hibernation,

$$LJ_{act} = (LA_{act}^{1/16} \times 0.87)^{10} \quad (3; \text{as in Krebs 1999, eqn. 14.2})$$

Sensitivity and elasticity analyses were conducted on the model. Sensitivity measures the change in  $\lambda$  resulting from a small change in a focal parameter whereas elasticity is the proportional change in  $\lambda$  resulting from a proportional change in a focal parameter (Benton and Grant 1999, Caswell 2001). Thus, elasticity and sensitivity are related such that elasticity equals the sensitivity of a parameter  $\times$  the parameter value divided by  $\lambda$ . Direct comparisons of both sensitivity and elasticity values among parameters present some problems; however neither is biased – they simply ask slightly different questions (Caswell 2001). I multiplied the elasticity of each parameter by its coefficient of variation (CV; Sokal and Rohlf 1995), a measure of yearly variation in the parameter. The resulting value (the actual elasticity [AE] coefficient) provided a relative index of the overall effect of a parameter on  $\lambda$  in the natural population (Steen and Erikstad 1996).

To evaluate the robustness of model results to changes in parameter values, I conducted Monte Carlo simulations. For these simulations, I assumed the standard deviation of each parameter was 20% of the mean value and values were normally distributed about the mean. For the boreal forest site, I set adult and juvenile winter survival to be equal within each randomization (Karels *et al.* 2000). I calculated the 95% confidence limits of  $\lambda$  based on 500 randomizations and conducted sensitivity and elasticity analyses on the first 50 parameter value sets to determine if the relative rankings of the parameter sensitivities changed with the parameter values used.

Because the CV values for squirrel survival and reproductive rates in the boreal forest were based on 7 to 12 years of measurements whereas CV values for rates from squirrels living in the alpine were based on only 3 years, I also established the robustness of each parameter's AE-coefficient ranking. For each parameter, I calculated the CV for every 3-year interval for the boreal forest data set. I then conducted a Monte Carlo simulation (500 randomizations) for the boreal forest model using the mean 3-year CV

and the measured standard deviation to determine if each parameter's AE-coefficient ranking was dependent on the specific CV values used or if the relative rankings were robust to realistic changes in CV associated with fewer years of sampling.

### Statistical Analysis

Population sizes and 95% confidence limits were estimated using the jackknife estimator in the program CAPTURE (Otis *et al.* 1978) as recommended by Menkens and Anderson (1988) and Boulanger and Krebs (1994). I estimated total and adult population sizes separately. Separate estimates were calculated for each of the two grids at each site, and then a mean density for each site was calculated.

Comparisons of traits between sites were made using t-tests, except for (1) mass, for which structural size was a covariate in a one-way analysis of covariance, (2) ratio of juveniles to adult females, in which year and habitat were variables in a log-linear analysis, and (3) yearling lactation rates, which were compared through contingency table analysis (likelihood ratio  $\chi^2$ ). Prior to analyses, data were checked for normal distribution and equality of variances and all proportion data were arcsine transformed (Krebs 1999). If variances were not equal, (Levene's test,  $\alpha = 0.05$ ), I used a Welch's test to compare means (Sall *et al.* 2001). Unless otherwise stated, all values are reported as mean  $\pm$  1 standard error. Mean survival and reproductive rates (except yearling lactation rates) are an average of yearly rates. Morphological means and yearling lactation rates are from data from all years combined. Statistics were performed using JMP version 3.2.1 (SAS Institute Inc., 1997). For the demographic model, Monte Carlo simulations and sensitivity and elasticity analyses were conducted using PopTools version 2.4 (Hood 2002).

## **Results**

### Population Trends

At both sites, ground squirrel distribution was patchy (van Dishoeck 1997, T. Karels *unpublished data*), but the grids were large enough to incorporate areas of both high and low local density, and thus represent the overall density in the two habitats. In late summer, total ground squirrel density tended to be 30-70% lower at the low-elevation

boreal forest site than at the higher elevation site, although adult density at the two sites was similar in most years (Figure 2.1). At both study sites, ground squirrel density (total and adults) declined between 1998 and 1999. At the forest site, adult and total squirrel density continued to decline until 2000 after which densities remained stable. In the alpine, adult squirrel density remained stable between 1999 and 2002 even though total squirrel density increased during this time because of an increased number of juveniles in the population.

### Morphology

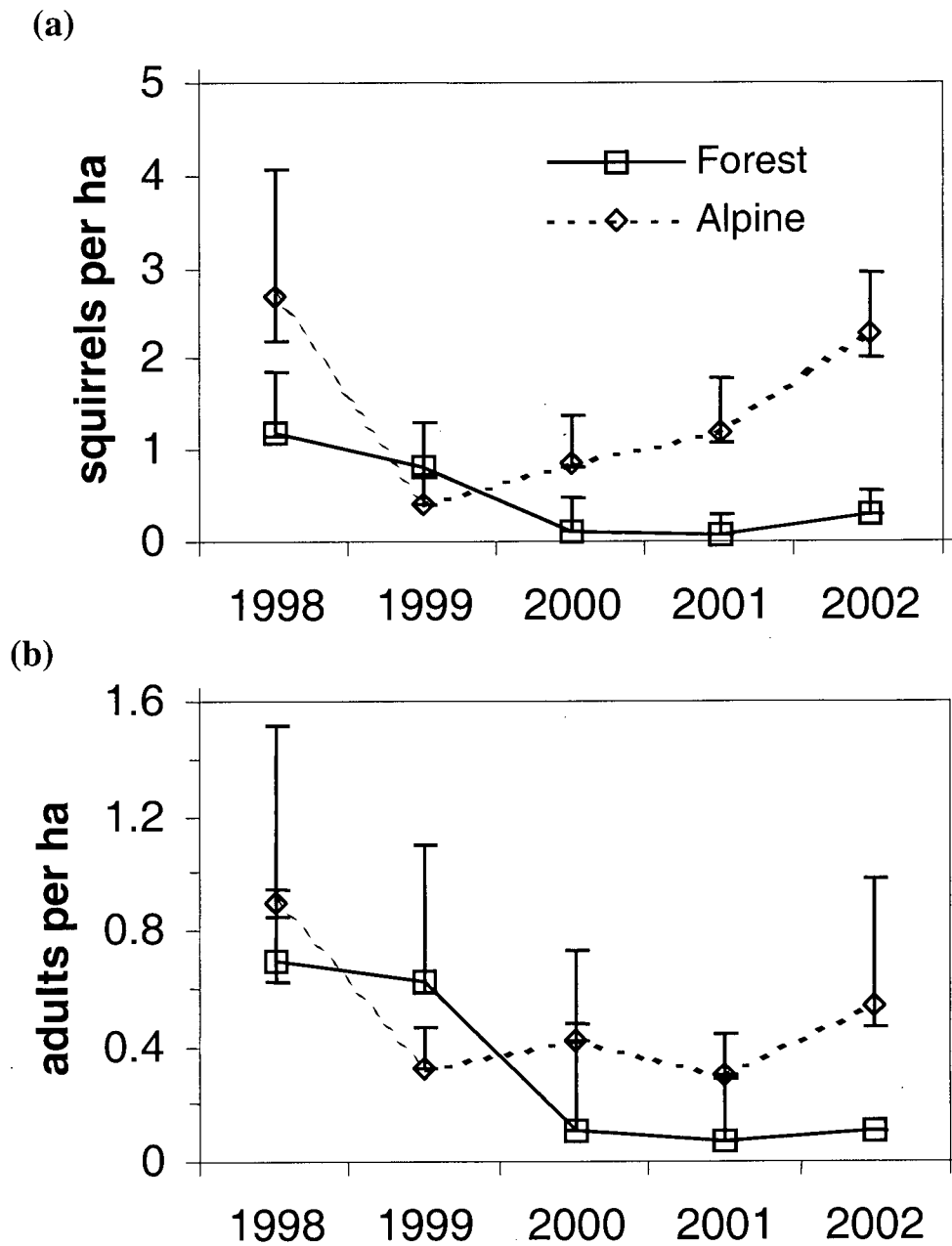
Adult male arctic ground squirrels living in the forest were structurally smaller (as measured by zygomatic arch breadth) than their alpine counterparts (Table 2.2). Although adult females showed the same trend when data analysis was restricted to data from concurrent years (1999 – 2002), analysis using all data available for the forest site detected no difference in structural size of females between the two sites. In late summer, both male and female adult arctic ground squirrels living at the forest site were heavier for a given structural size than squirrels living at the alpine site (Table 2.2). This indicates that ground squirrels living in the forest were in better body condition in late summer than those living in the alpine.

### Survival

Minimum annual survival of females did not differ between the forest and alpine site (Table 2.3). However, seasonal survival differed significantly - adult females in the forest had 28% higher winter survival but 38% lower summer survival than females in the alpine (Table 2.3). Although mean winter survival was higher at the boreal forest site for juveniles as well, the difference was not significant.

### Reproduction

Juveniles in the forest emerged from their natal burrows approximately 1 week earlier than those in the alpine (Table 2.4). Eighty-one percent of yearlings caught had



**Figure 2.1** Numerical trends of total (a) and adult (b) arctic ground squirrels at a low elevation boreal forest site and a high elevation alpine site, 1998 - 2002. Censuses were conducted on 2 grids at each site in late July or early August of each year. Error bars are the mean upper and lower 95% confidence limits associated with the population estimates for each grid.

**Table 2.2** Structural size (as measured by zygomatic arch breadth) and mass of adult arctic ground squirrels living at a low-elevation boreal forest site and a high-elevation alpine site in late summer. Sample sizes are provided in brackets.

	Zygomatic Arch Breadth (mm)				Mass (g)	
	Forest	Alpine	<i>t</i>	<i>P</i>	Forest	Alpine
<u>Female</u>						
All Years	36.0 ± 0.2 (101)	36.2 ± 0.3 (42)	-0.42	0.67	543 ± 6 (101)	501 ± 10 (42)
1999 - 2002	34.3 ± 0.3 (11)	36.2 ± 0.3 (42)	-3.38	0.002	568 ± 19 (11)	494 ± 9 (42)
<u>Male</u>						
All Years	37.9 ± 0.3 (70)	39.3 ± 0.4 (22)	-2.71	0.008	660 ± 12 (70)	567 ± 21 (11)
1999 - 2002	36.3 ± 0.5 (11)	39.3 ± 0.4 (11)	-5.06	<0.0001	661 ± 28 (11)	569 ± 18 (11)
<u>One-way ANCOVA - Mass</u>						
	All Years			1999 - 2002		
	<i>F</i>	d.f.	<i>p</i>	<i>F</i>	d.f.	<i>p</i>
<u>Female</u>						
Covariate: zygomatic arch	38.3	1	<0.0001	15.5	1	0.0003
Habitat	12.4	1	0.0006	10.7	1	0.002
<u>Male</u>						
Covariate: zygomatic arch	20.0	1	<0.0001	14.2	1	0.0007
Habitat	11.2	1	0.0012	6.3	1	0.017

**Table 2.3** Minimum survival rates of female arctic ground squirrels (with 95% confidence limits) at a low-elevation boreal forest site and a high-elevation alpine site. Summer survival was assumed to represent survival during the 16-week active season, whereas winter represented the other 36 months, during which females were hibernating. Survival was estimated for each of  $n$  years, and these yearly rates were averaged. Mean sample sizes used to calculate yearly rates can be found in Appendix 3.

	Forest		Alpine		
	yearly mean	$n$	yearly mean	$n$	$t$ $p$
Annual survival (%)					
Adult	34.1 (9.6 – 64.6)	9	27.1 (19.4 – 35.5)	4	0.31 0.76
Juvenile	31.9 (5.5 – 67.4)	7	40.2 (0.1 – 94.5)	4	0.25 0.81
Winter survival (%)					
Adult	68.4 (53.8 – 81.3) <sup>a</sup>	12	40.4 (39.6 – 41.2)	3	13.8 <sup>b</sup> 0.003
Juvenile	<sup>a</sup>		54.9 (0.9 – 100)	3	0.13 <sup>b</sup> 0.75
Adult summer survival (%)	48.2 (38.1 – 58.3)	12	86.5 (53.5 – 100)	3	3.14 0.008

<sup>a</sup> Adults and juveniles were pooled when calculating winter survival for the boreal forest site as previous studies found no effect of age on winter survival (Karels *et al.* 2000).

<sup>b</sup> Welch's  $F$  ratio

**Table 2.4** Reproductive traits of female arctic ground squirrels living at a low elevation boreal forest site and high elevation alpine site. Except for yearling lactation rate, reproductive rates were obtained for each of  $n$  years, and these yearly rates were averaged. Mean sample sizes used to calculate yearly rates can be found in Appendix 3. Rates are reported as mean (95% confidence limits).

	Forest		Alpine		
	yearly mean <sup>a</sup>	$n$	yearly mean <sup>a</sup>	$n$	$t$ $p$
Yearlings lactating <sup>b</sup> (%)	76.2	21	88.2	17	
Lactation rate (%)	73.8 (64.7 – 81.9)	7	98.3 (93.4 – 100)	3	4.61 0.002
Weaning success <sup>c</sup> (%)	73.7 (46.7 – 93.4)	5	77.1 (53.1 – 94.2)	3	0.19 0.86
Litter size	3.3 ± 0.3	5	3.9 ± 0.5	3	1.01 0.31
Reproductive output (juveniles/female)	1.5 ± 0.3	7	3.0 ± 0.8	3	2.38 0.045
Earliest date of juvenile emergence	June 17 ± 1.3 <sup>d</sup>	6	June 25 ± 1.2	3	3.61 0.009

<sup>a</sup> For % yearlings lactating, values are for all years combined, not the yearly mean, and  $n$  is the number of females, not number of years

<sup>b</sup> Minimum % of known yearlings that lactated between June 1-15 (forest) or June 8-22 (alpine); likelihood ratio  $\chi^2 = 0.94$ ,  $d.f. = 1$ ,  $p = 0.33$

<sup>c</sup> Proportion of lactating females that successfully weaned litters

<sup>d</sup> Juvenile emergence data from 1992 (July 4) was eliminated from the analysis as bad weather delayed breeding by 2 weeks relative to latest date seen in other years (Hubbs and Boonstra 1997); mean if 1992 data included = 19 June,  $p = 0.23$

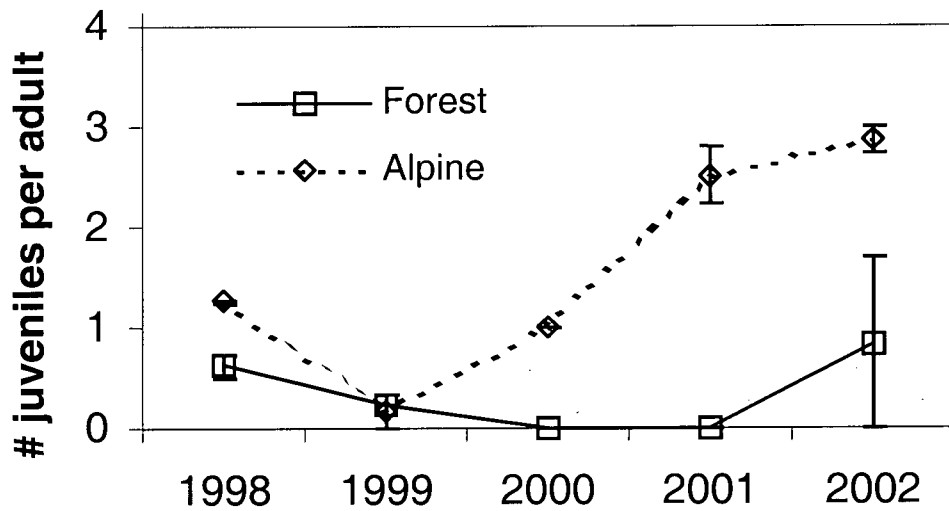
lactated, and no difference was detected between the two sites in the percent of yearlings that lactated (Table 2.4). However, overall reproductive output (number of juveniles weaned per adult female) in the boreal forest was only 50% of the reproductive output in the alpine due to a significantly lower proportion of adult females giving birth at the forest site (74% versus 98%) and a trend towards smaller litter sizes at the forest site (3.3 versus 3.9 young/litter; Table 2.4). Detailed reproductive traits were measured in different years at the two sites (Appendix 1) but a second measure of reproductive output supports the finding of reduced reproduction at the forest site. From 1998 to 2002, the ratio of juveniles to adult females caught was significantly lower in the boreal forest than in the alpine (Figure 2.2; log-linear analysis, year: Wald  $\chi^2 = 11.6$ , d.f. = 4,  $p = 0.02$ , site: Wald  $\chi^2 = 6.3$ , d.f. = 1,  $p = 0.01$ ).

#### Demographic model

Although the arctic ground squirrel population in the alpine appears to be stable over the long term ( $\lambda = 1$ ), the boreal forest population does not appear to maintain itself ( $\lambda < 1$ , Table 2.5). Sensitivity analysis indicates that in the forest, population growth rate is sensitive to small changes in adult survival during the active season whereas in the alpine, population growth rate is sensitive to small changes in adult and juvenile winter survival (Table 2.5, Figure 2.3). Growth rate of neither population is sensitive to small changes in reproductive output. In terms of the sensitivity of the growth rate to proportional changes in parameter values (elasticity), growth rate is most sensitive to changes in survival of adults in the active season in both populations (Table 2.5, Figure 2.3).

In the forest population, reproduction and active season survival varied greatly from year to year, whereas in the alpine population, juvenile winter survival was highly variable (Table 2.5). As a result, for the boreal forest population the AE-coefficient (elasticity x coefficient of variation) for adult active season survival is 50% higher than the next highest AE-coefficient (adult winter survival, Table 2.5, Figure 2.4). In contrast, in the alpine juvenile winter survival AE-coefficient is twice as high as the next highest AE-coefficient (reproductive output, Table 2.5).





**Figure 2.2** Trends in reproductive output, as indexed by the ratio of juveniles to adult females in late summer, at the low elevation forest site and high elevation alpine site, 1998 – 2002. Values are the mean  $\pm$  1 S.E. of two study grids at each site.

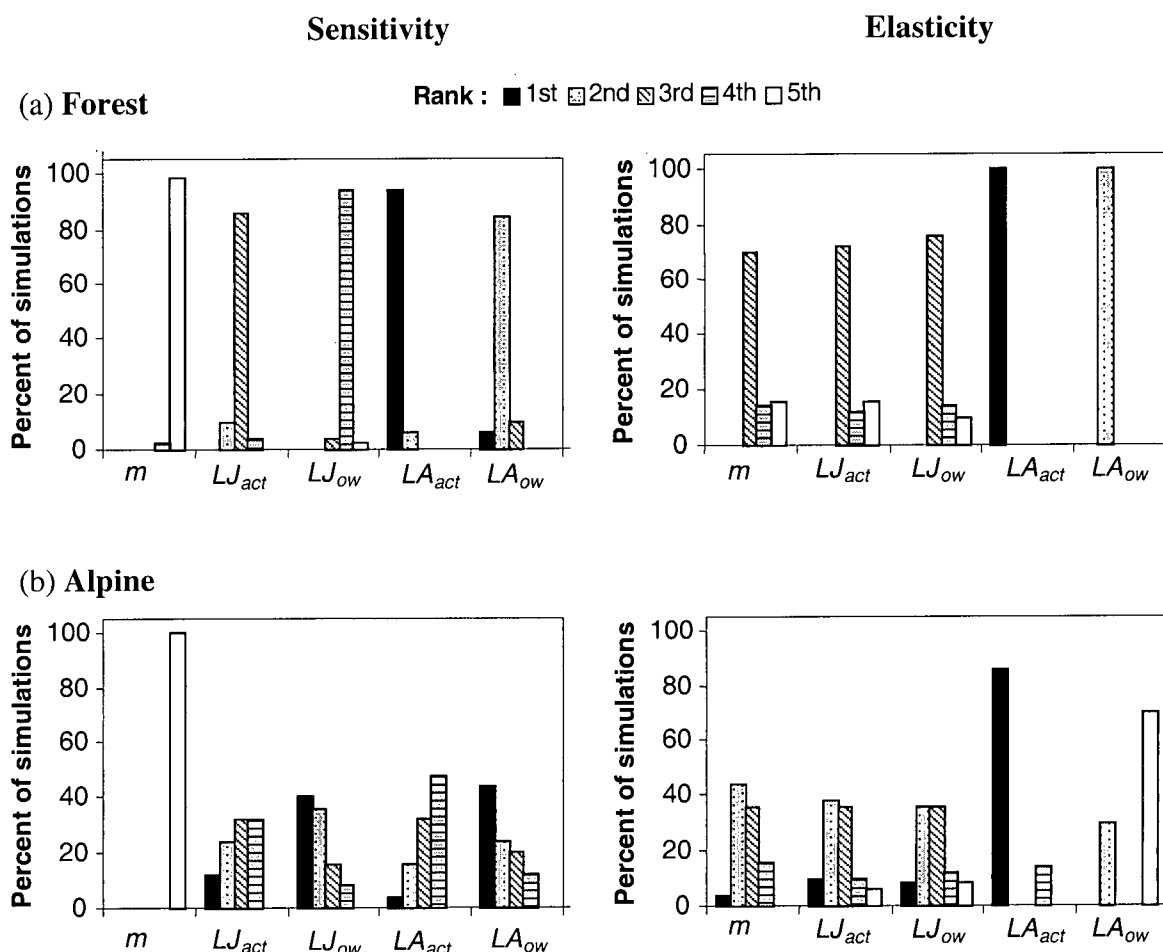
**Table 2.5** Sensitivity, elasticity, and actual elasticity (AE) coefficients of arctic ground squirrel population growth rate to demographic parameters. The parameters were measured at a low-elevation forest site (a) and high-elevation alpine site (b).

(a) Low elevation forest site					
Parameter	Value	Sensitivity	Elasticity ( $e_i$ )	CV <sub>i</sub> <sup>a</sup>	AE <sup>b</sup>
Reproductive output ( $m$ )	1.5	0.13	0.33	47.3	0.15
Juvenile active season survival ( $LJ_{act}$ )	0.471	0.41	0.33	35.7	0.11
Juvenile winter survival ( $LJ_{ow}$ )	0.752	0.26	0.33	30.7	0.11
Adult active season survival ( $LA_{act}$ )	0.530	0.93	0.84	35.7	0.30
Adult winter survival ( $LA_{ow}$ )	0.752	0.53	0.67	30.7	0.21
Growth rate ( $\lambda$ from eqns 1 and 2)	0.6				
$\lambda$ 95% confidence limits <sup>c</sup>	0.3 – 0.9				
(b) High elevation alpine site					
Parameter	Value	Sensitivity	Elasticity ( $e_i$ )	CV <sub>i</sub> <sup>a</sup>	CV <sub>i</sub> * $e_i$ <sup>b</sup>
Reproductive output ( $m$ )	3.0	0.20	0.59	44.8	0.26
Juvenile active season survival ( $LJ_{act}$ )	0.683	0.87	0.59	21.3	0.12
Juvenile winter survival ( $LJ_{ow}$ )	0.604	0.99	0.59	98.1	0.57
Adult active season survival ( $LA_{act}$ )	0.950	0.76	0.71	21.3	0.15
Adult winter survival ( $LA_{ow}$ )	0.444	0.95	0.41	1.7	0.01
Growth rate ( $\lambda$ from eqns 1 and 2)	1.0				
$\lambda$ 95% confidence limits <sup>c</sup>	0.6 – 1.6				

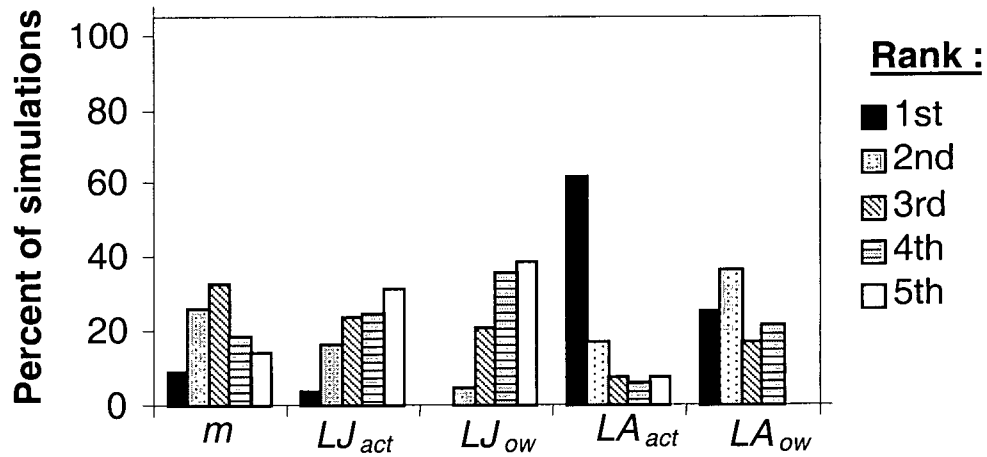
<sup>a</sup> Observed coefficient of variation

<sup>b</sup> Actual elasticity (AE) coefficient =  $CV_i \times e_i$

<sup>c</sup> Based on Monte Carlo simulation (500 iterations)



**Figure 2.3** Robustness of the relative rankings of  $\lambda$  sensitivities and elasticities to different parameter value sets ( $m$  = reproductive output,  $LJ_{act}$  = juvenile female active season survival,  $LJ_{ow}$  = juvenile female winter survival,  $LA_{act}$  = adult female active season survival, and  $LA_{ow}$  = adult female winter survival). Sensitivity and elasticity analyses were conducted on 50 different parameter value sets generated from Monte Carlo simulations. In cases where parameter rankings were equal, all tied parameters were assigned the highest rank for that value.



**Figure 2.4** Robustness of the relative rankings of actual elasticity (AE) coefficients to changes in  $CV_i$  values based on 500 replications in a Monte Carlo simulation ( $m$  = reproductive output,  $LJ_{act}$  = juvenile female active season survival,  $LJ_{ow}$  = juvenile female winter survival,  $LA_{act}$  = adult female active season survival, and  $LA_{ow}$  = adult female winter survival). In cases where parameter rankings were equal, all tied parameters were assigned the highest rank for that value.

## Discussion

Although the low-elevation boreal forest and higher elevation alpine sites are geographically close (approximately 30 km apart), arctic ground squirrels living at the two sites differed in a number of ways. Adult males living in the boreal forest were structurally smaller than males living in the alpine, yet males and females living in the boreal forest were heavier than those living in the alpine. The general trend along elevation gradients for most vertebrate species (Sandercock and Martin *manuscript in preparation*, Badyaev and Ghalambor 2001) predicted older age at first reproduction and lower reproductive output at higher elevation and increased adult survival at higher elevation. However, in this study, no difference in age at first reproduction was detected, and reproductive output was higher, not lower, at the higher elevation alpine site. Adult female survival in the boreal forest was significantly lower in the summer but significantly higher during the winter compared with adult female survival in the alpine. These differences in survival between sites cancelled each other out over the course of a year, resulting in no difference in annual survival between sites. Although population trends were similar for adults at the two sites, since seasonal survival differed between the sites, different mechanisms may be responsible for the trends in numbers seen, a conclusion supported by the results from the model.

A weakness of the current study is that the years of data collection varied between the two sites and comparisons between years of concurrent study (1998 – 2002) were hindered by small sample sizes in the boreal forest. In many instances, year effects could not be statistically controlled or evaluated. However, the data set for the boreal forest spanned many years and captured the range of natural variation, minimizing this problem. A second potential bias is that for survival and reproduction analyses, I considered rates from all years as equal even though the sample sizes from which the yearly rates were calculated varied among years. The study results are not affected by this decision. For most rates, unweighted means were similar to means weighted by sample size and in cases where they differed, they did so in a direction equal in both habitats or in a way that increased, not diminished, the magnitude of differences seen (Appendix 4).

This study was conducted at two sites, one at each elevation, and therefore may simply represent site differences as opposed to differences associated with elevation. However, several pieces of evidence indicate that the results may not simply be an artifact of site differences. Although the two grids studied at the alpine site were geographically close (<500 m apart), the two main study grids at the boreal forest site were >15 km apart, and would thus account for spatial variability in this habitat. Additionally, many of the factors affecting the boreal forest population appear to be related to changes in predation pressure (discussed below), which in turn is influenced by abundance of snowshoe hares and alternate prey, a characteristic common throughout much of the boreal forest. Most importantly, the main results from this study are consistent with results from a study conducted on arctic ground squirrels in 1975-1977 (Green 1977). Green studied two populations of *S. parryii plesius*, one in a low elevation open meadow site (800 m) and one on a high elevation sub-alpine plateau (1525 m) only 5 km away. Similar to my study, Green reported that the pregnancy rate and the percent of females that weaned litters were lower at the low-elevation site than the high-elevation site (pregnancy rates: 55% at low elevation, 73% at high elevation; weaning success: 73% at low elevation, 75% at high elevation). In contrast to my study, Green did not detect any difference in mean litter size at juvenile emergence between the two sites (3.5 and 3.6 at low and high elevations respectively) and found slightly higher annual survival of adult females at the higher elevation because of higher winter survival at the higher elevation site (active season survival: low elevation = 0.85, high elevation = 0.83; winter survival: low elevation = 0.73, high elevation = 1.0).

### Population Trends

Although changes in numbers of adults at both sites followed similar trends from 1998-2002, differences in seasonal survival and reproduction (discussed below) indicate the demographic factors underlying these changes may have varied. The results of the model support the hypothesis that different demographic processes underlie the population dynamics at the two study sites. AE-coefficients combine the proportional sensitivity of a parameter with how much it varies in the population (Steen and Erikstad 1996) and can provide an index of the ability of different demographic factors to

influence population numbers over the time period studied. For the boreal forest population, adult active-season survival had the highest AE-coefficient, indicating that this parameter may have contributed greatly to the changes in numbers. For the alpine population, changes in juvenile winter survival may have played a dominant role in creating the trends in population numbers seen.

Based on the model, the alpine population is on average stable ( $\lambda = 1$ ) whereas the boreal forest population is a sink ( $\lambda < 1$ ) and must rely on neighbouring source populations to supply immigrants (Pulliam 1988, Pulliam and Danielson 1991). This source-sink relationship may be constant over time, or alternatively, neighbouring ground squirrel populations may undergo a cycle of source-sink dynamics over time in concert with the snowshoe hare cycle. Direct evidence that the boreal forest may be ground squirrel sink habitat is that in 2000 the ground squirrel population living on one of the boreal forest grids went extinct and the site remained vacant for the remainder of the study. This local extinction corresponded with very low densities on the second boreal forest grid.

Sink populations have also been reported for Uinta and European ground squirrels. In the case of Uinta ground squirrels, emigrants from a lawn maintained the squirrel population in a nearby area of mixed shrubs and grass (Slade and Balph 1974), but a source population was not conclusively established in the European ground squirrel example (Hoffmann et al. 2003). Large open meadows adjacent to the boreal forest may function as source populations in my study. These open meadows have higher local densities (Lacey *et al.* 1997) than the forest (Karels *et al.* 2000, Boonstra *et al.* 2001), and the females living in the open areas (Lacey *et al.* 1997) have higher reproductive rates than those living in the forest (Hubbs and Boonstra 1997, Karels *et al.* 2000). This potential source sink relationship between open meadows and boreal forest should be further explored empirically and theoretically. Specifically, whether or not such a relationship varies with the phase of the snowshoe hare cycle, and whether or not populations in open meadows could supply the required number of immigrants needs to be determined.

## Morphology

Based on Bergmann's rule, I predicted that ground squirrels living at the higher elevation site would be larger than those living at lower elevation. Adult male ground squirrels living in the alpine site were structurally larger than those living in the boreal forest. The same trend was detected for adult females when the analysis was restricted to concurrent years of study (1999-2002), but sample sizes in the boreal forest during these years were low and the result may be an effect of sampling error. If I used all data available for the boreal forest population, I could detect no difference in structural size between adult females living in the boreal forest and alpine. In Columbian ground squirrels (*S. columbianus*), adult structural size does not vary with elevation although slower growth rates at higher elevation result in a negative association of skeletal size with elevation for the yearlings (Dobson 1992).

Bergmann's rule predicts that races living in colder environments should be larger (Begon *et al.* 1990). The usual explanation for the observed relationship of increasing size with colder environments is that a decreased surface area to mass ratio results in less body heat loss to the environment. Male arctic ground squirrels at the alpine site were structurally larger but weighed less than their lower elevation counterparts, which would lead to an increased, not decreased, surface area to body mass ratio, so this cannot explain the difference in size observed. I can think of two potential explanations why adult males at the alpine site may be larger than those living at the boreal forest site. Arctic ground squirrel densities tend to be higher in tundra and open areas than in the boreal forest (Carl 1971, Lacey *et al.* 1997, Hik *et al.* 2001 compared with Karels *et al.* 2000 and Boonstra *et al.* 2001). This may lead to more competition among males for mates and selection for larger body size. A second explanation is that there may be differences in male age structure between the two sites. If males do not obtain their maximum size by the end of their first summer as adults, differences in mean structural sizes may arise from differences in age structure. At what age males obtain maximum size is unknown for this species because juvenile and adult male dispersal makes multi-year data on individual males rare. However, juvenile males do not reach adult size prior to their first



hibernation and continue to grow in their second summer when they are yearlings (Chapter 4).

In this study, differences in ground squirrel mass were associated with elevation. Mass changes with elevation have also been documented for golden-mantled ground squirrels (*S. lateralis*; Bronson 1979) and Columbian ground squirrels (*S. columbianus*; Zammuto and Millar 1985, Dobson and Murie 1987, Dobson 1992), with mass being greater at lower elevations for most sex and reproductive classes. Only one of these studies, however, accounts for structural sizes in its comparisons (Dobson 1992). As for arctic ground squirrels (this study), Dobson (1992) observed both adult male and female *S. columbianus* were heavier for a standardized structural size at lower elevations (i.e. ground squirrels at the lower elevation were in better physiological condition). Peak food availability for arctic ground squirrels was similar at the two sites used in this study (Hik *et al.* 2001). However, the growing season (as indexed by snow free period) is much shorter at the alpine site (Table 2.1). As a result, total seasonal food availability may have differed between the sites and is therefore a likely cause of the observed differences in ground squirrel mass across elevation.

### Survival

Annual female survival was similar between the sites, yet seasonal survival between the two sites differed significantly. Female active season mortality, which is most often caused by predators (Carl 1971, Hubbs and Boonstra 1997, Byrom *et al.* 2000), was significantly higher in the boreal forest than in the alpine. Predator density is higher at the boreal forest than the alpine site (Hik *et al.* 2001) and may explain the lower active-season survival of females living at this site. In addition to predation pressure, arctic ground squirrels in the boreal forest may be less able to detect and avoid predators than their alpine counterparts. Ground squirrels rely on vision to detect predators at a distance (Balph and Balph 1966, Slade and Balph 1974, Hubbs *et al.* 1996). In the boreal forest, visibility can be obscured by vegetation and deadfall, which in turn affects which burrow systems remain occupied after periods of high depredation (Karels and Boonstra 1999). In the alpine tundra, vegetation height is usually lower than the eye level of an alert ground squirrel (25 cm; Karels and Boonstra 1999) and rarely affects visibility.

Unlike active-season survival, winter survival was higher at the forest site than it was in the alpine. Winter mortality occurs during hibernation and is assumed to result from the physiological demands of hibernation (Green 1977, Karels and Boonstra 2000, Karels *et al.* 2000) but occasionally is the result of grizzly bear depredation (E. Gillis *personal observation*, Carl 1971). There are several potential explanations for the increased winter mortality at the alpine site relative to the boreal forest site. In late summer, ground squirrels at the alpine site weighed less than squirrels at the forest site. This indicates less fat or lean body mass, both of which are metabolized for energy during hibernation (Buck and Barnes 1999a). Pre-hibernation weight is positively associated with winter survival in some *Spermophilus* spp., particularly for juveniles (Michener 1974, Slade and Balph 1974, Murie and Boag 1984), but was not found to be associated with winter survival of *S. parryii* (Green 1977, Karels 2000). Probably, there is a threshold pre-hibernation weight above which individuals have adequate energy stores to survive a winter, and it is only in years in which some individuals do not attain this threshold that the association between pre-hibernation weight and winter survival can be observed.

In the boreal forest, food and predation interact to limit the population (Hubbs and Boonstra 1997, Karels *et al.* 2000) but in some arctic tundra habitats, the number of suitable hibernacula and burrow systems may limit the population (Carl 1971). Whether suitable hibernacula are limiting at the alpine site is unknown. If they are limiting, in addition to intraspecific competition, interspecific competition for winter space may occur. A second hibernating species, hoary marmots, lives at the alpine site but not the boreal forest site. Marmots and ground squirrels hibernate very close to each other (T. Karels and E. Gillis, *unpublished data*), so may have similar microhabitat requirements for hibernacula (see Karels 2000 and Buck and Barnes 1999b for microhabitat characteristics of arctic ground squirrel hibernacula). In addition to competition for winter habitat, there may be competition between the two hibernating species for food resources containing specific fatty acids known to reduce the physiological costs of hibernation (Geiser and Kenagy 1993, Karels 2000, Karels *et al.* 2000). Adult marmots weigh approximately 10 times more than adult ground squirrels, and during the time period of this study, marmot densities increased by 30% in the alpine study area, setting

the conditions for interspecific competition, if it exists, to occur (T. Karels and D.S. Hik, *unpublished data*).

### Reproduction

Contrary to the general trend for vertebrates (Sandercock and Martin, manuscript in prep.), including other *Spermophilus* spp. (Bronson 1979, Dobson 1979, Zammuto and Millar 1985), arctic ground squirrels at the higher elevation site did not delay their age of first reproduction and had greater reproductive output than squirrels at the lower elevation site. The discrepancy between my results and those of other studies may occur because in this study, habitat changed with elevation. Arctic ground squirrels living in the boreal forest show higher levels of free cortisol and glucose in their blood than those living at the alpine site, an indication that squirrels in the forest are chronically stressed. This is most likely due to higher perceived predation risk caused by a greater abundance and diversity of predators in the forest as well as increased stress associated with the inability to detect predators visually from a safe distance (Hik *et al.* 2001). Chronic stress can suppress reproduction (Boonstra *et al.* 1998), and Hik *et al.* (2001) therefore predicted that reproductive output would be reduced in the boreal forest relative to more open areas. Indeed, in a 3-year study (1988 – 1990) in 5-ha open meadow at low elevation (650 m) approximately 30 km south of my boreal forest study site, Lacey *et al.* (1997) reported a reproductive output of 3.6 young per females (calculated from Lacey *et al.* 1997). This value was higher than the maximum reproductive output observed for a single year in the boreal forest of 2.5 young per female (Karels 2000) and demonstrates the potential impact of habitat on reproduction.

### Life-history trade-offs

Among vertebrates, populations living at higher elevations generally have lower reproduction but higher female survival than populations of the same species living at lower elevations (i.e. high elevation populations are more “k-selected”). This indicates that a life-history trade-off between survival and reproduction that is apparent for at least two species of ground squirrels (*S. lateralis*; Bronson 1979, *S. columbianus*; reviewed in Dobson and Murie 1987), but does not occur in *S. richardsonii* (Michener and Locklear

1990a). Likewise, I found no such apparent trade-off in arctic ground squirrels – females living at higher elevation had higher reproductive output but equal annual survival to female squirrels living at a lower elevation. Similarly, Karels (2000) did not find a trade off between individual survival and reproduction in arctic ground squirrels living in the boreal forest.

Intraspecific life-history patterns associated with elevation gradients have been used to test life-history theories such as r-K (Pianka 1970) and bet-hedging (Stearns 1976) theories (Zammuto and Millar 1985). Reciprocally, these theories have been used to explain the life-history patterns observed along elevation gradients (Bronson 1979, Sandercock and Martin manuscript in prep.). Both r-K and bet-hedging theories make predictions as to the life-history strategy organisms should adopt based on the stability and predictability of the environments in which they live (Pianka 1970). Debate as to whether high or low elevation environments are more predictable and stable makes *a priori* predictions and interpretation of life-history trends in the context of these theories problematic (Zammuto and Millar 1985). Indeed, a basic assumption of r-K theory, that the maximum growth rates differ between populations, is often not tested before applying this theory to populations living along elevation gradients. When tested, the assumption has not been met (Dobson and Murie 1987).

Increasingly, evidence suggests that the apparent life-history trade offs along elevation gradients are the result of phenotypic plasticity (Bronson 1979, Sorci *et al.* 1996, Dobson and Murie 1987). Given this, placing life-history patterns along elevation gradients in the context of phenotypic responses to environmental conditions may prove more productive than placing them in the context of the evolved life-history strategies. Assuming that my results can be extrapolated beyond my particular sites and that they represent true life-history trends for arctic ground squirrels along the elevation gradient, the discrepancy between my results (higher reproductive output at higher elevations, no difference in survival between high and low elevations) and the general trend for vertebrate species can be explained as a phenotypic response to environment. Arctic ground squirrels evolved in open arctic tundra habitats (Nadler and Hoffmann 1977), and they have evolved a suite of vocal, visual, and behavioural anti-predator tactics that are effective in open habitats (Balph and Balph 1966, Slade and Balph 1974, Hubbs *et al.*

1996, Karels and Boonstra 1999). The low elevation boreal forest, in which visibility is reduced, may simply be suboptimal habitat in which reproduction is reduced. Delayed reproduction probably does not occur at higher elevations for this species because arctic ground squirrels evolved in an environment similar to the alpine environment - the short growing season in the alpine is still sufficiently long for arctic ground squirrels to reach maturity as yearlings. Based on this explanation, I predict that species that exhibit delayed reproduction and lower reproduction at higher elevations have evolved under conditions more similar to lower elevation environmental conditions and are thus less well adapted to higher elevation conditions. I hypothesize that variations in life-history traits along elevation gradients are a phenotypic response to deviations from optimal conditions as opposed to evolved life-history strategies.

This hypothesis could be supported or rejected using previously published data, by relating the direction of change of life-history traits at different elevations for individual species to deviations from environmental conditions under which they have evolved. If such a study indicates that my hypothesis is reasonable, it provides an explanation other than evolved changes in life-history traits (such as r-K theory and bet hedging) to explain trends in survival and reproduction observed along elevation gradients. This alternate hypothesis could be tested in the field experimentally transplanting individuals between high and low elevation sites.

#### Future directions for research

Local factors, such as habitat type, appear to play a vital role in the population dynamics of arctic ground squirrels. However, the time scale of this study was not sufficiently long to detect the impact of the large-scale regional environmental trends that may affect both populations. These phenomena, such as El Niño and the Pacific Ocean decadal oscillation, fluctuate on the time scale of years and decades respectively. Adult populations in both habitats started to decline in the same year and remained low and stable for the remainder of the study. The concordance of population trends at the two sites may indicate that in addition to the local factors affecting population demography, a larger scale factor may also operate through different mechanisms in the two populations. Alternatively, the similarity of population trends at the two sites may simply be a

coincidence. Population trends of arctic ground squirrels in the boreal forest appear to be driven, in part, by changes in predation pressure associated with the snowshoe hare cycle (Hubbs and Boonstra 1997, Byrom *et al.* 2000, Boutin *et al.* 1995). The dominant boreal forest ground squirrel predators are rarely seen at the alpine study site (D. Hik *unpublished data*), so probably do not synchronize ground squirrel population trends in the two habitats. However, until longer concurrent data sets are obtained for these populations, the relative impact of large-scale environmental trends that affect both populations cannot be assessed.

Based on results from the model, the boreal forest habitat appears to be unable to maintain a stable ground squirrel population. The importance of immigration into this habitat should be evaluated empirically and theoretically. Given that changes in ground squirrel survival are related to changes in predation pressure and the snowshoe hare cycle in the boreal forest and predictably fluctuate over time (Hubbs and Boonstra 1997, Boutin *et al.* 1995), source-sink dynamics between the forest and adjacent open areas may also fluctuate during the 10-year snowshoe hare cycle. The forest population may be able to sustain itself during periods of low predation pressure, and rely on immigration only during or just prior to periods of high predation. Thus, any model should incorporate the temporal variability in survival associated with predictable changes in the predator regime. If the average population growth rate of arctic ground squirrels in the boreal forest habitat really is less than one in the absence of immigration, continuous boreal forest may be a factor limiting the southern distribution of arctic ground squirrels. It will be difficult for arctic ground squirrel populations inhabiting the forest to adapt to this environment if immigration is required for population persistence, and changes in boreal forest distribution due to climate change and fire suppression may impact ground squirrel densities.

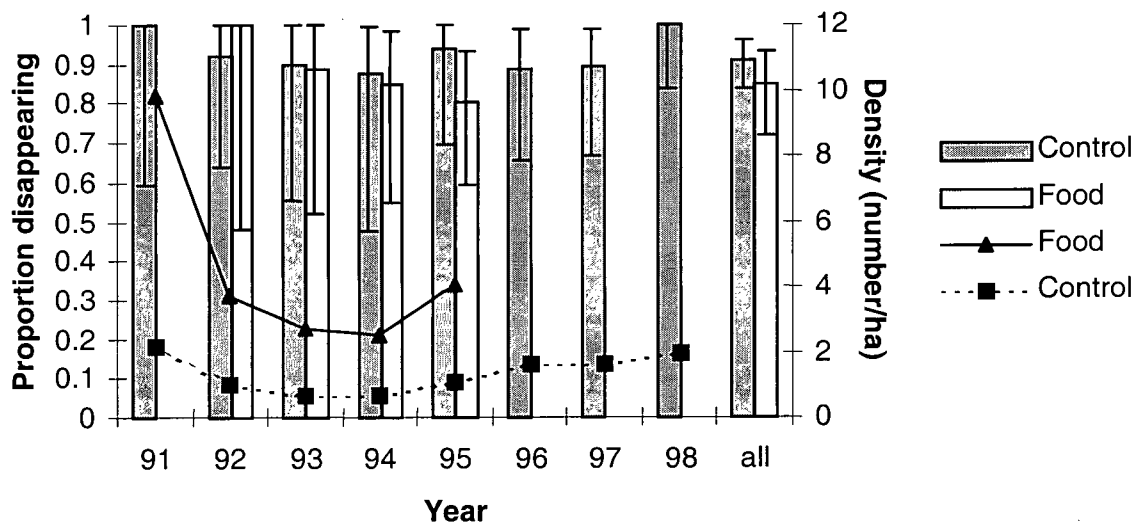
### Chapter 3: Disappearance of adult male arctic ground squirrels: Mortality and dispersal

#### Introduction

Pulses of disappearance of animals from populations arise from seasonal variation in mortality and dispersal. In small mammals that have a distinct breeding season, periods of high disappearance may arise from age-specific juvenile dispersal or mortality (Cockburn *et al.* 1985, Boyce and Boyce 1988, Nunes and Holekamp 1996, Byrom and Krebs 1999, O'Donoghue 1994, Gillis 1998), adult seasonal mortality (Lee and Cockburn 1985, Michener and Locklear 1990a, Boonstra *et al.* 2001b), or breeding dispersal (Green 1977, Wolff and Lidicker 1980, Boyce and Boyce 1988, Michener and Locklear 1990a). Identifying peak periods of disappearance and whether death or dispersal is the cause of this disappearance may provide insights into the life-history strategies utilized by a population.

The most spectacular example of adult male disappearance in mammals occurs in 9 species of *Antechinus* and *Phascogale*, marsupial dasyurids (Lee and Cockburn 1985). Competition for females during the mating season is so intense that all males become physiologically stressed, their immune systems become compromised, and they are killed by parasites or disease during or immediately after the mating season. In *Antechinus stuartii*, 100% of adult males disappear over just a 5 – 10 day period (Lee and Cockburn 1985). A similar, but less dramatic, trend in disappearance has been identified in at least two species of North American ground squirrel, the arctic ground squirrel (*Spermophilus parryii*, Boonstra *et al.* 2001b) and the Richardson's ground squirrel (*Spermophilus richardsonii*, Michener and Locklear 1990a).

Live-trapping studies of *S. parryii* have revealed that in most years, up to 90% of males that breed in an area during the spring disappear before the subsequent breeding season the following spring, irrespective of squirrel density or food availability (Figure 3.1, Carl 1971, Lacey 1991). Similarly, approximately 80 – 90% of adult male *S. richardsonii* disappear annually (Michener and Locklear 1990a). In both species, adult female disappearance over the same period is approximately 50%, much less than of their male counterparts (Michener and Locklear 1990a, Byrom and Krebs 1999). Half of



**Figure 3.1** Mean proportion of adult males (bars  $\pm$  95% confidence limits) that disappeared from one spring trapping session to the next and adult population density (lines) during a long term study in southwestern Yukon (Karels *et al.* 2000). On control grids, 8, 14, 11, 9, 17, 20, 21, and 21 males were monitored in 1991 to 1998 respectively, and on food grids 5, 10, 15, and 30 males were monitored in 1992 to 1995 respectively. The data from all years was combined for "all" (control  $n = 99$ , food  $n = 52$ ). Data courtesy of T. Karels, R. Boonstra, and the Kluane Boreal Forest Ecosystem project



the breeding males disappear during or shortly after the breeding season (Michener and Locklear 1990a, Boonstra *et al.* 2001b), and possibly die as a direct or indirect result of intense intrasexual competition for mates (Michener and Locklear 1990a, Boonstra and McColl 2000, Boonstra *et al.* 2001b). The proximate cause and location of death, however, is not known. A second peak of disappearance of adult males in arctic ground squirrels occurs shortly after juveniles emerge from natal nests in late summer (Carl 1971, Green 1977, McLean 1982, Lacey 1991). This corresponds to a period when immigrant adult males are caught on trapping grids (Green 1977, Lacey 1991). Losses of males at these times must be partially due to dispersal but exact dispersal rates, dispersal distances, and the long-term survival of dispersers have not been quantified in this species.

My objectives in this study were to quantify the disappearance of adult male arctic ground squirrel as a function of date and season, and to partition the cause of disappearance into components explained by death and dispersal. Based on the results from previous live trapping studies, I predicted two peaks of disappearance, one associated with high mortality during the mating season and one associated with breeding dispersal (and possibly mortality) by adult males just after juveniles emerge from natal nests 8 weeks later. I used inter-individual variation in a range of morphological, behavioural, and condition variables to identify the factors associated with an individual's probability of dying or dispersing.

## **Methods**

### General methods

From June 2000 to August 2002, I studied arctic ground squirrels at an alpine study site in the Ruby Ranges, near Kluane Lake, southwestern Yukon (1700 – 2200 m, 61° 20' N, 138° 25' W). The annual cycle of arctic ground squirrels is comprised of two distinct periods – winter (September to mid-April), during which time squirrels are hibernating, and the active season (mid-April to September), during which time squirrels are continuously euthermic and above ground daily. The active season can be further subdivided into the breeding and non-breeding portions. For males, the mating season begins with the establishment of mating territories when they emerge from hibernation in

mid-April (Carl 1971, Lacey and Wieczorek 2001). Copulations occur over a two to three week period as soon as females emerge from hibernation, about two weeks after the males first emerge. During the mating season, food is often unavailable because vegetation is still covered by snow or dormant (Buck and Barnes 1999a, Lacey *et al.* 1997, E. Gillis *personal observation*).

The arctic ground squirrels I studied lived in an area that was a mosaic of boulderfields (36%), patches of moss, lichens, and bare ground (37%), and vascular plants (*Salix*, *Carex*, *Dryas*, *Cassiope* spp. 37%; Hik, McColl & Boonstra 2001; McIntire & Hik 2002). Potential ground squirrel predators included red fox (*Vulpes vulpes*), golden eagle (*Aquila chrysaetos*), northern harriers (*Circus cyaneus*), wolverine (*Gulo gulo*) and grizzly bear (*Ursus arctos*; D.S. Hik, *unpublished data*). Over the three years of the study, density of adult ground squirrel in late summer was relatively constant but lower than in previous years (Chapter 2).

In order to monitor male survival and dispersal movements of ground squirrels during the active season, I live trapped adult males and fitted them with 1.5-g transmitters (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada). These transmitters had a battery life span of approximately 6 months and signal range of approximately 500m in most of the study area. . Because there was the potential for males to disperse to areas where I would be unable to locate them to remove their radio collars, I fitted the collars as loosely as safely possible, and I used soft plastic tubing (outer diameter 6mm), which would collapse as males gained weight around their neck, as the collaring material. I located collared males every 1 to 7 days, either during the day, when animals were active, or at night when animals were in their sleeping burrows. I recorded male locations  $\pm 10$  m relative to permanent grid stakes placed in the study area at 50 m intervals. If a male was found dead, I identified the cause of death using evidence on and near the body.

I live-trapped radio-collared ground squirrels throughout the active season to monitor their reproductive status, changes in body mass, and adjust radio collar fit as animals changed mass. I categorized all males whose testes were descended as reproductive. I also measured the breadth of each male's zygomatic arch (a measure of structural size,  $\pm 0.5$  mm) on every capture. Each male was trapped, on average ( $\pm 1$  S.E.),  $6.3 \pm 0.4$  times in 2000,  $6.0 \pm 1.0$  times in 2001, and  $7.0 \pm 0.9$  times in 2002.

## Survival

### *Active season survival*

I divided the active season into the mating season, which began on emergence from hibernation in April or May and ended May 31, and the non-mating season. The non-mating season started on June 1, by which time all females had mated and males no longer had descended testes. This period ended when radio collars were removed the last week of July (2002) or the second week of August (2000 and 2001), after the males had established their fall territory but before they entered hibernation.

For each year, I used a Kaplan-Meier procedure that permitted staggered entry of animals into the study to describe the cumulative probability of survival as a function of time (Pollock *et al.* 1989). I knew the mortality date of all males that died to within one week, and assumed the male died the day after it was last known to be alive if I did not locate the body the day the animal died. I removed animals from the analysis on the day they had their collars removed. For animals whose signals were lost, I removed them from the analysis on the day they were last known to be alive because their final fates were not known. I also removed males from the analysis during the time they were not collared if I temporarily removed collars for longer than two weeks. If males were subsequently re-collared, they re-entered the study as "new" individuals. In order to compare survival among time periods that varied in length, I standardized survival to 7-day survival using the program Ecological Methodology (Krebs 2001, Krebs and Kenney 2001).

### *Winter survival*

I estimated winter survival as the proportion of adult males alive in August that were trapped in April or May of the following year. Adult male arctic ground squirrels establish and defend fall territories, on which they hibernate, in July and August (Carl 1971, E. Gillis *personal observation*). In 2000 and 2001, I used telemetry to identify the main burrows used by collared males in July and August, near where they would hibernate. I trapped these areas extensively in April and May the following year, and if a male was not trapped, I assumed that he had died. I excluded from the analysis males that hibernated in peripheral areas not extensively trapped in early May ( $n = 4$  in 2000, 2 in 2001) because some males shifted their home range shortly after emerging from

hibernation (this chapter and Chapter 4). Disappearance of these males may have been caused by dispersal as opposed to death.

### Dispersal

#### *Detection of dispersal and dispersal date*

I defined a disperser as an individual who left a home range and established a new, temporally and spatially distinct home range (after Lidicker and Stenseth 1992). I identified potential dispersers using two methods, fuzzy cluster analysis and shifts in sleeping burrows, and then conducted home range overlap analysis to identify which of the potential dispersers were true dispersers.

Fuzzy cluster analysis is similar to traditional "hard" cluster analysis except instead of each point being assigned to a cluster, each point is ranked on a continuous scale of 0 to 1 as to the certainty with which it belongs to each cluster. Zero indicates that the point does not belong to a given cluster and one indicates that the point definitely belongs to a particular cluster (Odeh *et al.* 1992). The level of "fuzziness" (i.e. the extent to which points are "forced" to belong to a cluster) is defined by the parameter  $\Phi$ , where  $\Phi = 1$  is the equivalent of a hard cluster analysis and all points have a certainty value of 1 for one cluster and 0 for all other clusters. If  $\Phi$  is greater than 1, points do not have to belong to any cluster, and the certainty with which they belong to each cluster will range from 0 to 1. Researchers consider  $\Phi = 2$  to be a moderate level of fuzziness (Odeh *et al.* 1992, Schaefer *et al.* 2001). I conducted two fuzzy cluster analyses on all telemetry locations for each male using the program FuzMe ( $\Phi = 2$ ; Minasny and McBratney 2002). In the first cluster analysis, I stipulated two clusters for each male (representing 1 dispersal movement), and in the second, and I stipulated three clusters for each male (representing 2 dispersal movements). I then examined, for each individual, the dates associated with the locations assigned to each cluster to determine if locations belonging to the same cluster (with a cluster certainty  $\geq 0.7$ ) were temporally, as well as spatially, distinct. If they were, the male had potentially dispersed, which I confirmed using methods described below. If locations of males that were spatially clustered were not temporally clustered as well, I assumed the clusters to represent areas of high use within a male's home range (e.g. a burrow system or foraging location).

Fuzzy cluster analysis will not detect dispersal if only a few locations are obtained for the animal after dispersal, for example, if the animal died or had a collar removed shortly after dispersing. Therefore, for males not identified as potential dispersers using fuzzy cluster analysis, I examined their sleeping locations to determine if large ( $>150$  m) permanent shifts in sleeping locations had occurred. If they had, I considered the male to have potentially dispersed.

After I identified potential dispersal events, I estimated the dispersal date using all telemetry locations for each male. In all cases, I defined the potential dispersal date as the date the animal left the previous home range, which was always known to within one week. I confirmed that dispersal had occurred by overlaying the home ranges of the potential disperser before and after the dispersal date. Home ranges were calculated using a 90% minimum convex polygon based on all day and night locations and kernel center (Kenwood and Hodder 1990). If these home ranges had 0% overlap, I assumed the male had dispersed.

As with survival, I used a Kaplan-Meier procedure that permitted staggered entry of animals into the study to describe the cumulative probability of dispersal as a function of time for each year (Bennetts et al. 2001). If a male had his collar temporarily removed for more than two weeks, I removed him from the analysis for the period he was not collared. In contrast to survival analyses, in which a male must be eliminated from the sample analysis after he dies because he is no longer at risk of death, animals may disperse more than once in a season. Thus, if a collared male dispersed, he remained as part of the study group until his collar was removed in August, after he had established his fall territory but prior to hibernation.

#### *Dispersal distance*

For all males that had two temporally and spatially distinct home ranges, I identified the main sleeping burrow used by the male before and after dispersal. Dispersal distance was the linear distance between these two burrows.

#### Correlates of survival and dispersal

To determine what factors were associated with mating season survival, winter survival, and dispersal, I conducted nominal logistic regressions with fate (dead or alive,

dispersed or did not disperse) as the dependent variable and potential correlates, described below, as independent variables. All regressions were performed in JMP version 3.2.1 (SAS Institute Inc., 1997), with the most parsimonious of the competing models identified using the second order Akaike's information criterion,  $AIC_c$  (Christensen 1990, Burnham and Anderson 1998). Prior to being entered into a model, I ensured that independent variables were not correlated ( $\alpha = 0.05$ ).

#### *Correlates of mating season survival*

I investigated the potential correlation between mating-season survival and year, age of male (yearling or  $\geq 2$ ), an index of movement rate during the mating season, and number of females in the male's core (50%) home range. I included only males I collared before May 15 in the analysis.

I used data obtained from live trapping to determine the age for each radio-collared male. For some males, I knew the year they were born because I first trapped them when they were juveniles. Therefore, I could calculate exact age. Some other males, who were not captured as juveniles, grew in structural size (as measured by zygomatic arch width) during the summer of the year they were first captured. I therefore considered them to be yearlings in the year they grew, and  $\geq 2$  years old in subsequent years. All other males were assumed to be yearlings in the year they were first caught ( $n = 3$  in 2001,  $n = 1$  in 2002).

As an index of movement rate, I used dispersion of the 1<sup>st</sup> five non-sleeping locations I obtained for each male during the mating season. I calculated dispersion by taking the mean distance between all possible pairs of the five locations for each male (i.e. the mean Euclidean distance between points, Conner and Leopold 2001). If males died after being located only 4 times, I used the dispersion of the 4 locations ( $n = 2$ ), but excluded from the analysis males for whom I obtained less than 4 locations during the breeding season.

To determine the spatial location and size of the male's core home range, I used all April and May non-sleeping locations, eliminating the 50% of locations farthest from the kernel center of the range (50% adaptive kernel home range as recommended by Hubbs and Boonstra 1998). I established core home range sizes using this method only

for males who did not disperse during the breeding season and for whom I had  $\geq 15$  daytime locations, the minimum required for reliable estimates of home range size for this species (Hubbs and Boonstra 1998). Core home range size was, however, highly correlated with my index of movement rate ( $r^2 = 0.72$ ,  $n = 9$ ,  $t = 4.2$ ,  $p = 0.004$ ). Therefore, for males for which I had  $<15$  non-sleeping locations in the mating season, I estimated the size of the core home range using the regression equation from the relationship (50% home range (ha) =  $0.00217 \times \text{dispersion} + 0.609$ ). For males with estimated core home range sizes, I assumed a circular core home range centered on the kernel center of all mating season locations (Worton 1987, 1989).

The location at which each female ( $n = 141$ ) mated was determined in one of two ways. For a female whose young were located either through radio-telemetry (Chapter 2) or by the emergence of juveniles, I assumed she mated where her litter was located (55% of females). For other females, I used the arithmetic center of all trapping locations in May for each female, or if the female was not trapped in May, the mean of all June-July trapping locations, to determine her breeding location (23% and 22% of females respectively).

#### *Correlates of winter survival*

I investigated the potential correlation between winter survival and year, age of male (yearling or  $\geq 2$  years old), and an index of fall body condition (residuals of mass in August regressed on breadth of zygomatic arch). In 2001, I also had conclusive information on each male's mating season location and dispersal history. I therefore conducted a second set of regressions using winter survival as the dependent variable and age (yearling or  $\geq 2$  years old), male dispersal (dispersed or did not disperse), and the number of females in the male's core home range as independent variables.

#### *Correlates of dispersal*

I examined the potential correlation between dispersal and year, age of male (yearling or  $\geq 2$  years old), the number of adult females within 100 m of the male, and the presence of juvenile females, presumably daughters, within 100 m of the male. I restricted analyses to those males who were collared before and survived until juvenile emergence (June 25, Chapter 2) as males collared after this time may have already

dispersed and males that died before this time might have dispersed had they survived. I also excluded males who had collars removed before July 11, the date after which no dispersal was detected, as their dispersal fate was unknown.

To establish the number of females within 100m of a male, the male location I used depended on whether or not the male had dispersed. For dispersers, I used main sleeping burrows prior to dispersal, and for non-dispersers, I used mating locations (as established by methods previously described). For non-dispersers that were not collared during the mating season, I used the location of the main sleeping burrows used just after collaring.

I established adult female locations by methods previously described. For locations of juvenile females ( $n = 159$ ), I used the location of their natal nest if it was known (34% of juvenile females) or their first trap location if it was not (66% of juvenile females).

### Statistics

Means are reported as mean  $\pm$  1 S.E. and survival estimates are reported with 95% confidence limits based on either Greenwood's standard error for Kaplan-Meier estimates (Pollock *et al.* 1989) or binomial confidence intervals for proportion data (Krebs 1999). Differences were considered to be statistically significant using  $\alpha = 0.05$ . All home range analyses were done using Ranges V (Kenwood and Hodder 1990) and spatial relationships between males and females were established using ArcView GIS 3.2 (Environmental Systems Research Institute, Inc., 1999; distances calculated using Nearest Features, with Distances and Bearings v. 3.6 extension, J. Jenness, US Forest Service, 2002).

### **Results**

During the 3 years of the study, 49 adult males were radio-collared, eleven of whom were radio-collared in two years (Table 3.1). The average number of times each male was located varied among years, ranging from approximately 19 in 2000 to 30 in 2002 (Table 3.2).



**Table 3.1** Sample sizes and monitoring dates of radio-collared adult male arctic ground squirrels. Animals with "fate unknown" disappeared and could not be located or death could not be confirmed. Numbers in brackets are the number of individuals that were also collared the previous year.

Year	Dates monitored	# individuals		Fate unknown	# Died
		Collared	Collared before June 1		
2000	May 29 – Aug 18	23	4	0	2
2001	Apr 28 – Aug 13	20 (8)	18	4	6
2002	Apr 27 – Jul 27	17 (3)	17	4	2

**Table 3.2** Average number of times ( $\pm 1$  SE) radio-collared males were located during the day and at night, when males were in sleeping burrows. Dates squirrels were monitored and sample sizes can be found in Table 3.1.

Year	Entire active season		Mating season only (< June 1)	
	daytime	sleeping	daytime	sleeping
2000	15.5 $\pm$ 1.3	3.9 $\pm$ 0.4	0.5 $\pm$ 0.3	0
2001	15.4 $\pm$ 3.1	5.4 $\pm$ 1.1	8.2 $\pm$ 1.4	1.9 $\pm$ 0.3
2002	19.2 $\pm$ 2.6	11.7 $\pm$ 1.8	13.8 $\pm$ 1.8	6.1 $\pm$ 0.8

## Survival

Survival rates of adult males varied during the active season, differing substantially between the mating and non-mating portions (Table 3.3, Figures 3.2 and 3.3). Males rarely died between June and mid-August; however, during the mating season, mortality was high and peaked late in the mating season (mid to late May; Table 3.3, Figure 3.2). Of the 9 radio-collared males who died during the mating season, I was able to establish the cause of death for all except one that died in 2002. Six males were killed by predators (one fox kill in 2000, four fox kills and one avian kill in 2001), one drowned (2001), and one died as the results of wounds obtained in fights with other males (2002). Only one radio-collared male died during the non-mating portion of the active season (2000), and he was killed by an avian or mammalian predator.

Survival of adult males also differed between the active season and over winter. Male survival was, on average, 4% per week lower during the mating season than winter (Table 3.3). The mating season of 5 weeks was, however, much shorter than the winter period (33 weeks). As a result, the probability of a male surviving the entire mating season was actually 30% higher than his probability of surviving the entire winter (Figure 3.3).

Of all correlates investigated in isolation and combination, age alone was the best predictor for both mating season and winter survival (Appendices 7 and 8). During the mating season, yearlings had a 63% higher probability of surviving than males  $\geq 2$  years old (Figure 3.4,  $r^2 = 0.28$ ,  $n = 23$ , likelihood ratio  $\chi^2 = 8.41$ ,  $p = 0.04$ ). Yearlings also had higher winter survival, although the difference was smaller and the trend was not statistically significant (Figure 3.4,  $r^2 = 0.09$ ,  $n = 24$ , likelihood ratio  $\chi^2 = 2.96$ ,  $p = 0.09$  for 2000 and 2001 combined,  $r^2 = 0.58$ ,  $n = 8$ , likelihood ratio  $\chi^2 = 6.09$ ,  $p = 0.01$  for 2001 only).

## Dispersal

Thirty-four males were collared for a sufficient time period to evaluate whether or not they dispersed. In total, 12 males left established home ranges and re-established new, spatially and temporally distinct home ranges a total of 13 times. Dispersers moved on average  $400 \pm 50$  m (range 160 – 750 m, Figure 3.5).

**Table 3.3** Comparison of adult male survival (standardized to 7-days) during the active season (mating and non-mating season) and during the winter. The 95% confidence interval associated with the estimate is provided in brackets. Average survival is reported as mean  $\pm$  1 S.E.

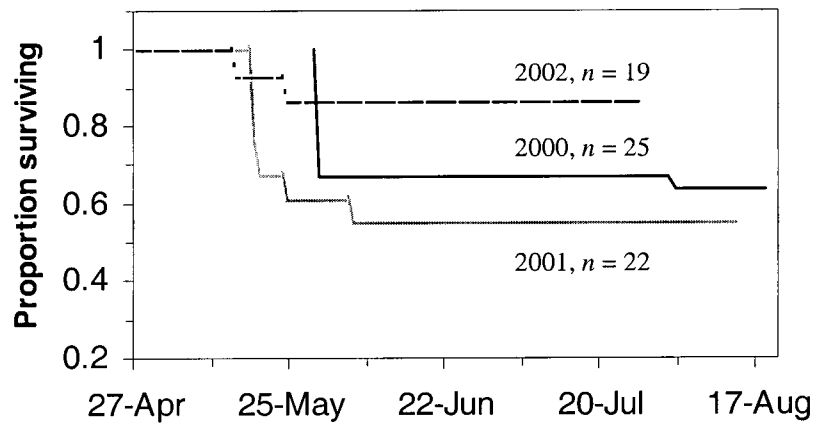
	Active Season		Winter <sup>3</sup>
	mating <sup>1</sup>	non-mating <sup>2</sup>	
2000	--	0.996 (0.987-1.00)	0.979 (0.957-0.991)
2001	0.899 (0.800-0.964)	1.00 (1.00-1.00)	0.971 (0.928-0.992)
2002	0.971 (0.927-1.00)	1.00 (1.00-1.00)	--
Average	0.935 $\pm$ 0.036	0.999 $\pm$ 0.002	0.975 $\pm$ 0.004

<sup>1</sup> Sample sizes: 2001  $n$  = 19, 2002  $n$  = 17

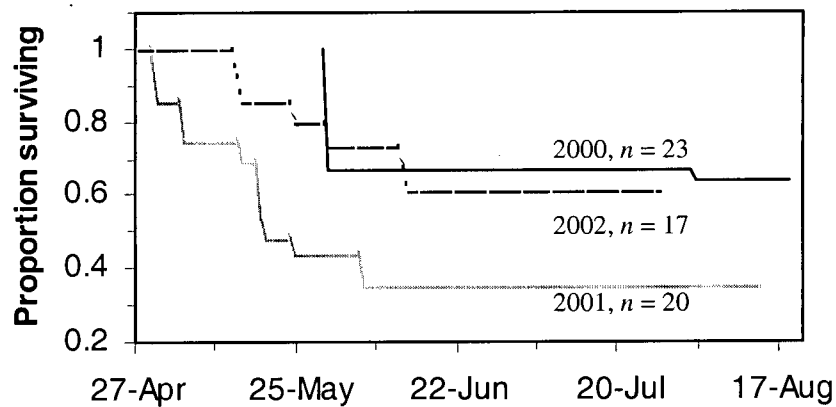
<sup>2</sup> Sample sizes: 2000  $n$  = 24, 2001  $n$  = 11, 2002  $n$  = 14

<sup>3</sup> Sample sizes: 2000  $n$  = 16, 2001  $n$  = 8

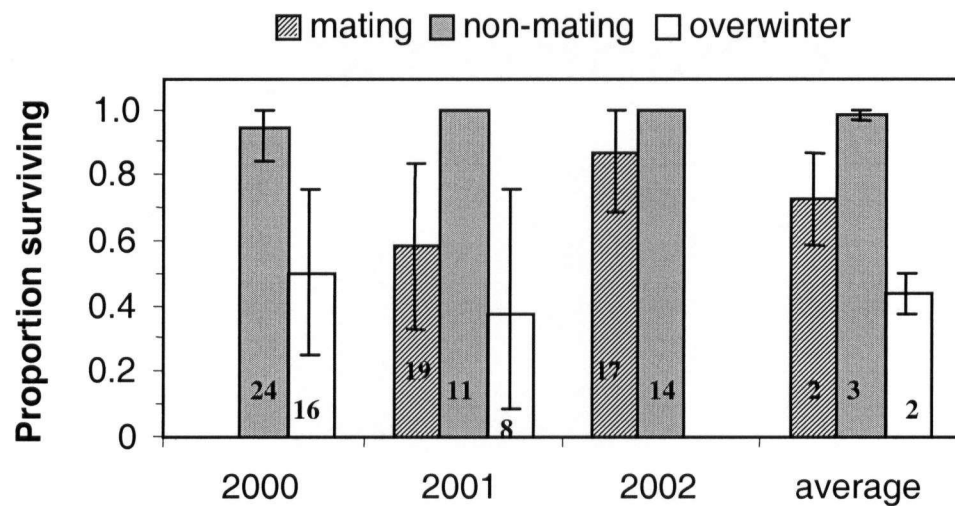
(a)



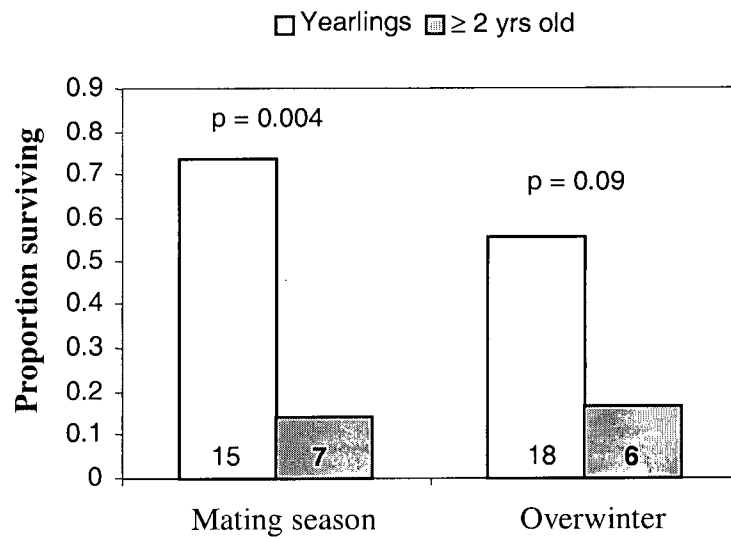
(b)



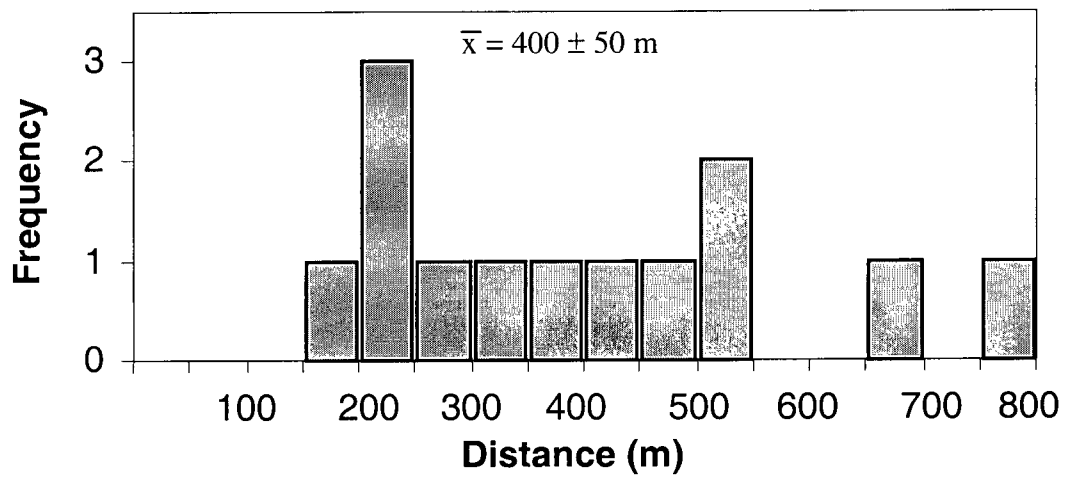
**Figure 3.2** Kaplan – Meier survival curves for radio-collared males for each of the three years : (a) animals with unknown fates censored from the analysis and (b) animals with unknown fates assumed to have died. The 95% confidence intervals associated with the yearly survival curves are provided in Appendices 5 and 6.



**Figure 3.3** Survival of adult males by season, assuming the mating season was 5 weeks, the non-mating portion of the active season was 14 weeks, and hibernation was 33 weeks. Error bars represent the 95% confidence interval associated with estimates. Average survival is mean  $\pm$  1 S.E. Sample sizes are provided on bars.



**Figure 3.4** Effect of age on the proportion of males that survived the mating season and winter. Sample sizes are provided on bars.



**Figure 3.5** Distribution of distances between pre- and post- dispersal sleeping burrows for males that left established home ranges in order to establish new, spatially and temporally distinct home ranges.



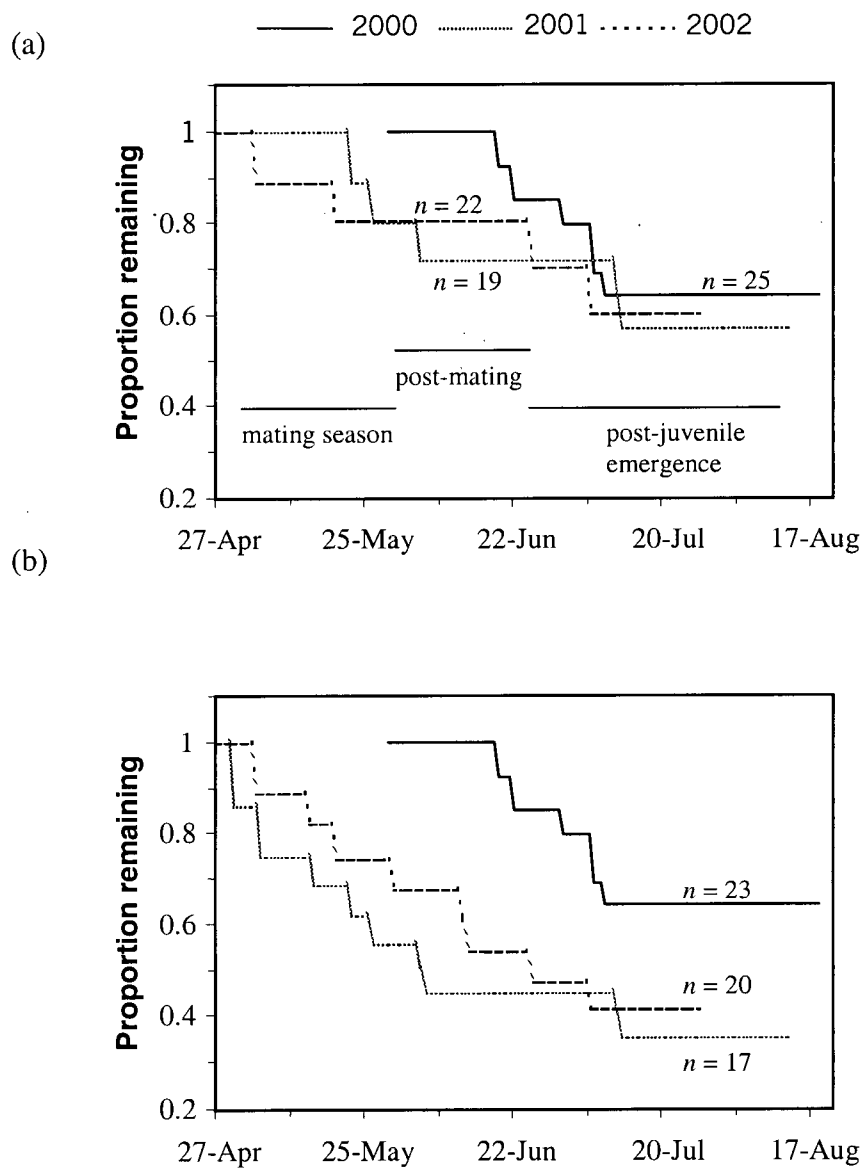
Males dispersed throughout the early part of the active season, but not after July 11 (Figure 3.6). Three of the dispersal events occurred during the mating season, 5 occurred between the end of the mating season and the emergence of juveniles, and the remaining 5 occurred shortly after juvenile emergence. Two of these dispersal events were made by one male who moved twice in 2002, in early May and again in July.

None of the potential correlates examined (year, age of male, male's proximity to females, or the presence of daughters nearby) independently or in combination predicted very well the probability of a male dispersing (Appendix 11). The two most parsimonious statistical models (year only and age only) were very similar in their predictive value, as indicated by almost identical  $AIC_c$  values, but each explained only 5% of the variation whether or not an animal dispersed. Neither factor was statistically significant (year only,  $r^2 = 0.05$ ,  $n = 34$ , likelihood ratio  $\chi^2 = 2.2$ ,  $p = 0.33$ ; age only,  $r^2 = 0.05$ ,  $n = 34$ , likelihood ratio  $\chi^2 = 2.1$ ,  $p = 0.14$ ).

## Discussion

As predicted, during the active season there were two peak periods of disappearance of adult males from the arctic ground squirrel population I studied. The first peak was late in the mating season (mid to late May), and was mainly caused by mortality, although some dispersal also occurred during this time. The second peak, just prior to and shortly after the emergence of juveniles from natal nests (June 25, Chapter 2) was a result of dispersal. The best predictor of male death was age. Yearlings had lower mating season and winter mortality than older ( $\geq 2$  years old) males.

Although this study lasted only 2 ½ years and was focussed on one site, the timing of disappearance of males is similar to other studies of arctic ground squirrels, and many of the trends in survival and dispersal I quantified have been predicted by other researchers, as I will discuss below. Thus, although variation in actual survival and dispersal rates is certain to exist among populations, I am confident that the trends in timing and correlates of survival and dispersal I discuss are representative of arctic ground squirrels living in open, tundra habitats.



**Figure 3.6** Kaplan –Meier dispersal curves for radio-collared males for the three years of study: (a) animals with unknown fates censored from the analysis and (b) animals with unknown fates assumed to have dispersed. The 95% confidence intervals associated with the yearly dispersal curves are provided in Appendices 9 and 10.

The annual disappearance rate of 80% of adult males is remarkably similar to rates reported for other populations in previous studies (Carl 1971, Lacey 1991). Although less than the 48% mortality predicted from live-trapping studies in the boreal forest (Boonstra *et al.* 2001b), mortality was very high during the mating season in this study, with an average of 28% of males dying in the five weeks after hibernation. Most males that disappeared during the remainder of the active season dispersed. Only 2% of males that survived the mating season died during the remainder of the active season, but 35% dispersed. Winter mortality among males was high. Fifty to 63% of the adult males that survived the mating season died during winter, a mortality rate similar to that reported for a population inhabiting a lower elevation boreal forest approximately 35 km away (50 – 83%, Hubbs and Boonstra 1997).

Increased mortality of males during the mating season is a trait common among ground squirrels (*S. richardsonii*, Michener and Locklear 1990a; *S. parryii*, Boonstra *et al.* 2001b, my study; *S. columbianus*, Neuhaus and Pelletier 2001; *S. tereticaudus*, Dunford 1977; and *S. beldingi*, Sherman and Morton 1984). This increased mortality is thought to be the result of competition among males for females during the mating season (Schwagmeyer 1990), which seems counterintuitive given there are frequently two to eight times more females than males in a population (Dobson 1984). Each female, however, is only in oestrus for a few hours on one day, so at any given time, the operational sex ratio (receptive females to reproductive males) is extremely male biased (Michener and McLean 1996, Millesi *et al.* 1998). It is this male-biased operational sex ratio that sets the stage for intense intrasexual competition among males, even among males within a species of territorial ground squirrels. For example, even though most male arctic ground squirrels physically defend territories on which potential mates reside (McLean 1983, Green 1977, Lacey and Wiczorek 2001), fighting intensifies when the females on males' territories are in oestrus. This is because males who defeat the territory holder can mate with oestrous females and father their litters (Lacey and Wiczorek 2001). Fighting can be so severe that males die as a result of the wounds they incur (Watton and Keenleyside 1974, Holmes 1977).

The proximate cause of mortality of males during the breeding season is not known for most *Spermophilus* spp. For arctic ground squirrels, Boonstra *et al.* (2001)

suggested that males die from infections or illnesses because their immune systems are weakened during the breeding season by the effects of chronic stress associated with the prolonged intense fighting.' This phenomenon is responsible for the 100% mortality of males during the breeding season in *Antechinus* (Lee and Cockburn 1985, Scott 1987). My results, however, do not support the direct link between reduced immune system function and death. Most males that died during the mating season in my study were depredated. Mortality may have been indirectly caused by chronic stress, however, if the physiological changes associated with chronic stress affected male behaviour in a way that increased their susceptibility to predation (Boonstra *et al.* 2001b). Several factors that may directly increase the males' susceptibility to predation have been observed during the breeding season. These include behavioral changes, such as increases in movement rates and decreases in vigilance behaviours (McLean 1983), morphological change, such as high weight loss (Buck and Barnes 1999a), environmental changes, such as the loss of cryptic colouration against a background of snow, and decreased access to burrow systems still under snow (Carl 1971, E. Gillis *personal observation*).

The probability of a male dying either during the breeding season or over winter was dependent upon whether he was a yearling or  $\geq 2$  years old. Regardless of age, all males trapped during the breeding season were reproductive (Chapter 4), indicating that all males would be involved in intrasexual competition for mates. Older males ( $\geq 2$  years old) were, however, more likely to die than yearlings during the mating season.

Even though males in both age cohorts would have invested energy into reproduction, older males may have a higher mortality rate during the breeding season if they invested more resources in reproduction, and if a trade-off between reproduction and mating season survival existed. Two measures of reproductive effort, rate of loss of body mass and severity of wounds, indicate the former condition was met (Chapter 4). It is also likely a trade off between survival and reproduction does exist for males during the mating season, as available energy resources are limited. During the mating season, fresh food resources are not yet available (Buck and Barnes 1999a, E. Gillis *personal observation*), and males rely on energy from their body reserves, built up by eating cached seeds, just before emerging in the spring (Buck and Barnes 1999a). The increased proportion of energy invested into reproduction by older animals relative to yearlings

may have increased the susceptibility of older males to depredation and dying in fights with other males (Chapter 4).

Physically, older males that survived through the mating season seemed to recover from their higher reproductive effort during the post-mating portion of the active season. Survival of both yearlings and older males was very high during this time, and despite their much higher rate of mass loss during the breeding season, older males were in similar physical condition to yearlings just prior to hibernation (Chapter 4). Despite their apparent recovery, however, older males were much less likely to survive the winter. One potential explanation is that the physiological effects incurred during the mating season had a long-term survival cost which was realized under the physiological demands of hibernation (Chapter 4).

None of the factors that I examined, either in isolation or in combination, were useful in predicting the probability that an adult male would disperse. Animals may disperse for a number of non-exclusive reasons – to increase their access to resources, to increase their access to mates, or to prevent inbreeding (Greenwood 1980). Dispersal of reproductively mature animals is rare in small mammals (Greenwood 1980), and among those species in which it does occur, it occurs at a low rate in only some years (Wolff and Lidicker 1980, Lurz *et al.* 1997, Berteaux and Boutin 2000). This indicates that even if adult animals are prone to disperse, they may use a proximate cue in the local environment to disperse (Ims and Hjermann 2001, Ronce *et al.* 2001). As a result, the proximate and ultimate causes of breeding dispersal in ground squirrels are not clear (Holekamp 1984a), but dispersal is probably a response to a combination of factors that I could not adequately measure and incorporate in the models. The causes of dispersal in male arctic ground squirrels are investigated more thoroughly in Chapter 5.

An unexpected result in my study was the timing of dispersal for many of the males. McLean (1983) suggested that adult males should disperse as soon after mating as possible in order to secure a high quality fall territory, but that many males delay dispersal in order to protect their current offspring from being killed by immigrant males. I therefore predicted that most adult males would delay dispersal until after juveniles emerged, as has been reported in other studies (McLean 1983, Lacey 1991). Although some males did delay dispersal until after juvenile emergence, many males in my study

dispersed from the area on which they bred prior to juvenile emergence (Figure 3.6). Other studies have indicated that a few males may disperse during or shortly after the mating season (Green 1977, McLean 1983), but "early dispersers" were much more common in my study than previously reported.

One possible explanation for the higher frequency of early dispersal in my study is that there were many males in my study population that had minimal reproductive success. McLean's (1983) hypothesis to explain the timing of dispersal leads to the prediction that males that are less successful reproductively should disperse early in the season but males that are more successful reproductively should delay dispersal until after juvenile emergence, at which time their many offspring are no longer at risk of infanticide. Likewise, breeding dispersal should occur earlier in years when local male density is sufficiently low to reduce the probability of infanticide. Although I have a limited sample size, I have indirect evidence to support the first prediction. It appears that older males had a higher reproductive success than yearlings (Chapter 4). Among males that dispersed, only one of five older males dispersed before juveniles emerged. In contrast, 4 of the 7 yearlings that dispersed did so before juvenile emergence. A limited number of years and similar densities among years in my study prevents testing the second prediction with my data. However, the high frequency of dispersal before juvenile dispersal in my study relative to other studies is consistent with this prediction because squirrel densities at my study site were much lower than densities at sites of previous studies (Green 1977, McLean 1983).

In summary, the annual disappearance rate of adult male arctic ground squirrels averaged 80%. There were two periods of peak disappearance during the active season – late in the mating season, the result of males dying, and just prior to and shortly after the emergence of juveniles from natal nests, the result of post-breeding dispersal. Winter mortality of adult males was also high – an average of 57% of males that were alive at the end of the active season died during the winter.

Though movement rate, year, and one measure of reproductive success (number of females in male's core home range) did not appear to be related to mortality, age was a useful predictor of mortality both in the mating season and winter. Older ( $\geq 2$  years old) males experienced higher mortality than yearlings, possibly a result of a higher

investment in reproduction that reduced both immediate and long-term survival. In contrast to survival, I found no factors closely associated with dispersal.

Survival and timing of dispersal may be closely linked to male reproductive effort and success. I explore this, as well as the potential links between dispersal, age, and reproductive success, in more detail in Chapters 4 – 6.

## **Chapter 4: Variation in mating behaviours among adult male arctic ground squirrels**

### **Introduction**

From an evolutionary standpoint, the reproductive success of any individual is the relative contribution it makes to the future gene pool. Although conceptually useful, this definition of success is of little practical use in most field studies, so reproductive success is more commonly measured as the number of offspring an individual produces. In invoking this working definition, the "future gene pool" is restricted to the next generation only, and it is assumed that differences in reproductive success that arise after one generation persist.

The dilemma for sexually reproducing animals is how to allocate reproductive energy to maximize reproductive success over a lifetime. Lifetime reproductive output is a function of both the number of times an individual reproduces and the number of offspring produced in each reproductive attempt. This allocation "decision" is further complicated in that energy used for reproduction is not available for other purposes. Thus a trade-off exists between current reproduction and future survival and reproduction.

In polygynous species, males invest little energy in parental care and can increase their reproductive success by concurrently siring many offspring with many different females. Each offspring can be fathered by only one male, however, and therefore most of the energy a male has available for reproduction is used to acquire successful matings (i.e. matings that result in offspring). In species in which there is little or no sperm competition and no female choice, a male can increase the number of successful matings simply by increasing the number of females with which he mates. In these species, males with different attributes simultaneously attempt to maximize the number of matings they acquire. This can result in the evolution of multiple mating tactics, each of which is beneficial under a restricted set of conditions (Clutton-Brock 1989, Brockmann 2001).

In some species, all males compete using the same basic tactic, but more often individual males of the same species employ alternative mating tactics (Emlen and Oring 1977, Rubenstein 1980, Brockmann 2001). In species in which intraspecific variation



occurs, even if one tactic predominates other tactics can persist as a result of spatial and temporal variation in environmental conditions, frequency dependent selection, and behavioral changes of individuals in response to intrinsic or extrinsic factors (Rubenstein 1980, Brockmann 2001).

Spatial and temporal variation in environmental conditions allows some tactics to be more successful than others in different places or times. The relative success of an individual's tactics may depend on local male density, male quality (size, dominance and experience), tactics of other males, local female distribution, and the ratio of reproductive males to females (Emlen and Oring 1977, Clutton-Brock 1989, Schwagmeyer 1990, Brockmann 2001). As long as conditions vary in space or time, no one tactic can drive the others to extinction and multiple strategies can persist (Rodenhouse *et al.* 1997). Likewise, frequency-dependent selection results in different tactics being successful under different conditions. In this case, the varying condition is the frequencies of the various tactics. As a tactic becomes more common, its success will decrease compared to other tactics until its value and frequency declines. When the tactic becomes less common, its relative success will start to increase again (Zamudio and Sinervo 2000, Brockmann 2001).

Alternative mating tactics can also persist in populations if individuals irreversibly or reversibly switch tactics within or between mating seasons (Brockmann 2001). In particular, age can play a key role. Age can affect male size and experience, and animals of certain ages may exploit tactics unavailable to others. Age affects the relative amount of energy an individual should invest in current reproduction because residual reproductive output declines with age. Life-history theory assumes a trade-off between current reproduction and future survival (Stearns 1992), thus, the relative amount of energy an individual should invest in current reproduction versus survival should increase with age (Pianka 1976).

Mating tactics used by males in polygynous species can be placed into one of two broad categories, defense polygyny or non-defense polygyny (Dobson 1984, see Clutton-Brock 1989 for a similar but more detailed classification scheme). Males employing defense polygyny exclude other males permanently or temporarily from an area that either contains one or more females, or contains resources that attract females to the

defended area. In contrast, males engaging in non-defense polygyny compete not for space, but for social status or for female choice in order to secure copulations.

Many hypotheses proposed to explain the evolution of mating tactics and systems make specific predictions about the role of environmental conditions (such as the distribution of females, sex ratio, density) in determining the tactic (Dobson 1984 and references therein, Clutton-Brock 1989). Studies of sciurid rodents (*Spermophilus*, *Cynomys*, and *Marmota*) have made valuable contributions to the exploration of this relationship between environmental conditions and mating tactics (Dobson 1984, Schwagmeyer 1990). Within this family, examples of species representing all mating systems, from monogamy to promiscuity, are represented (Dobson 1984, Holmes 1984, Boellstorff *et al.* 1994). Among *Spermophilus* spp., both male defense and non-defense polygyny occur (Schwagmeyer 1990) and within some species, there is also considerable intraspecific variation in mating tactics (Carl 1971, Murie and Harris 1978). These species provide an opportunity to determine if explanations used for interspecific variation in mating tactics apply to intraspecific variation as well (Dobson 1984).

One ground squirrel species in which alternative male mating tactics may co-exist is the arctic ground squirrel (*Spermophilus parryii*). Arctic ground squirrels are herbivorous, hibernating small mammals (ca. 500-700 g) found throughout northern North America (Banfield 1974). They spend approximately 8 months of the year (September to mid-April) hibernating singly in underground nests. Adult males emerge from hibernation in mid-April, approximately 2 weeks before the females (Carl 1971, Lacey 1991), and some establish mating territories on which they breed (Carl 1971, Lacey and Wiczorek 2001). Mating occurs over a two to three week period as females emerge from hibernation, when fresh food is often unavailable because the vegetation is still covered by snow or is dormant (Buck and Barnes 1999a, E. Gillis *personal observation*). Like other *Spermophilus* species, the adult population is female biased due to poor survival of males during juvenile dispersal the first year of life (Byrom and Krebs 1999). However, a very short female oestrous period, lasting only a few hours (Lacey *et al.* 1997), creates a strongly male-biased operational sex ratio. Litters of females are usually sired by only one male (Lacey *et al.* 1997) so severe competition among males for mates occurs (Carl 1971, Green 1977, Michener and McLean 1996). On average, 50%

of adult males disappear during each mating season (Boonstra *et al.* 2001b), many of whom die (Chapter 3). Some adult males that survive continue to defend their breeding territories until young of the year have emerged from their natal nests, approximately 8 weeks after mating (Carl 1971, Green 1977, Lacey *et al.* 1997). This behaviour possibly prevents other males from entering the area and killing the young (McLean 1983).

The mating tactic of arctic ground squirrels has been categorized as territorial (Dobson 1984 and references therein, Lacey and Wiczorek 2001). However "floater" (i.e. non-territorial) males are also present during the once-a-year mating season (Carl 1971). Territorial males defend areas on which multiple females reside during the mating season (McLean 1983). The main reproductive benefit to a male holding a territory is his superior opportunity to obtain a majority of first copulations with females in his territory and to sire her offspring. For example, in one study, 70 % of females residing on a male's territory copulated first with the territory holder (Lacey and Wiczorek 2001). Even if a female subsequently mated with other males, the father of her young was almost always the first male with whom she mated (90% of cases, Lacey *et al.* 1997). However, 30% of females' first copulations were "extra-pair" copulations acquired by neighboring males who defeated the resident male territory holder in antagonistic interactions on the day the female was in oestrus (Lacey and Wiczorek 2001). Success in siring young by the non-territorial "floater" males that have been observed in some populations is still unknown. Thus, although territoriality is the most conspicuous and best studied strategy in this species, territorial defense may be only one of several mating tactics used by males.

The objectives of this study were to describe, for arctic ground squirrels, the spatial distribution of males during the mating period, to determine if age influenced the mating tactic males employ, and to identify correlates of male reproductive effort. Specifically, I wanted to (1) measure the home range size during the mating season for male ground squirrels living in alpine habitat and determine if older males obtained higher quality breeding territories than yearlings, (2) identify physical differences associated with age that may affect male mating success or tactic, and (3) identify factors correlated with indices of male reproductive effort and movement rate during the mating season. In other chapters of this thesis, I relate the variation in mating behaviour to mating season and winter survival (Chapter 3) and use variation in reproductive effort as

an integral component relating age, survival, and dispersal tactics of male arctic ground squirrels (Chapter 6).

## Methods

I studied arctic ground squirrels for two sequential mating seasons (late April to June, 2001 and 2002) at an alpine study site in the Ruby Ranges, near Kluane Lake, southwestern Yukon (1700 – 2200 m, 61° 20' N, 138° 25' W). The study area was a mosaic of boulderfields (36%), patches of moss, lichens, and bare ground (37%), and vascular plants (*Salix*, *Carex*, *Dryas*, *Cassiope* spp. 37%; Hik *et al.* 2001, McIntire and Hik 2002). Densities of adult ground squirrel at the time of the study were relatively low compared to previous years but similar between the two years of this study (0.31 adults/ha in 2001 and 0.54 adults/ha in 2002, Chapter 2).

The general procedure I followed was to trap and radio-collar adult male ground squirrels in order to monitor their movements, mass changes, and reproductive condition during the mating season. I then related these variables to other internal (e.g. age) and external (e.g. proximity to females) variables using a variety of statistical tests, described in more detail below. Before I conducted any parametric test, I checked data for normality and homogeneity of variances. If the assumptions for parametric tests were violated, I used non-parametric statistics. All statistics were performed in JMP version 3.2.1 (SAS Institute Inc., 1997) and unless otherwise stated, all numbers are reported as mean  $\pm$  1 S.E.

### General Methods

I trapped adult male ground squirrels as they emerged from hibernation and fitted them with 1.5-g transmitters (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada). I assumed that the collars did not affect male behaviour as collars weighed <0.3% of the body of males and fit snugly around their neck. I located all males radio collared before 15 May every 1 to 7 days throughout the mating season (emergence from hibernation until May 31, by which time all females had emerged and mated). Males were located both during the day, when they were active, and at night, when they were in sleeping burrows (2001:  $11.7 \pm 1.9$  locations/male ( $9.6 \pm 1.6$  by day,  $2.3 \pm 0.4$  at night),

2002:  $22.1 \pm 2.7$  locations/male ( $15.4 \pm 1.9$  by day,  $7.2 \pm 0.8$  at night). On each occasion, location was recorded to the nearest 10 m relative to permanent grid stakes placed in the study area at 50 m intervals.

I monitored the reproductive status and changes in the masses of males throughout the mating season by live-trapping radio-collared ground squirrels every one to two weeks (each male trapped  $3.1 \pm 0.5$  times in 2001,  $4.1 \pm 0.4$  times in 2002). Animals were tagged with uniquely numbered eartags on their first capture, and on this and subsequent captures, identity, reproductive condition (testes descended = reproductive, testes abdominal = non-reproductive), weight ( $\pm 5$ g), and zygomatic arch breadth (the width of the skull at the widest point  $\pm 0.5$ mm) were recorded.

#### Breeding home range size and male spacing

I was interested in three aspects of male spacing during the breeding season – home range size, breeding locations, and the distance between breeding locations.

I calculated breeding home range sizes only for males who did not disperse during the breeding season (Chapter 3) and for whom I had  $\geq 15$  daytime locations, the minimum required for reliable estimates of home range size for this species (Hubbs and Boonstra 1998, E. Gillis *unpublished data*). All home ranges were calculated using Ranges V (Kenwood and Hodder 1990) after I had excluded sleeping locations from the data. I calculated the breeding home range size in 3 ways to facilitate comparison to previous studies. First, I calculated the a minimum convex polygon (MCP) home range size excluding the 5% of points farthest away from the arithmetic center (95% MCP). Secondly, I calculated the adaptive kernel home range excluding the 5% of points farthest away from the kernel center (95% kernel). Lastly, I calculated male's core home range as the adaptive kernel home range size excluding the 50% of points farthest away from the kernel center, as recommended by Andreassen *et al.* (1993) and Hubbs and Boonstra (1997).

I considered the center of all locations I had obtained for the male during the breeding season to be the male's mating location (as calculated by the kernel mean, Worton 1989). I evaluated the spacing of males during the mating season by calculating the distance between each male's mating location and the mating location of his nearest

male neighbour. One male was located in an area that was not extensively trapped during the mating season, so I eliminated him from this analysis because I could not conclusively identify his nearest neighbour.

#### Effect of age on physical attributes and the territory quality of male arctic ground squirrels

I used data obtained from live trapping to determine the age of each radio-collared male. I knew the year that some males were born and therefore their exact age because I first trapped them when they were juveniles. Some males that had not been captured as juveniles, grew in structural size (as measured by zygomatic arch width) during the summer of the year they were first captured. I therefore considered them to be yearlings in the year they grew, and  $\geq 2$  years old in subsequent years. I assumed all other males were yearlings in the year they were first caught ( $n = 3$  in 2001,  $n = 1$  in 2002).

In order to determine if yearling males differed from older males ( $\geq 2$  years old) in attributes that may affect reproductive effort, I compared the structural size, mass, body condition, and two indices of breeding territory quality between the two age cohorts.

#### *Physical Attributes*

I compared structural size between yearlings and older males by comparing their zygomatic arch widths. For each male, I used the zygomatic arch measurement taken the first time he was trapped each year because some yearlings grew in structural size after, but not during, the mating season (E. Gillis *unpublished data*).

Comparison of mass and body condition (mass corrected for structural size) between the two age classes at the start of the breeding season was complicated by the fact that not all males were trapped on the same day or on the day they emerged from hibernation. Therefore, I estimated the mass of each male for a standardized date near the start of the breeding season. To do this, for males caught more than once during the mating season, I regressed mass against date ( $r^2 = 0.79 \pm 0.06$ ,  $n = 17$ ) and estimated mass on May 1 for each male using the resulting regression equation. The estimated masses were reasonable proxies for true masses, as indicated by a comparison of the

estimated mass on May 1 to the actual mass for 15 males trapped April 27 – May 1. The average difference between estimated and actual mass on May 1<sup>st</sup> was  $16.5 \pm 3.8\text{g}$ , which was the equivalent of  $2.7 \pm 0.6\%$  of male total body weight ( $n = 15$ ).

Comparison of body condition (mass corrected for structural size) between the two age groups was further complicated by the presence of a significant interaction between zygomatic arch width and year in an analysis of covariance with mass as the dependent variable ( $n = 28$ ; year:  $F = 4.54$ ,  $p = 0.04$ , 1 *df*, ZA:  $F = 23.5$ ,  $p < 0.001$ , 1 *df*, year  $\times$  ZA:  $F = 4.53$ ,  $p = 0.04$ , 1 *df*). This interaction meant that the slope of the linear relationship between mass and structural size varied significantly between years and data from different years could not be combined in an analysis of covariance. I therefore compared the residuals of mass regressed on zygomatic arch, calculated separately for each year, between age classes (Schulte-Hostedde *et al.* 2001). This method standardized the condition index between years, allowing me to combine data from both years prior to comparing the age classes.

#### *Breeding territory quality*

I assumed that the quality of a male's breeding territory could be measure by his access to females, so I compared two indices of access to females between yearling and older males. The first index was the number of females in each male's core home range (50% adaptive kernel or equivalent, Chapter 3). The second index was the male's proximity to females as measured by the mean distance from a male's mating location to the breeding location of the nearest 3 females. I chose to use his proximity to the nearest 3 females because the sex ratio averaged 1 male: 3 females during this study (1:3.5 in 2001, 1:2.8 in 2002, E. Gillis *unpublished data*). If females and males are uniformly distributed, all males should be equally close to 3 females. However, if females are clumped and some males live near clumps while others live far from clumps, there will be large variation in the mean distance from a male's mating location to the breeding location of the nearest 3 females. Males with a smaller mean distance will have more convenient access to females nearby.

The location at which each female ( $n = 100$ ) mated was determined in one of two ways. For a female whose young were located either through radio-telemetry (Chapter 2)

or by the emergence of juveniles, I assumed she mated where her litter was located (56% of females). For other females, I used the arithmetic center of all May trapping locations for each female, or if the female was not trapped in May, the mean of all June-July trapping locations as her breeding location (29% and 15% of females respectively).

#### Correlates of reproductive effort and male movement

Both reproductive effort and male movement may vary among individuals using different mating tactics. I examined several internal and external attributes (described below) associated with males to see if any were correlated with either of two indices of reproductive effort or one index of movement, and thus potentially correlated with different mating tactics. All regressions were performed in JMP version 3.2.1 (SAS Institute Inc., 1997), with the most parsimonious of the competing statistical models identified using the second order Akaike's information criterion,  $AIC_c$  (Christensen 1990, Burnham and Anderson 1998). Prior to being entered into a model, I ensured independent variables were not correlated. All tests were two-tailed except for the effect of age on reproductive effort, which was one-tailed since I predicted older animals would invest more in reproduction than yearlings.

#### *Reproductive effort*

The two indices of reproductive effort I used were rate of mass loss during the mating season and severity of injuries during the mating season. Increased mass loss is associated with an increase in the number of mates acquired by males in the European ground squirrel (Millesi *et al.* 1998). I calculated rate of mass loss for male arctic ground squirrels caught more than once during the breeding season by regressing mass against date for each male over the time period he lost weight. The slope of the regression line was the rate of mass loss in  $g\ day^{-1}$ . Males varied in mass at the start of the breeding season, so I normalized each male's measurement by dividing the rate of mass loss by the male's estimated mass on May 1<sup>st</sup>. The resulting value was the % spring body weight lost  $day^{-1}$ . I assumed that males losing a greater proportion of their body mass per day were allocating a greater proportion of their available energy to reproduction.



I also assumed that males with a higher reproductive effort would have a greater number and more severe wounds because intense competition among males for mates often leads to fighting among males (Carl 1971, Green 1977, Michener and McLean 1996). I recorded details of any wounds observed on males when they were trapped. The severity of wounds each male sustained during the mating season was assigned to one of 4 categories:

- (1) none
- (2) minor (one or two small cuts)
- (3) moderate (multiple deep lacerations or minor broken bones (e.g. broken toes))
- (4) severe (blinding, injuries affecting mobility, or multiple, deep facial lacerations that exposed the underlying bone)

I examined 4 factors to see if any were associated with either of the reproductive effort indices - year, age, spring body condition, and mean distance from each male's breeding location to the breeding location of the nearest 3 females (proximity to females as described above). I included year to account for any potential weather effects, and I included age because optimal reproductive theory predicts older animals should invest more heavily in reproduction. Male body condition may influence the mating tactic of males by affecting the amount of energy a male can allocate to reproduction, and a male's proximity to females affects the amount of effort required to acquire or defend females. To determine which factors were associated with each reproductive effort index, I conducted standard least squares regression for mass loss and nominal logistic regression for wounding level with the reproductive effort index as the dependent variable and potential correlates as independent variables.

#### *Movement rate*

As an index of movement rate, I used dispersion of the first five non-sleeping locations I obtained for each male during the mating season. I calculated dispersion by taking the mean distance between all possible pairs of the five locations for each male (i.e. the Euclidean distance between points, Conner and Leopold 2001). If males died after being located only 4 times ( $n = 2$ ), I used the dispersion of the 4 locations, but excluded from the analysis males for whom I obtained less than 4 locations during the

breeding season. I used standard least squares regression to examine the potential effect of year, age, spring body condition, and the male's proximity to nearest 3 females.

## **Results**

### Breeding home range size and male spacing

Home-range size during the breeding season varied considerably among males, with actual values depending on the estimation method used (Table 4.1). Average breeding home range size estimated by the 95% minimum convex polygon method was three times smaller than that estimated by the 95% kernel method (4 and 12 ha respectively, Table 4.1). When the outermost 50% of locations were eliminated from the home range estimate for any individual ("core" home range as estimated by 50% kernel home range estimate), the home range estimate was only 1/10 the size of the home range size when only 5% of the locations were eliminated (95% kernel home range, Table 4.1).

Males did not center their areas of activity close to each other during the breeding season. On average, males' centers of activity were almost 200 m away from the centers of activity of their nearest neighbours (mean  $193 \pm 20$  m,  $n = 26$ , range 55 – 425m). This distance did not differ between years (Kruskal Wallis test,  $z = 1.1$ ,  $p = 0.26$ ).

### Age effects

Irrespective of age, all males trapped during the mating season had descended testes, indicating they were all in reproductive condition. However, yearlings and older ( $\geq 2$  years old) males did differ in other physical attributes that may have affected their mating tactics and reproductive success.

### *Physical Attributes*

Upon emergence from hibernation, yearlings were structurally smaller than older males (Table 4.2). Not surprisingly, they also weighed 15% less than older males (Table 4.2). The weight of yearlings was slightly lower than expected based on differences in structural size alone, resulting in a significantly lower body condition (Table 4.2).

**Table 4.1** Breeding home range sizes (mean  $\pm$  1 S.E.) of adult male arctic ground squirrels estimated three different methods (95% minimum convex polygon (MCP), 95% adaptive kernel, and 50% adaptive kernel). Estimates for 8 of the 10 squirrels were from males collared in 2002 and 2 from males collared in 2001. Sizes did not differ between years ( $p > 0.10$ ).

	n	mean size (ha)	range (ha)
95 % MCP	10	4.01 $\pm$ 0.56	0.98 – 7.21
95 % Kernel	10	12.41 $\pm$ 2.52	2.46 – 26.92
50 % Kernel	10	1.36 $\pm$ 0.26	0.37 – 3.07

**Table 4.2** Effect of age on physical attributes and breeding territory quality of adult male ground squirrels (sample sizes provided in brackets). No year effects were detected ( $p > 0.10$ ), so data from 2001 and 2002 were pooled prior to analysis. Zygomatic arch width (ZA) is a measure of structural size and the body condition index used was the difference between the actual mass and the expected mass based on the regression of mass against ZA for each year.

	yearlings	$\geq 2$ years old	t	p <sup>1</sup>
% reproductive	100 (20)	100 (15)	n/a	n/a
Zygomatic arch (mm)	$38.8 \pm 0.5$ (15)	$40.5 \pm 0.5$ (13)	2.7	0.006
Estimated mass on May 1 <sup>st</sup> (g)	$490 \pm 19$ (12)	$590 \pm 23$ (13)	3.3	0.002
Body condition index (g)	$-26.2 \pm 12.3$ (12)	$16.2 \pm 17.3$ (13)	1.9	0.04
Mean distance to 3 closest females (m)	$134 \pm 13$ (14)	$121 \pm 21$ (15)	0.5	0.30
# females in 50% home range	$0.8 \pm 0.2$ (13)	$1.3 \pm 0.4$ (12)	$0.9^2$	0.19

<sup>1</sup> one-tailed test

<sup>2</sup> non-parametric Kruskal Wallis test used, z-score provided

### *Breeding territory quality*

Breeding territory quality, in terms of a male's proximity to females, did not differ significantly between yearlings and older males (Table 4.2). On average, males had  $1 \pm 0.2$  females in their core home range (range 0 – 4,  $n = 25$ ). Yearlings tended to have fewer females in their core home ranges than older males, but again this difference was not statistically significant (Table 4.2).

### Correlates of reproductive effort and male movement

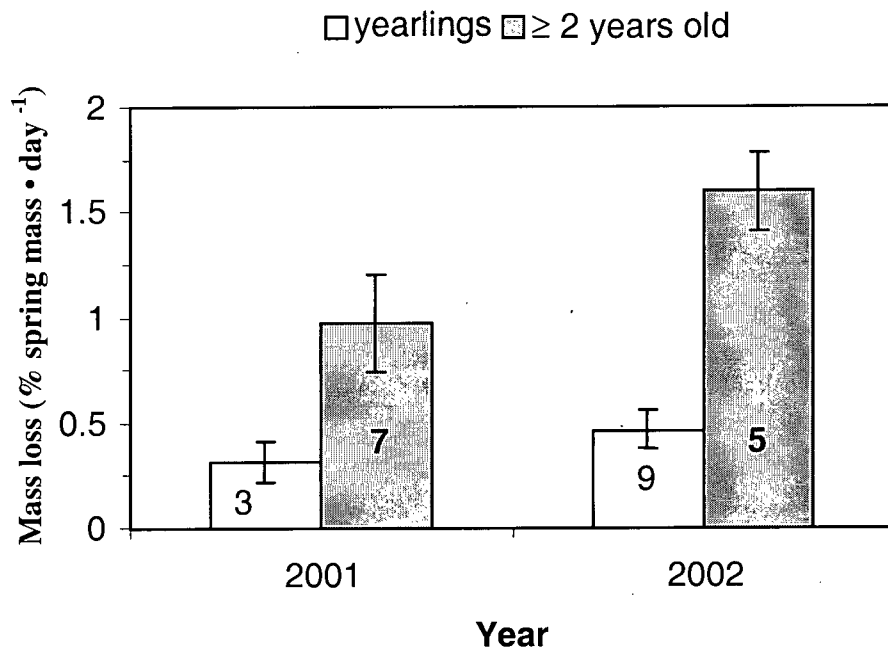
#### *Reproductive effort*

Variation in the two measures of reproductive effort I used, mass loss and level of wounding, were best predicted by different factors.

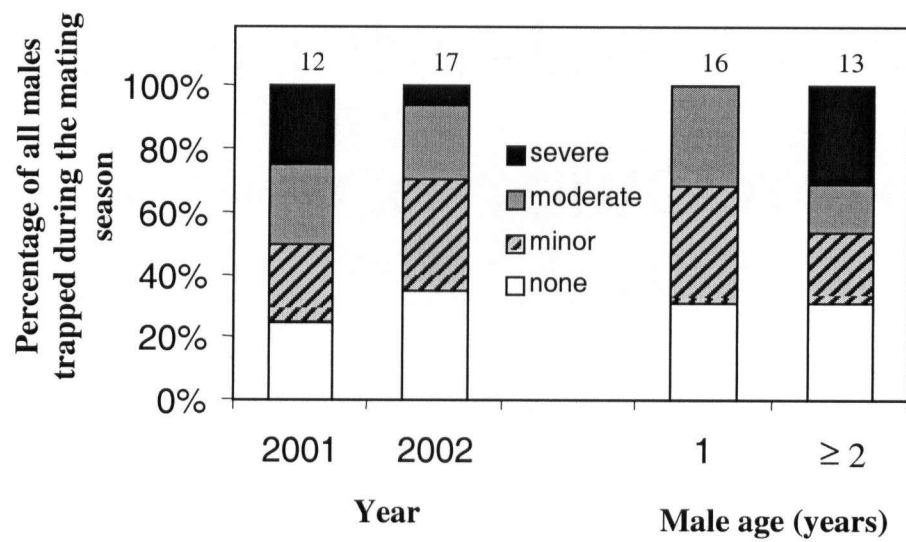
*Mass loss* — The rate at which males lost weight in the breeding season was highly variable. On average, males lost  $5.0 \pm 0.9 \text{ g} \cdot \text{day}^{-1}$  ( $n = 24$ ) but mass changes ranged from a loss of  $12 \text{ g} \cdot \text{day}^{-1}$  to a gain of  $3 \text{ g} \cdot \text{day}^{-1}$ . After correcting for differences among individuals in initial mass, the mass loss corresponded to an average of  $0.83 \pm 1.6\%$  loss of spring body weight per day ( $n = 24$ , range - loss of  $2.2\% \text{ day}^{-1}$  to gain of  $0.8\% \text{ day}^{-1}$ ).

Although it did not account for much of the variation in rate of mass loss during the breeding season, there was a trend towards lower mass loss in 2001 than 2002 (Figure 4.1). The most parsimonious statistical model explaining the variation in mass loss among males included only age as a factor ( $r^2 = 0.28$ , Appendix 12). Older males lost mass at a faster rate than yearling males ( $n = 24$ ,  $F = 8.4$ ,  $p = 0.004$ ,  $df = 1$ , Figure 4.1). Little of the variation in the rate of mass loss was explained by variation in male body condition in the spring or proximity of males to females (Appendix 12).

*Level of wounding* — During the breeding season, males were frequently observed fighting with each other, and 69% of males trapped during the breeding season had wounds, presumably incurred in male-male fights ( $n = 29$ ). Although yearlings frequently had minor or moderate levels of wounding, severe wounding was restricted to older males (Figure 4.2).



**Figure 4.1** Effect of age on mass loss by males during the breeding season. The year effect was not statistically significant but the age effect was ( $\alpha = 0.05$ ).



**Figure 4.2** Wounding rates and wound severity during the mating season as a function of year and age of male. Sample sizes provided above bars.

Due to small sample sizes, I combined categories 1 and 2 (no and minor wounds) and categories 3 and 4 (moderate and severe wounds) for statistical analysis. Although year, age, and spring body condition were not good predictors of the probability a male would sustain moderate to severe injury during the mating season, male proximity to the nearest 3 females was (Appendix 13,  $r^2 = 0.36$ ,  $n = 24$ , likelihood ratio  $\chi^2 = 11.7$ ,  $p < 0.0006$ ). Males living in closer proximity to females were more likely to incur moderate to severe wounds (Figure 4.3).

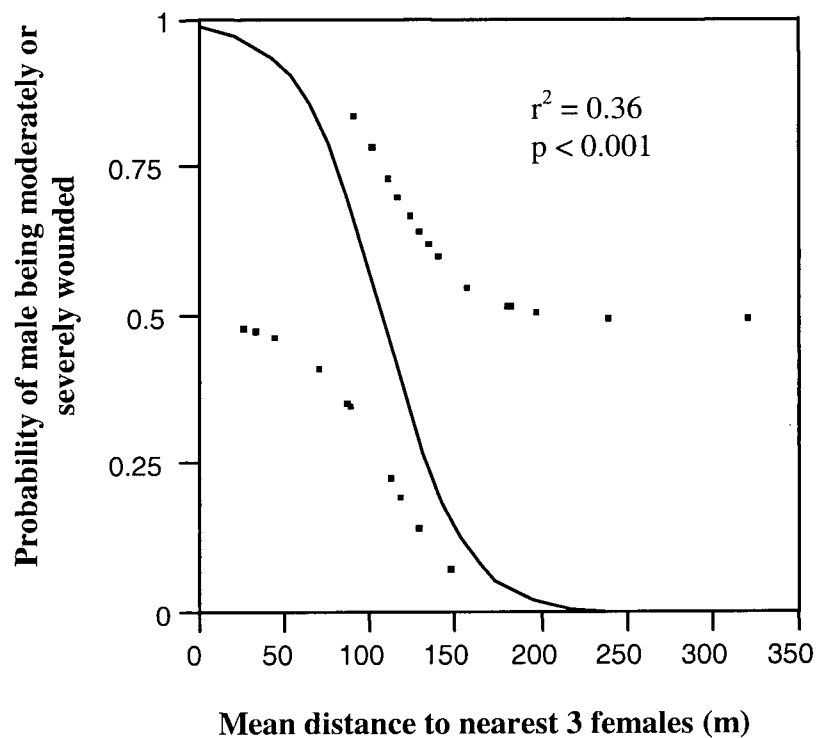
### *Movement*

Although some males were sedentary, others traveled extensively during the breeding season (dispersion of 1<sup>st</sup> five locations ranged from 96 – 1179 m, mean =  $449 \pm 48$  m,  $n = 25$ ). None of the factors (year, age, spring body condition, proximity to females) or a combination of the factors that I considered explained more than 13% of the variation among males' dispersion of locations (Appendix 14). In fact, the most parsimonious statistical model included only the average distance to the nearest 3 females as a factor. Although not statistically significant over the entire range of values, there was a trend for males in closer proximity to females to be more sedentary ( $r^2 = 0.09$ ,  $n = 25$ ,  $F = 2.2$ ,  $p = 0.15$ , Figure 4.4). The trend was highly statistically significant when the average distance to the nearest 3 females was below 135 m ( $r^2 = 0.64$ ,  $n = 17$ ,  $F = 26.7$ ,  $p = 0.0001$ , Figure 4.4).

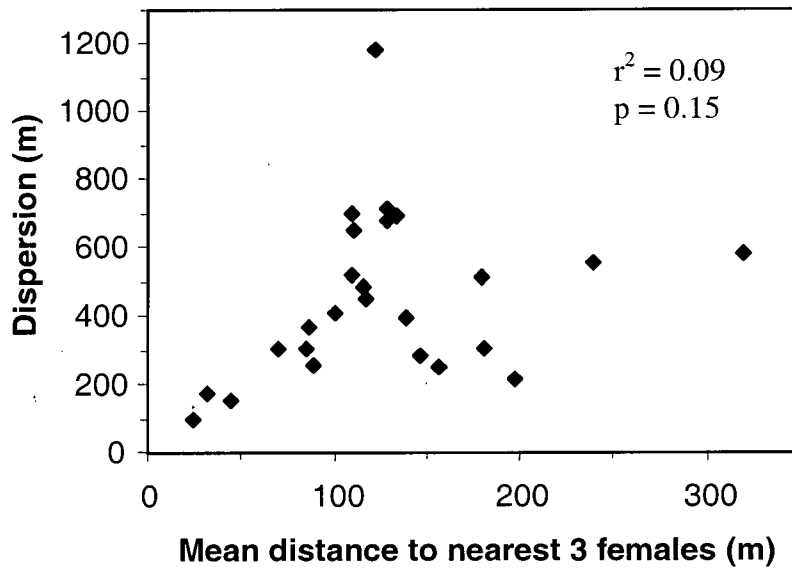
### **Discussion**

Continuous variation existed among male ground squirrels in several internal and external factors that I examined during the mating season. This suggests that individual males may employ different mating tactics, although I was unable to identify and define distinct male mating tactics. One factor associated with variation in many of the traits was age. Although all males trapped during this study were in reproductive condition, older ( $\geq 2$  years old) males were structurally larger, heavier, and were in better body condition than yearlings at the start of the breeding season. Males of both age classes had similar movement and injury rates, but relative to yearlings, older males lost more weight, sustained more serious injuries, and tended to have more females in their





**Figure 4.3** Relationship between a male's proximity to females and the probability of being moderately or severely wounded during the breeding season ( $n = 24$ ). Points are the data for individual males (points below line are males that were moderately or severely wounded) and the curve is for the best logistic regression fit.



**Figure 4.4** Relationship between male movement rate, as measured by the dispersion of the 1<sup>st</sup> five telemetry locations obtained for each male, and the mean distance from the male to the nearest 3 females during the mating season ( $n = 25$ ). For  $x$ -values  $< 135$  m,  $r^2 = 0.64$ ,  $n = 17$ ,  $p = 0.001$ .

core home ranges. These differences suggest that older animals invested more effort in reproduction.

This study encompassed only two breeding seasons at one locality, but the generality of the results is greatly strengthened by previous studies on arctic ground squirrels and will be discussed in more detail below. In particular, differences in physical attributes between yearlings and older males and high levels of wounding have been observed in other populations. However, previous studies have not attempted to directly link these measurements to reproductive effort.

#### Breeding home range size and male spacing

Core and 95% home range size estimates for males in this study, who lived in the alpine at low population density, were much larger than observed at higher population density or in the boreal forest (Table 4.3). A variety of factors, including density, female distribution, food availability, season, and habitat may affect home range size of arctic ground squirrels (Carl 1971, McLean 1983, Hubbs and Boonstra 1998, Lacey and Wieczorek 2001). Exactly which factor or combination of factors is responsible for the differences among studies is not known. However, within a site, home-range sizes of arctic ground squirrels are larger in years of lower densities (Lacey and Wieczorek 2001), so the lower density of squirrels at my study site is probably partially responsible for the larger home range sizes.

In the current study, I was unable to map the home ranges of all males during the breeding season because many males died before I had obtained sufficient locations (Chapter 3). However, I was able to establish that males centered their breeding season activity approximately 200 m from the closest adjacent male. Therefore, there was a low probability that their core home ranges, which averaged only 1.4 ha, overlapped extensively. Similarly, Carl (1971) and Lacey and Wieczorek (2001) found that males maintained distinct core areas of activity during the breeding season. In contrast to core home ranges, at a spacing of 200 m between home range centers, 95% home ranges (12 ha, Table 4.1) would have overlapped extensively among males. This result is consistent with a study by McLean (1983) in which 62% of a male's home range overlapped the home ranges of other males, but inconsistent with a another study in which only 7 – 15%

**Table 4.3** Comparison of published home range size estimates for male arctic ground squirrels. Differences in methods of data collection and home range estimation existed among studies (see table footnotes) so not all estimates are directly comparable. Estimates followed by the same symbol have been estimated using the same estimation methods.

Home range size (ha)	Core home range size (ha)	Squirrel density (adults•ha <sup>-1</sup> )	Season	Habitat	Ref
3.06 ± 1.03*	0.60 ± 0.49*	1.5	active	Forest	1
1.33 ± 0.69*	0.08 ± 0.08*	15.2	active	Forest + food <sup>a</sup>	1
12.41 ± 2.52*	1.36 ± 0.26*	0.4	mating	Alpine tundra	4b
0.14 ± 0.07**		6.4	mating (1988)	Meadow	2
0.05 ± 0.03**		12.8	mating (1989)	Meadow	2
4.01 ± 0.56**		0.4	mating	Alpine tundra	4a
1.83 ± 0.24	1.23 ± 0.30	~ 2.9	mating	Arctic tundra	3

<sup>a</sup> Squirrels were living in an area on which food was supplemented

Sources:

1. Hubbs and Boonstra, 1998. 95% and 50% kernel home range estimates based on locations from radio-telemetry.
2. Lacey and Wieczorek, 2002. 95% MCP (arithmetic mean) based on locations from scan sampling.
3. Carl, 1971. Based on maps drawn from observations and trapping.
- 4a. This study. 95% MCP (arithmetic mean) based on locations from radio-telemetry.
- 4b. This study. 95% and 50% kernel home range estimates based on locations from radio-telemetry.

of males' home ranges overlapped those of other males (Lacey and Wieczorek 2001). Differences among studies may be biologically based, caused by changes in spacing behaviour associated with changes in density, or they could be method based (use of telemetry versus scan sampling; Table 4.3).

### Age effects

Regardless of age, all males trapped during this study had descended testes, indicating that they were sexually mature and capable of producing sperm in the current breeding season. Not all male arctic ground squirrels breed as yearlings in all populations and years, however (Green 1977, McLean and Towns 1981, Lacey 1991, Buck and Barnes 1999a). Spatial and temporal variability in breeding by yearlings is common in many other ground squirrel species as well (e.g. *S. beldingi*, Barnes 1984, *S. citellus*, Millesi *et al.* 1998, Millesi *et al.* 1999, *S. lateralis*, Bronson 1979, *S. tridecemlineatus*, Schwagmeyer and Brown 1983, and *S. columbianus*, Zammuto and Millar 1985). Factors that influence a yearling male's reproductive status may be his mass (Barnes 1984, Bushberg and Holmes 1985, Kenagy *et al.* 1989, Millesi *et al.* 1998) or his social interactions with other males (Slade and Balph 1974, Green 1977), either during the breeding season or the previous fall. For arctic ground squirrels, it has been proposed that in order for yearling males to breed in the spring, they must have obtained a threshold mass and cached enough seeds the previous summer (Buck and Barnes 1999a). Seeds cached by males prior to hibernation (Krog 1954, McLean and Towns 1981) may influence male reproductive success (Buck and Barnes 1999a). The seeds are eaten during a 1-2 week period when males are euthermic prior to spring emergence, probably completing spermatogenesis, and they allow males to replace all the mass they lose during hibernation (Barnes 1987, Buck and Barnes 1999a). Because fresh vegetation is unavailable to males during the mating season, the seed caches are the only way for males to recover from hibernation before undertaking the energetically demanding breeding season.

Although the difference in structural size between yearling and older males that I report has not been previously documented, the difference in mass has (Buck and Barnes 1999a). In Buck and Barnes's (1999a) study, the lighter weight of yearlings at spring

emergence corresponded to a lighter weight when they entered hibernation as juveniles the previous fall (Buck and Barnes 1999a). Juveniles are unlikely to obtain the same mass as adults prior to hibernation because they must devote more energy to growth than adults (Kenagy *et al.* 1989). In their first active season, that lasts only 3 months, juvenile males must grow, disperse, acquire and defend a fall territory, and obtain sufficient body resources to survive hibernation (Carl 1971, Byrom and Krebs 1999). Given limited time and resources, most yearlings cannot attain their maximum size in the summer they are born and are therefore smaller and lighter than older animals after their first winter in hibernation.

#### Correlates of reproductive effort and male movement

On average, males lost mass during the mating season, with older males losing more mass than yearlings. Male arctic ground squirrels lose mass during the mating season regardless of the year or location. Several studies, conducted both near where the current study was conducted and further north, have reported males losing 11 – 21% of body mass during the breeding season (Green 1977, McLean and Towns 1981, Buck and Barnes 1999a) with older males losing more than yearlings (Lacey 1991, Buck and Barnes 1999a). I therefore tentatively conclude that older males have higher reproductive effort than yearlings because in European ground squirrels (*S. citellus*) males that lost more mass during the breeding season had acquired more mates (Millesi *et al.* 1998).

The high incidence of wounding among male arctic ground squirrels is also not restricted to this study (see also Green 1977, Holmes 1977) and indeed is a common trait in many ground squirrel species (Evans and Holdenreid 1943, Sherman and Morton 1984, Michener and Locklear 1990b, Millesi *et al.* 1998). While wounding during the mating season is common among male ground squirrels, it is much less common among females, and wounds on females tend to be less severe (Michener and Locklear 1990b, E. Gillis *unpublished data*). Presumably, the high levels of wounding on males during the mating season is the result of intrasexual competition for females as the rate of antagonistic interactions among males is higher during the mating season than during the remainder of the active season (Carl 1971, Green 1977). In my study, males were more likely to have moderate or severe wounds if they were in closer proximity to females, an indication that

males near females fight more than males without females nearby. Such intense fighting can be costly. Some male arctic ground squirrels are killed directly by other males during the mating season (Chapter 3, Watton and Keenleyside 1974, Holmes 1977) and males that are severely wounded during fights may die indirectly of fighting if their wounds increase their susceptibility to depredation or infection (Sherman and Morton 1984, Chapter 3).

Male movement rate, as measured by the dispersion of the 1<sup>st</sup> five locations obtained for each male, was positively related to their proximity to females. This result indicates that males living far from females may have moved to areas where females lived during the mating season while males that were already close to females were able to restrict movement to a smaller area. I did not measure territorial behaviour directly, but this relationship may represent a gradient of territoriality, with males in close proximity to females being territorial and those that are not near females becoming "floaters" (Carl 1971). A gradient of territorial behaviour associated with female distribution would also explain the relationship between the probability of males having moderate or severe wounds and their proximity to females, because strongly territorial males would presumably fight more than less territorial males.

Although the relationship between male movement and proximity to females was very strong when the distance to the nearest three females averaged <135m, there was little relationship between male movement and proximity beyond this distance (Figure 4.4). It appears that after some threshold, males are increasingly unwilling to travel to gain access to female. Such a trend may arise from an increased risk of predation caused by very high movement rates or distances. Alternatively, females living far from some males presumably have other males living closer to them. The probability of a distant male successfully mating with these females may be very low, and therefore it may not be beneficial for males to travel very large distances to find mates.

#### Implications of results and future studies

My results demonstrate the potential of age to affect the mating tactics of male arctic ground squirrels. In this study, older males had a higher reproductive effort than yearlings, a finding that may be general among *Spermophilus* spp. Older males may also

have greater reproductive effort or success than younger males in *S. columbianus* (Murie and Harris 1978), *S. lateralis* (Kenagy *et al.* 1989), *S. beecheyi* (Evans and Holdenreid 1943), *S. citellus* (Millesi *et al.* 1998), and *S. tridecemlineatus* (Schwagmeyer and Brown 1983), but possibly not in *S. richardsonii* (Michener and Locklear 1990a,b).

Differences in reproductive effort between younger and older males may arise from an evolved response or simply be a plastic response of individuals to their own size. Optimal reproductive theory predicts that species should evolve so that older males allocate more of their resources to reproduction than yearlings because older animals have a lower residual reproductive value (Pianka 1976). Older male arctic ground squirrels do have a lower probability of surviving the mating season and subsequent winter than yearlings (Chapter 3), so this may lead to selection for older males to invest more heavily in current reproduction. However, poor survival may be a consequence of high reproductive investment, as opposed its cause (Boonstra *et al.* 2001b).

An alternative explanation is that younger males are just "making the best of a bad situation" (Brockmann 2001). Boonstra *et al.* (2001) predict that a low probability of survival between mating seasons, such as that experienced by both yearling and older male arctic ground squirrels (Chapter 3), should result in all individuals investing as much energy in current reproduction as possible, regardless of their probability of success. It is therefore likely that both yearlings and older adults invested as many resources as possible into reproduction, but yearlings are constrained in their investment by their smaller size.

The current evidence indicates that the differences in reproductive effort between yearlings and older male arctic ground squirrels may be related more to size, which is correlated with age, than to an evolved response associated with age *per se*. For example, because of their lighter weight, yearlings are unlikely to win antagonistic encounters with older, heavier males (Watton and Keenleyside 1974, Murie and Harris 1978, Dobson 1983, Schwagmeyer and Brown 1983) and so may engage in them less.

If size determines reproductive effort, then within each age class a positive relationship between size and reproductive investment should exist. I did not have the sample sizes needed to test this prediction directly with my data. However, when non-reproductive yearlings are present in a population, they are smaller than the reproductive



yearlings, providing some evidence that reproductive effort is related to mass within, as well as between, age groups (Buck and Barnes 1999a, Bushberg and Holmes 1985, Kenagy *et al.* 1989, Millesi *et al.* 1998). Further support for the size hypothesis comes from the Richardson's ground squirrel (*S. richardsonii*), a species that is closely related to arctic ground squirrels and with a very similar life-history. Unlike arctic ground squirrels, Richardson's ground squirrel yearlings are the same size as adult males at spring emergence, and mating season wounding rates and annual disappearance rates do not differ between the two age groups (Michener and Locklear 1990a, b).

I have documented differences among individuals in several parameters related to mating tactics (e.g. home range size, movement rates, and reproductive effort). Although I could not quantitatively evaluate its frequency, it appears that individual male arctic ground squirrels may also alter how they acquire mates within the mating season. For example, McLean (1983) reported that some males changed from defending a territory to defending a particular female on the day that a female was in oestrus. Likewise, at least two of the males I studied drastically altered their mating tactics late in the breeding season. Both held and vigorously defended small territories near high-density patches of females during the initial portion of the breeding season. Once all females in their territories had emerged from hibernation and bred, the two males began to roam, often >300 m from their initial territories, to areas in which females were still emerging and mating (*E. Gillis unpublished data*). The shifting of reproductive behaviour by an individual within one season may allow future studies to better identify the conditions under which males adopt particular mating tactics.

Recognizing the importance of age in the reproductive investment of arctic ground squirrels will allow future studies to address four key questions through experiments. First, what is the relative contribution of age versus size to reproductive investment by males? To answer this question, sizes and masses of males can be experimentally manipulated. Weight and size of yearlings can be increased through food supplementation of juveniles the previous year (Bushberg and Holmes 1985), and older males can also be supplemented with food. Once a large mass gradient within each age cohort is established, researchers can determine if there is a relationship between mass and reproductive effort within, as well as between, each age cohort. The interaction of

seed caches and mass in determining reproductive condition can also be determined by providing some fed and control males with seeds to cache prior to hibernation.

Secondly, what is the physiological basis of increased reproductive effort by older males? In particular, the role of testosterone should be investigated. In arctic ground squirrels, simulated stressors can increase testosterone levels (Boonstra *et al.* 2001b). If natural stressors, such as male-male conflict, produce a similar response, the increase in testosterone may lead to increased aggression, particularly among large older males. If winning antagonistic encounters increases the probability of future encounters, a positive feedback loop will be created. However, such a response may lead to chronic stress, reducing future survival (Scott 1987, Boonstra *et al.* 2001b).

Thirdly, is there really a trade off between current reproductive investment and mating season and winter survival? This question can be experimentally tested if yearlings can be "made" to invest more heavily in reproduction, by increasing size as suggested above, and if older males can be prevented from becoming reproductive through castration.

Lastly, if the trade off between reproduction and survival is the case, how does the increased reproductive effort of older males decrease their subsequent winter survival? Endocrinological evidence indicates that males are chronically stressed during the reproductive season (Boonstra *et al.* 2001b), probably due to high levels of antagonistic interactions with other males. Whether or not the stress levels differ between adults and yearlings during the mating season is not yet known, but should be investigated. If stress levels differ between ages and are correlated with reproductive effort, as I suggested above, it may provide the link between the age and size of male, his reproductive investment, and the resulting survival during the mating season and the subsequent winter (Chapter 3).

Mating effort may be the factor that links many aspects of a male arctic ground squirrel's life-history that appear to be related to age. It may help explain differences between yearlings and older males in breeding season and winter survival (Chapter 3) and trends in dispersal (Chapter 5). Mating effort may also affect timing of breeding dispersal and indirectly affect the probability that a male commits infanticide (Chapter 6).

Given its potential effects, further studies examining mating effort, reproductive success, and their consequences on male survival and behaviour are warranted.

## **Chapter 5: Breeding dispersal of male arctic ground squirrels**

### **Introduction**

Howard (1960) first promoted the idea that there are two distinct reasons why animals disperse: either they are forced out or they leave voluntarily. While this seems obvious now, the dominant view over the preceding 40 years was that dispersal was inherently risky and therefore no animal would voluntarily disperse. Howard's idea that dispersal could be an evolved behaviour opened the door for ecologists to explore its possible benefits.

Since 1960, the concept of voluntary dispersal has been extended beyond Howard's early conception of "hard-wired" (innate) dispersal. Today, voluntary dispersal applies to any situation in which animals could breed if they remained philopatric but they disperse. Involuntary dispersal refers to situations in which animals must disperse to at least have an opportunity to reproduce successfully (Lidicker and Stenseth 1992). As dispersal involves some costs, the question becomes what motivates voluntary dispersal and the risks associated with it. In the case of "hard-wired" innate dispersal, the answer lies in past selection and this is difficult to evaluate in the present. When variability among individuals exists in the propensity to disperse, it is feasible to determine the proximate factors (i.e. triggering cues) that are associated with dispersal. Identifying the proximate causes of dispersal can be the first step in understanding its ultimate, evolutionary causes and benefits (Lidicker and Stenseth 1992).

Individual differences in the propensity to disperse are generally associated with the age and the sex of the animal (Greenwood 1980). The motivations of adults and juveniles undoubtedly vary given that they differ in social status, experience, resource requirements, future reproductive potential, and past reproductive success. Those differences are so striking that it is essential to recognize two distinct types of dispersal, natal and breeding. Natal dispersal is the dispersal of individuals from where they were born to the location of their first attempt at reproduction (Howard 1960) and breeding dispersal is the dispersal of reproductively mature adults from one breeding site to another, either within or between breeding seasons (Greenwood 1980).

Dispersal may be triggered by either external or internal cues (Ims and Hjermann 2001), such as interactions with conspecifics (Christian 1970, Bekoff 1977, Cockburn *et al.* 1985, Wolff 1993) or body mass and hormonal cues (Nunes and Holekamp 1996, Nunes *et al.* 1999). Because breeding dispersers are reproductively mature, reproductive success may also be a cue to disperse. In general, adult birds disperse in response to reproductive failure (Haas 1998) and adult small mammals disperse in response to reproductive success. For example, female red squirrels are more likely to disperse if offspring are present on their territory. (Berteaux and Boutin 2000) and male Belding's ground squirrels that have a high reproductive success are more likely to disperse before the next breeding season (Sherman 1977).

For dispersal to be adaptive, it must increase, on average, the fitness of individuals who disperse. Three ultimate hypotheses have frequently been used to explain how dispersers could increase their fitness beyond the fitness they would have achieved had they remained philopatric: (1) dispersers avoid close inbreeding (inbreeding avoidance hypothesis; Shields 1987, Johnson and Gaines 1990), (2) dispersers increase their access to mates (mate acquisition hypothesis; Greenwood 1980, Dobson 1982), and (3) dispersers increase their access to resources and thereby improve their chances of surviving and breeding (resource acquisition hypothesis; Greenwood 1980, Dobson 1982). These hypotheses need not be mutually exclusive (Dobson and Jones 1985). For example, Hoogland (1982) demonstrated that adult male black-tailed prairie dogs dispersed to increase their access to unrelated females since their reproductively mature daughters would not mate with them, which is a combination of the inbreeding avoidance and mate acquisition hypotheses.

A fourth hypothesis, specific to breeding dispersal, proposes that some adults disperse so their offspring can remain and breed on the natal territory (Lambin 1997, Berteaux and Boutin 2000). This is often referred to as the bequeathal hypothesis. Bequeathal of the natal territory can increase a parent's fitness in circumstances where territories are vital for survival and breeding, and when the probability of adults obtaining territories is much higher than it is for their offspring (Berteaux and Boutin 2000).

The most difficult ultimate hypothesis to test is that dispersal has evolved in response to adverse affects following close inbreeding, and thus for inbreeding avoidance

(Moore and Ali 1984, Packer 1985). Using a simple model to compare the probability of dying during dispersal to the probability that offspring would die as a direct result of close inbreeding, Bengtsson (1978) concluded that dispersal could be selected as an inbreeding avoidance mechanism in small groups of animals in which potential mates were close relatives. The inbreeding avoidance hypothesis, however, has proven difficult to test empirically because reduction in inbreeding is a necessary consequence of dispersal, regardless of what proximal factors motivated the disperser to leave.

Strong support for the inbreeding avoidance hypothesis has, therefore, been limited to species for which inbreeding avoidance is the only possible benefit to dispersal such as in two species of Australian marsupials in the genus *Antechinus* (Cockburn *et al.* 1985). In these species, the only condition under which juvenile males remain at their natal sites is if their mothers die and their sisters disperse. Juvenile males are not forced out by their fathers and would not compete with their fathers for mates or resources even if they remained because male generations are discrete. All juvenile males disperse, regardless of litter size, and adult females recruit unrelated males into their nests, to replace their juvenile sons. As a result, local density and per capita resource availability remain constant before and after dispersal. Thus, in *Antechinus* species, the resource acquisition and mate acquisition hypotheses can be eliminated as reasons for juvenile male dispersal, and this provides strong support for the inbreeding avoidance hypothesis. The biological peculiarity that permits this strong test of the inbreeding avoidance hypothesis is the death of all adult males. An equivalent peculiarity permits the testing of the inbreeding avoidance hypothesis in arctic ground squirrels.

Up to 90% of arctic ground squirrel (*Spermophilus parryii*) males that breed in an area disappear before the following spring (Chapter 3, Carl 1971, Hubbs and Boonstra 1997) compared with less than 50% of females (Byrom and Krebs 1999). Half of the breeding males disappear shortly after the breeding season, with some dying as a result of intense intrasexual competition during the mating season and others dispersing (Chapter 3, Boonstra *et al.* 2001b). The remaining adult males disappear either before females emerge from hibernation in the spring or after juveniles emerge from their natal nests in late summer (Carl 1971, Green 1977, McLean 1983, Lacey 1991). During this second peak of disappearance, immigrant adult males are often caught on trapping grids (Green

1977, Lacey 1991) so loss of males at these times must be partially due to dispersal (Table 5.1). Although most adult males disperse, not all do, making it possible in principle to identify proximate cues associated with dispersal and philopatry.

Some adult males that disperse from trapping grids abandon territories that they have successfully established, mated on, and defended for at least two months (Carl 1971, Green 1977, McLean 1983). Thus they are not subordinate individuals. It is improbable that male arctic ground squirrels disperse in order to increase their access to food because providing supplemental food does not decrease the proportion of males that disappear (Figure 5.1 in Chapter 3). Adult males do not bequeath their territories to their sons as 60 to 100% of juvenile males also disperse during the summer they are born (Byrom and Krebs 1999).

Because the resource acquisition and bequeathal hypotheses cannot explain why adult male ground squirrels disperse, the arctic ground squirrel system affords an opportunity to evaluate the inbreeding avoidance and mate acquisition hypotheses independently and in combination. My objective was to test the hypotheses that adult male ground squirrels disperse (1) to avoid inbreeding; (2) to increase access to females; and (3) to increase access to unrelated females. I used natural variation among individual propensity to disperse to test predictions on which males should disperse based on each hypothesis (Table 5.2). Specifically, I compared (i) male reproductive condition during the breeding season, (ii) mating success, (iii) reproductive success, and (iv) the number of females within 100 m of the male's spring versus fall location between males that did and did not disperse.

## **Methods**

### The study species

Arctic ground squirrels are herbivorous, hibernating small mammals (ca. 500-700g) found throughout northern North America (Banfield 1974). Populations have a female biased adult sex ratio (Green 1977), the result of high mortality of juvenile males during natal dispersal (Byrom and Krebs 1999). Unlike their male counterparts, juvenile females are philopatric (Byrom and Krebs 1999) and this philopatry results in spatially clustered female kin groups interspersed with unrelated adult males (McLean 1982).

**Table 5.1** Indices of male breeding dispersal rates from one spring to the next from trapping studies of arctic ground squirrels. Maximum dispersal rates are from studies in which disappearance due to death and dispersal were not differentiated. Minimum dispersal rate indices are from studies in which long distance dispersers may not have been trapped and therefore are not classified as dispersers. Sample sizes are the total number of resident males present in a given spring.

Parameter measured	Year(s)	n	Annual breeding dispersal rate	Min. or max. dispersal rate index	Reference
Adult male disappearance	1991-1998 average	2-21 91	0.88-1.00 0.91	Maximum	Figure 3.1 in Chapter 3
Adult male disappearance	1960	18	0.66	Maximum	Carl 1971
	1961	45	0.82		
	overall	63	0.77		
Adult males dispersing and disappearing	1987-1989	29	0.21	Minimum	Calculated from Table 4.1 in Lacy 1991
	1987-1989	29	0.93	Maximum	
Proportion of immigrants on study area	1991	23	0.26	Minimum	Hubbs and Boonstra 1997
	1992	16	0.12		
	overall	39	0.21		
Adult males trapped >100m from previous home range who did not return to home range	1977-1979	69	0.33	Minimum	Calculated from Figure 3 in McLean 1983



**Table 5.2** Conditions, as predicted by three hypotheses, under which adult males should disperse between breeding seasons. Predictions for the specific variables I measured are compared to the results in Table 5.6.

Hypothesis	Cue for Dispersal	Conditions under which male will disperse from breeding territory	Conditions under which male will remain on breeding territory
Extreme Inbreeding Avoidance	presence of juvenile females	daughters present on breeding territory	daughters absent on breeding territory
	presence of juveniles	juveniles present on breeding territory	juveniles absent on breeding territory
	mating success	previously mated with females on breeding territory	obtained no mates on breeding territory
	reproductive condition during breeding season	testes descended during breeding season	absent (still hibernating) or testes abdominal during breeding season
Access to Females	total number of females on territory	new territory contains more females (related + unrelated <sup>1</sup> ) than old (breeding) territory	potential new territory contains $\leq$ females than current territory
Access to Unrelated Females	number of unrelated females on territory	new territory contains more unrelated females than old (breeding) territory	potential new territory contains $\leq$ unrelated females than current territory

<sup>1</sup> unrelated female refers to any female that is not the male's daughter

Arctic ground squirrels spend approximately 8 months of the year hibernating singly in underground nests. Adult males emerge from hibernation in mid-April, approximately 2 weeks before the females (Carl 1971, Lacey 1991), and some establish mating territories on which they breed (Carl 1971, Lacey and Wieczorek 2001). Mating occurs over a two to three week period as females emerge from hibernation (Lacey *et al.* 1997) with 10 – 50% of males dying during the mating season each year (Chapter 3). Some adult males continue to defend their breeding territory until after young of the year have emerged from their natal nest, approximately 8 weeks after mating (Carl 1971, Green 1977, Lacey *et al.* 1997). This possibly prevents infanticide by other males (McLean 1983).

Adult males disperse during the mating season, immediately after the mating season, or just before or after juveniles emerge (Carl 1971, Green 1977, McLean 1983). After dispersing, adult and juvenile males establish and defend fall territories in which they forage, hibernate, and then mate the following spring (Carl 1971, McLean 1983). The first adult males to enter hibernation do so in late August, almost one month after adult females, and up to one month before juveniles (Carl 1971, Green 1977, McLean 1983, Lacey 1991).

## Methods

From early June 2000 to August 2002, I studied arctic ground squirrels at an alpine study site in the Ruby Ranges, near Kluane Lake, southwestern Yukon (1700 – 2200 m, 61° 20' N, 138° 25' W). The study area was a mosaic of boulderfields (36%), patches of moss, lichens, and bare ground (37%), and vascular plants (*Salix*, *Carex*, *Dryas*, *Cassiope* spp. 37%; Hik *et al.* 2001, McIntire and Hik 2002). Adult ground squirrel densities were relatively low compared to previous years, but similar for the duration of the study (Chapter 2).

Adult male ground squirrels were trapped once they emerged from hibernation and fitted with 1.5g transmitters (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada). All radio collared males were located every 1 to 7 days during the active season and their position ( $\pm 10$ m) was recorded relative to permanent grid stakes placed in the study area every 50m. Males were located both during the day, when active, and at

night when they were in sleeping burrows (2000, mean  $\pm$  1 S.E. =  $15.5 \pm 1.3$  day and  $3.5 \pm 0.4$  night locations/male,  $n = 23$ ; 2001,  $14.5 \pm 3.1$  day and  $5.4 \pm 1.1$  night locations/male,  $n = 20$ ; 2002,  $19.2 \pm 3.1$  day and  $11.7 \pm 1.8$  night locations/male,  $n = 17$ ). In addition to radio tracking, I live-trapped radio-collared ground squirrels throughout the summer to monitor changes in their reproductive condition and body mass. I considered males to be reproductive if their testes were descended, and not reproductive if their testes were abdominal.

I restricted analyses to those males that were collared and survived until juvenile emergence (June 25, Chapter 2) because males collared after this time may have already dispersed and males that died before this time might have dispersed had they survived. I also excluded males who had collars removed before July 11, the date after which no dispersal was detected, as their dispersal fate was unknown. I defined a disperser as an individual who left a home range and established a new, temporally and spatially distinct home range (after Lidicker and Stenseth 1992). I identified potential dispersers and dispersal dates using two methods, fuzzy cluster analysis (Odeh *et al.* 1992) and shifts in sleeping burrows. I then conducted home range overlap analysis of 90% minimum convex polygon home range estimates to ensure that an individual's pre- and post-dispersal home range did not overlap (Chapter 3).

I compared three measures of mating success between dispersers and non-dispersers. The first measure was simply whether or not a male was in reproductive condition during the mating season. The second measure was mass loss during the mating season based on the observation that European ground squirrels males that lost more mass during the breeding season had higher mating success (Millesi *et al.* 1998). I calculated rate of mass loss ( $\text{g} \cdot \text{day}^{-1}$ ) for individual male arctic ground squirrels caught more than once during the breeding season by regressing mass against the date for the duration of time over which each male lost weight (mean  $r^2 = 0.79 \pm 0.06$ ,  $n = 17$ ). My third measure of mating success was the number of females within a male's core home range during the mating season (50% adaptive kernel home range or equivalent, Chapter 3). Breeding locations for 56% of the 100 females were nest locations located by either radio-telemetry or by locating her young when they emerged from their natal nests (Chapter 2). For other females, I used the arithmetic mean of all May trapping locations

for each female or if the female was not trapped in May, the mean of all June and July trapping locations (29% and 15% of females respectively).

I also compared the reproductive success of dispersing and non-dispersing males. I assumed that all females within males' core home ranges mated with them. If any of those females weaned litters, I classified the males as successful. In no case did a female have a litter of only sons or only daughters (E. Gillis, *unpublished data*) so the presence of daughters was not examined separately from the presence of juveniles.

To determine if males that dispersed increased their access to females through dispersal, I calculated the differences in the number of females and unrelated females within 100m of each male's main sleeping burrow before and after dispersal. I also determined the proportion of dispersing males that increased, decreased, or did not change their access to females by dispersing. Using the same measure, I also compared access to females between dispersing and non-dispersing males in late summer (after July 10). Adult female location was established by methods described previously. Juvenile female location was the nest site location for juveniles whose mother could be identified (34% of juvenile females) and the first trap location for all other juvenile females (66% of juvenile females). I assumed all juvenile females in each male's core breeding home range were his daughters. I excluded from the analysis 5 males located on the periphery of the study area in late fall as I did not trap these areas extensively.

Mating season locations were known only for 2001 and 2002, so analyses including measures of mating and reproductive success are restricted to these two years. Males collared after May 15<sup>th</sup> in each of these years were also excluded from these analyses, as their exact breeding location was unknown. Age may influence mating effort and reproductive success (Chapter 3). Small sample sizes precluded keeping ages (yearlings versus  $\geq 2$  years old) separate for analyses, but I present results for ages separately to facilitate the observation of trends. Ages for adult males first captured as juveniles were known. Males first captured as adults were classified as yearlings in the year they were captured if they grew in structural size (as measured by zygomatic arch width) during the summer and as  $> 1$  year old in subsequent years. All other males were assumed to be yearlings the year they were first caught ( $n = 5, 3$ , and 1 in 2000, 2001, and 2002 respectively).

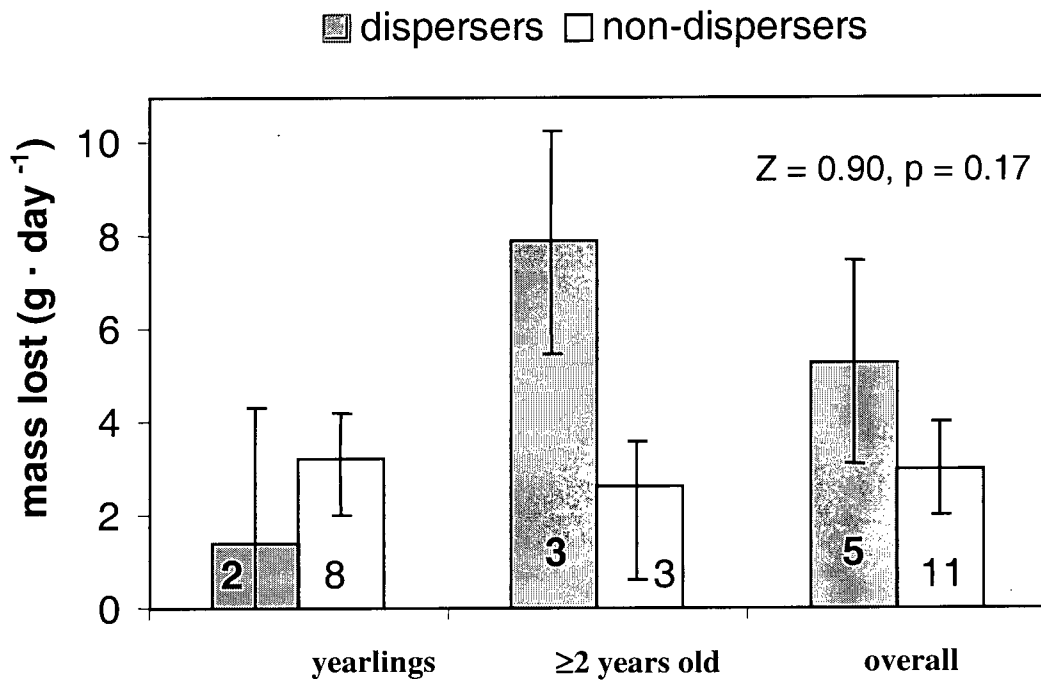
Unless otherwise stated, all numbers are reported as mean  $\pm$  1 S.E. Prior to parametric tests being performed, data were checked for normality and homogeneity of variances. When assumptions for parametric tests could not be met, non-parametric statistics were used. All tests were one tailed because predictions were one tailed (Table 5.2) and statistics were performed in JMP version 3.2.1 (SAS Institute Inc., 1997).

## Results

Dispersal fates could be established for 14 adult males in 2000, 9 adult males in 2001, and 11 adult males in 2002. During the 3 years of the study, 13 dispersal events occurred (Chapter 3). Due to high annual disappearance rates (Chapter 3), I knew the 2002 breeding locations of only two males for whom I also knew 2001 breeding locations. In both cases, males dispersed - one shortly after the breeding season in 2001 and the second just after spring emergence and before mating in 2002. As a result, for the 2002 breeding season, these males were 540 and 730 m respectively from the center of their 2001 breeding ranges. The male that dispersed just after spring emergence dispersed a second time, in July (Chapter 3). I eliminated the first dispersal event for this male from subsequent analyses as the dispersal cues used prior to breeding may have been based on the previous year as well as the current year's conditions and all analyses I investigated considered only cues from the current year.

All males trapped during the mating season had descended testes ( $n = 35$ ), and were in reproductive condition. Thus, reproductive condition during the mating season did not differ between dispersers and non-dispersers. However, males that dispersed lost on average almost twice as much body mass during the breeding season as non-dispersers, although this difference was not statistically significant at  $\alpha = 0.05$  (Figure 5.1). This trend occurred in the older cohort but not among yearlings (Figure 5.1).

On average, males had between zero and five females living within their core home range during the breeding season. This number did not differ significantly between dispersers and non-dispersers, but there was a very strong trend for dispersers to have fewer females on their breeding core home range than non-dispersers (Table 5.3). Correspondingly, dispersers had, on average, half the number of litters emerge within



**Figure 5.1** Comparison of mating success, as measured by rate of mass loss during the breeding season, between adult male ground squirrels that did and did not subsequently disperse. Bars represent  $\pm 1$  S.E. and sample sizes are provided on the bars. The Z-test statistic was from a non-parametric rank sums test (Kruskal-Wallis) and  $p$  value is for a one tail test.

**Table 5.3** Comparison of male arctic ground squirrel mating and reproductive success between dispersing and non-dispersing adult male arctic ground squirrels. Mating success was measured as the number of females in a male's core breeding home range, and reproductive success, was measured by the presence of weaned litters in a male's core breeding home range. Values are mean  $\pm$  1 S.E. and sample sizes are provided in brackets.

	mean number of females in core		mean number of litters in core		% males with litter weaned in	
	breeding range <sup>1</sup>		breeding range <sup>2</sup>		core breeding home range <sup>3</sup>	
	dispersers	non-dispersers	dispersers	non-dispersers	dispersers	non-dispersers
overall	0.4 $\pm$ 0.2 (5)	1.6 $\pm$ 0.5 (13)	0.4 $\pm$ 0.2 (5)	1.0 $\pm$ 0.2 (13)	40.0 (5)	69.2 (13)
yearlings	0 $\pm$ 0 (2)	1.7 $\pm$ 0.5 (10)	0 $\pm$ 0 (2)	1.1 $\pm$ 0.2 (10)	0 (2)	80.0 (10)
$\geq 2$ years old	0.7 $\pm$ 0.3 (3)	1.3 $\pm$ 1.3 (3)	0.7 $\pm$ 0.3 (3)	1.3 $\pm$ 0.7 (3)	66.7 (3)	33.3 (3)

<sup>1</sup> Overall difference not statistically significant (one tailed non-parametric Kruskal-Wallis test,  $Z = 1.5$ ,  $p = 0.08$ ).

<sup>2</sup> Overall difference not statistically significant (one tailed non-parametric Kruskal-Wallis test,  $Z = 1.4$ ,  $p = 0.09$ ).

<sup>3</sup> Overall difference not statistically significant (likelihood ratio  $\chi^2 = 1.3$ , one tailed  $p = 0.13$ ).

their core breeding home ranges as non-dispersers (Table 5.3), but once again this difference was not statistically significant. The percentage of males that had litters emerge on their core breeding home range did not differ between males that did and did not disperse (40 versus 70% respectively, Table 5.3).

In dispersing, the average number of females within 100 m of main sleeping burrows of the dispersing males decreased after dispersal for yearlings but it increased after dispersal for older males (Table 5.4). This difference between the age groups, however, was not significant (non-parametric Kruskal-Wallis test,  $Z = 0.22$ ,  $p = 0.41$ ) and overall, the average number of females within 100 m of a disperser before and after dispersal did not change. In contrast, the average number of unrelated females (number of females minus daughters) within 100 m of dispersers increased after dispersal for both yearling and older males (Table 5.4).

Mean values, particularly with small sample sizes, can be greatly skewed by outliers. Thus, it is useful to look at the consequences of dispersal, in terms of proximity to females, for each male separately. In dispersing, yearlings rarely increased the number of females in close proximity, but half of older males did increase their proximity to females (Table 5.5). This difference between the age groups, however, was not significant (log-likelihood  $\chi^2 = 2.2$ ,  $p = 0.17$ ) and overall, most dispersers had fewer females within 100 m after dispersal than they did before. The results were almost identical considering unrelated, as opposed to total females (Table 5.5).

On average, dispersers had more total and unrelated females within 100m of their main sleeping burrows prior to hibernation than non-dispersers although this difference was not statistically significant (Figure 5.2). The trend arose because on average, older dispersing males had almost twice the number of females within 100m of their non-dispersing cohorts (Figure 5.2). For yearlings, the trend was opposite and less strong, with dispersers having only 56% of the total females and 68% of the number of unrelated females of non-dispersers.

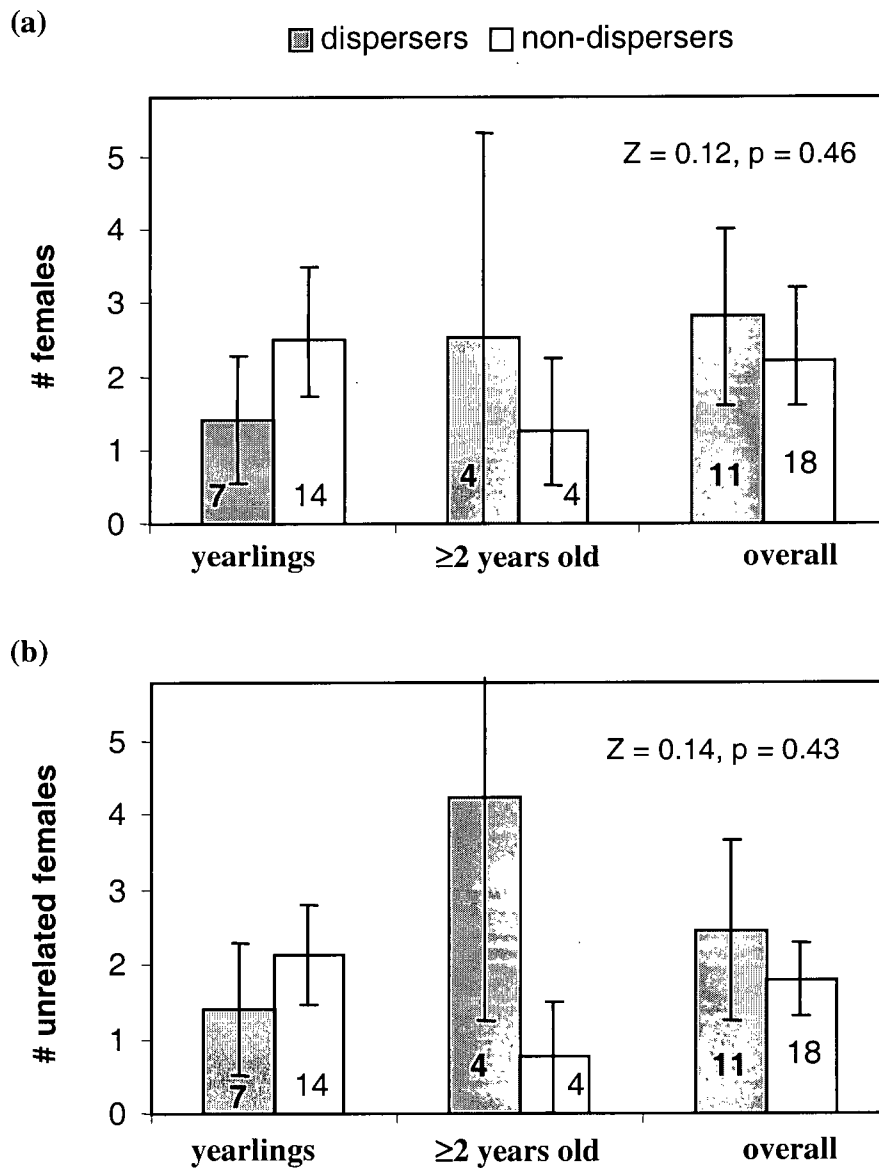


**Table 5.4** Mean ( $\pm 1$  S.E.) change in number of total females and unrelated females within 100m of the main sleeping burrows of dispersing arctic ground squirrel males pre- and post-dispersal. A positive value indicates an increase, while a negative indicates a mean decrease.

	<i>n</i>	change in total # of females		change in # of unrelated females	
		mean	range	mean	Range
overall	11	$0 \pm 1.5$	-5 – 11	$1.4 \pm 1.3$	-2 – 12
yearlings	7	$-1.4 \pm 1.4$	-5 – 6	$0.3 \pm 1.0$	-2 – 6
$\geq 2$ years old	4	$2.5 \pm 3.1$	-5 – 11	$3.3 \pm 3.1$	-2 – 12

**Table 5.5** The percent of arctic ground squirrel males that increased, did not change, and decreased the number of total females within 100m of their main sleeping burrows pre- and post-dispersal.

	<i>n</i>	total # of females			total # of unrelated females		
		increased	same	decreased	increased	same	decreased
overall	11	27.3	9.1	63.6	27.3	36.4	36.4
yearlings	7	14.3	14.3	71.4	14.3	42.9	42.9
≥2 years old	4	50.0	0	50.0	50.0	25.0	25.0



**Figure 5.2** Mean number of arctic ground squirrel females within 100 m of male's pre-hibernation main sleeping burrow. (a) Total females, (b) Unrelated females. Error bars are one S.E. and p values are for one tail test. Mean value for  $\geq 2$  years old dispersers when one outlier male with 13 total and unrelated females removed was  $2.5 \pm 1.5$  females and  $1.3 \pm 0.8$  unrelated females ( $n = 3$ ).

## Discussion

Due to high levels of natural variation and small sample sizes, I was unable to show statistically significant differences in previous mating and reproductive success between dispersing and non-dispersing adult male arctic ground squirrels. There were, however, several trends in the data that may be biologically significant because they were consistent within a cohort. Interestingly, the trends differed consistently between breeding yearlings and older animals (Table 5.6), and the overall trend was largely a function of the relative contribution of each age cohort to the overall sample sizes and the relative magnitude of the trend for each age cohort.

I found no evidence to support the hypotheses that yearlings dispersed to avoid mating with their daughters, to increase their access to mates, or to increase their access to unrelated mates (Table 5.6). Dispersal by yearlings was not positively related to the presence of potential daughters on the territory, mass loss during the mating season, reproductive condition during the mating season, or the number of females on the core breeding home range. Yearlings decreased their proximity to females by dispersing and had fewer females near them in the fall than non-dispersers.

Unlike yearlings, older ( $\geq 2$  years old) males may have dispersed to increase mating opportunities, to avoid mating with their daughters, or both (Table 5.6). Dispersers in the older age cohort were more likely to have their daughters born the current year on their breeding territories than non-dispersers, and tended to lose much more weight than non-dispersers during the mating season. This indicates that they may have had greater mating success. The number of females on the breeding territory however, was similar for dispersers and non-dispersers. Dispersers did increase their access to females by dispersing, and as a result, dispersers had more females nearby in the fall than non-dispersers.

Trends for yearlings and older males may differ for several reasons. Some of the dispersal by yearlings I observed may have been natal, not breeding, dispersal. Juveniles delay natal dispersal until they are yearlings if they do not attain a threshold body mass in the year they are born (Lacey 1991, Nunes and Holekamp 1996). In her study of arctic ground squirrels, Lacey (1991) reported 31.6% of juvenile males delayed dispersal until they were yearlings and suggested that up to 87% of males that moved to and acquired

**Table 5.6** Evaluation, based on my study of breeding dispersal in male arctic ground squirrels, of three hypotheses used to explain why animals disperse. Unrelated females refer to any female that is not the male's daughter. Because of small samples, none of the trends are statistically significant. However, << and >> indicate there was at least a two-fold difference in the groups being compared.

Hypothesis	Cue	Prediction <sup>1</sup>	Results (trends only, not significant)		
			overall	yearlings	> 1 year old
Extreme inbreeding avoidance	presence of daughters	% with daughters on territory: D > ND	D < ND	D < ND	D > ND
	presence of juveniles	% with juveniles on territory: D > ND	D < ND	D < ND	D > ND
	mating success	mass loss: D > ND # females in breeding territory: D > ND # litter emerged: D > ND	D > ND D << ND D << ND	D < ND D < ND D < ND	D >> ND D < ND D = ND
	reproductive condition	% reproductive: D > ND	D = ND	D = ND	D = ND
Access to females	# females on territory	# females nearby: D > ND before < after	D = ND before = after	D < ND before >> after	D > ND before << after
Access to unrelated females	# unrelated females on territory	# unrelated females nearby: D > ND before < after	D > ND before < after	D > ND before = after	D >> ND before << after

<sup>1</sup> D = dispersers, ND = non-dispersers, before = before dispersal, after = after dispersal

new burrow systems between the end of the mating season and the emergence of juveniles were non-reproductive yearlings. In a 3-year study conducted in the boreal forest, between 0 and 43% of males born on control areas each year did not disperse as juveniles (Byrom and Krebs 1999). If high rates of delayed natal dispersal occurred in my study, it would increase variability in the results for yearlings if the causes and cues for natal and breeding dispersal are different. For 2001 and 2002, I am confident that all yearling dispersal was breeding dispersal because all yearlings were reproductively mature and present during the mating season. Juvenile male arctic ground squirrels that delay dispersal until they are yearlings normally do not reproduce (Lacey 1991). In addition, for the 9 males for whom both natal nest site and yearling breeding locations were known, all 9 dispersed a minimum of 175m in their juvenile year (mean  $470 \pm 90$ m). Yearling data from 2000, however, may be confounded with delayed juvenile dispersal. If it is, it would make it harder to detect any real differences between attributes of breeding dispersers and non-dispersers because natal dispersers may use very different proximate cues than breeding dispersers, thereby increasing the variability in the data.

The differences in trends between yearlings and older males more likely reflect real differences in proximate dispersal cues used by the two age groups. Reproductive yearlings and older males may disperse for very different reasons. Yearlings presumably bred in the territories they secured the previous fall as juveniles, at which time they would have been less dominant than the larger adult males with established territories (Watton and Keenleyside 1974). It is therefore possible that they were forced to occupy the least favourable territories, and therefore disperse in order to obtain territories with better resources when they are yearlings. For some birds, male breeding dispersal to secure territories with better resources is restricted to the younger individuals (Greenwood and Harvey 1982, Payne and Payne 1993, Newton 2001).

If juveniles hibernate on poorer quality territories than adults, they may disperse as yearlings to obtain territories with better resources in order to increase their probability of surviving to the next breeding season. These resources are probably not related to access to females, as the core home ranges of yearlings and older males encompassed similar numbers of females (Chapter 4). Juveniles do, however, hibernate in hibernacula that experience colder temperatures than adults (Buck and Barnes 1999b). High quality

hibernacula, or places to dig them, are limited in some areas (Carl 1971, Lacey 1991), so juveniles may move when yearlings to acquire warmer hibernacula. Movement by yearlings to acquire territories with higher food resources is also possible, but unlikely, because addition of food addition has not decreased natal or breeding dispersal rates in other populations (Figure 5.1 in Chapter 3, Byrom and Krebs 1999).

Alternatively, the differences in trends of dispersers and non-dispersers between age cohorts may arise from differences in mating tactics and success between the two age cohorts (Chapter 3). Although such differences should not affect analyses that directly use measures of mating and reproductive success, it is possible that my measures are inaccurate. They were based on the relative spatial location of males, females, and offspring and I assumed males mated with all females in their core home ranges. It is likely, however, that resident males did not always father all juveniles in their territories (Lacey and Wieczorek 2001), and I have not accounted for the successful mating of males with females outside of their core breeding home ranges. Establishment of paternity for juveniles born at the site, through genetic analysis of tissue samples taken from all individuals in this study (E. Gillis *in preparation*), will provide a better measure of reproductive success and may provide clearer results.

Two other studies have attempted to identify differences between dispersing and non-dispersing adult male arctic ground squirrels (Green 1977, Lacey 1991). As in this study, Green (1977) found that the reproductive condition of individuals during the breeding season was unrelated to dispersal. Green (1977) detected no clear trends in amicable and antagonistic interaction rates between dispersing and non-dispersing adult males. In addition, males immigrating into an area from which other males had been removed were the same structural size and mass as males remaining on control areas. Likewise, Lacey (1991) found no difference between the structural size and the mass of resident males and males that immigrated to a study area during the time period when breeding dispersal was known to occur.

Breeding dispersal by males also occurs in black-tailed prairie dogs (*Cynomys ludovicianus* (Hoogland 1982) and most other *Spermophilus* species (*S. tridecemlineatus*, *S. tereticaudus*, *S. richardsonii*, *S. beldingi*, *S. armatus*, *S. beecheyi*, *S. columbianus*, Holekamp 1984a and references therein, *S. variegatus*, Shriner and Stacey 1991, *S.*

*townsendii*, Smith and Johnson 1985). Juvenile females are philopatric (Holekamp 1984a), so by dispersing between breeding seasons, males will not mate with their daughters. This opens the possibility that inbreeding avoidance is the reason males disperse. As such, one would expect dispersal to be proximally related to the reproductive or mating success of dispersing males. In my study, mating success in one season, as measured by mass loss, of older males may have been related to their dispersal before the next. Likewise, in Belding's ground squirrels there is high variability among males in mating success and mating success is linked with subsequent dispersal. The most successful Belding's ground squirrel males dispersed, but males that mated with few or none of the females living near them remained in the area to breed the following year (Sherman 1977, Sherman and Morton 1984). Breeding dispersal has also been cited as one of the four tactics used by black-tailed prairie dogs to avoid inbreeding (Hoogland 1982, Garrett and Franklin 1988). Thus, inbreeding avoidance remains a possible basis for breeding dispersal in ground squirrels. Female kin are spatially clumped (McLean 1982), however, so males that disperse not only avoid mating with their daughters but they avoid mating with other closely related females. Unless the presence of daughters can be shown to be the actual cue for dispersal, as Hoogland (1982) has shown for black-tailed prairie dogs, it is impossible to differentiate between these two potential ultimate causes of dispersal.

Research on breeding dispersal in small mammals has not yet been extensive. It has been documented for several species of ground and tree squirrels, mice, voles, and Eurasian badgers (Greenwood 1980 and Holekamp 1984a and references therein, see also Wolff and Lidicker 1980, Lurz *et al.* 1997, Berteaux and Boutin 2000, Hazell *et al.* 2000, Rajska-Jurgiel 2000, Devillard *et al.* 2003) but the proportion of animals that undertake breeding dispersal has been estimated for only a few species, (McLean 1983, Sherman and Morton 1984, Sandell *et al.* 1991, Devillard *et al.* 2003, Cheeseman *et al.* 1988). Excluding the ground squirrel studies previously discussed, only four studies have reported ways in which dispersers and non-dispersers differ. Dispersing adult male and female Damarland mole rats (*Crytonys damarensis*) were larger than their non-dispersing counterparts (Hazell *et al.* 2000) but dispersing adult feral cats (*Felis catus*) had lower body condition before reproductive maturity than non-dispersers (Devillard *et al.* 2003).



Dispersing red squirrels were older and had weaned more offspring prior to dispersal than non-dispersers (Berteaux and Boutin 2000). Only one study, conducted on *Microtus arvalis*, experimentally manipulated conditions to examine the effects of local conditions on breeding dispersal and concluded that breeding dispersal is the consequence of soil hardness. Female voles living in areas with hard soil were unable to extend burrows and construct nests, so they dispersed prior to parturition to an area with a soil type that facilitated nest construction (Boyce and Boyce 1988).

In contrast to breeding dispersal in mammals, breeding dispersal in birds has been examined extensively through observational (Greenwood 1980 and references therein) and experimental studies (e.g. Haas 1998, Hoover 2003). It appears that birds and mammals may differ in the conditions under which they disperse. Birds most often in disperse in response to reproductive failure (Greenwood and Harvey 1982, Payne and Payne 1993, Newton 2001), but small herbivorous mammals disperse after reproductive success (Sherman 1977, Hoogland 1982, Berteaux and Boutin 2000). As a result, breeding dispersal may have drastically different impacts on local and regional population dynamics of birds and mammals. If reproductive failure instigates dispersal, dispersing birds may be lower quality birds leaving high quality territories, or high quality individuals leaving low quality territories. In either case, high quality birds eventually settle in high quality territories and in a heterogeneous environment, and the differences in reproductive output between high and low quality habitats will be increased. In contrast, if reproductive success instigates dispersal, then dispersing individuals may be of high quality and high quality territories will be abandoned or passed on to offspring. If high quality individuals immigrate into low quality territories, or lower quality individuals immigrate into the vacant high quality territories, then in a heterogeneous environment, the difference in reproductive output between high and low quality habitats will be reduced. Whether or not breeding dispersal at the rates observed in natural populations could increase reproductive heterogeneity in heterogeneous environments for birds and decrease it in mammals is unknown and needs to be explored both empirically and theoretically.

In this study, overall results and results from the older cohort support more than one of the ultimate hypotheses investigated. Dispersal is a complex behavioural process

that involves three phases- emigration, transience, and settlement (Ims and Hjermann 2001). It is very likely that different factors affect each phase, and in combination multiple hypotheses are supported. For example, males may use their mating success as a cue to disperse, but then they may disperse in such a way as to maximize their access to females. This would potentially increase the number of females and unrelated females near them. In the absence of a clear ecological signal to disperse used by all males, the causes and the consequences cannot be untangled without experimental manipulation and it is difficult to support a single ultimate hypothesis. Unfortunately, in the absence of a clear cue associated with dispersal, it is difficult to design experiments to test the cause of dispersal because researchers do not know which cue to manipulate.

Only four mammal studies (of kangaroo rats (*Dipodomys spectabilis*), prairie voles (*Microtus ochrogaster*), red squirrels (*Tamiasciurus hudsonicus*), and feral cats (*Felis catus*)) have reported the survival or reproductive consequences of breeding dispersal (Belichon *et al.* 1997 and references therein, Berteaux and Boutin 2000, Devillard *et al.* 2003). All compared individuals who dispersed naturally to those who remained philopatric. As in this study, in which winter survival of male arctic ground squirrels was unrelated to dispersal and survival cost was unrelated to movement during the non-mating portion of the active season when most dispersal occurred (Chapter 3), these studies found no obvious survival cost to dispersal. This trend is consistent with studies of a variety of bird species. In contrast with the cases of breeding dispersal, in many species, including arctic ground squirrels, natal dispersal is associated with increased mortality (Belichon *et al.* 1997, Byrom and Krebs 1999). This may be because animals undergoing breeding dispersal may do so only if there is little or no cost associated with the process, as indicated by the results from a study on red squirrels in which breeding dispersal occurred more frequently when food availability was high (Berteaux and Boutin 2000).

If the true survival and reproductive consequences of dispersal for animals that would normally not disperse could then be examined, it may give some insight into why some individuals disperse and others do not. Given that it may be very difficult to identify a single ecological cue associated with breeding dispersal to manipulate in order to "force" animals to disperse or remain, future research should attempt to identify the

proximate physiological cause of dispersal. This has been done for natal dispersal of Belding's ground squirrels. Nunes *et al.* (1999) established that male juveniles disperse as a result of exposure to the testosterone they produce shortly after they are born.

Even though the results of my study are not conclusive, they do highlight several critical aspects of breeding dispersal in small mammals. Breeding dispersal is a complex, individual behaviour that is most likely to be condition and environment dependent (Imms and Hjermand 2001). It appears that age and mating strategy may influence the conditions under which male arctic ground squirrels will disperse and that the ultimate reasons why yearlings and older males disperse may be fundamentally different. As well, breeding dispersal may confer many concurrent benefits, such as inbreeding avoidance and obtaining a superior territory (either mates or other resources or both). However, these same benefits may be achieved by other behaviours, such as kin recognition (Hoogland 1982), alternative mating tactics, increasing foraging range, or subtle shifts in home range. Therefore comparison of naturally dispersing and philopatric individuals may not provide clear answers as to what ultimately causes breeding dispersal.

Despite being unable to definitely answer the question of why adult males disperse, the results of my study indicate that yearlings and older males differ in the cues they use to disperse as well as the reasons why they disperse. This result, along with the findings that the two age cohorts differ in survival rates (Chapter 3) and reproductive effort (Chapter 4), highlight the need for future studies on male arctic ground squirrel reproduction and dispersal to consider yearlings separately from older males. In the final chapter of this thesis (Chapter 6), I present a conceptual model suggesting that the casual relationships that give rise to the dispersal, reproductive, and survival differences between the two age groups.

## Chapter 6. General Discussion

### Summary

I studied arctic ground squirrels in the southwest Yukon at high elevation in alpine tundra to answer five main questions: (1) How do changes in elevation and habitat affect arctic ground squirrel demography? (2) What is the fate of adult males that disappear at very high rates? (3) What factors are correlated with a male's probability of death and dispersal?, (4) What factors are correlated with a male's reproductive tactic and success?, and (5) Why do adult males disperse?

In this chapter, I highlight the main conclusions of my research and discuss the generality of some of these conclusions. I also present a conceptual model relating male size, mating tactics, natal dispersal, breeding dispersal, and survival in male arctic ground squirrels. This model combines the findings of the current study with the results and interpretations of previous studies. Finally, I suggest further research that would address some of the key questions raised by the results of my study.

### Effect of elevation and habitat on ground squirrel demography (CHAPTER 2)

The demography of squirrels living at the boreal forest site and alpine site did differ (Chapter 2). Although annual adult female survival was similar between the forest and alpine sites, seasonal survival was not – survival over summer was lower but survival during the winter was higher in the forest than in the alpine. Reproductive output also varied between sites. Contrary to the trend for most birds and mammals, reproductive output of squirrels in the lower elevation forest was less than in the higher elevation alpine. These differences in yearly reproductive rates probably resulted differences in lifetime reproductive success because females at both sites were reproductively mature as yearlings and annual survival was similar between sites.

Survival and reproductive rates of arctic ground squirrels on each site were incorporated into demographic models, and the models revealed the factors underlying the difference in ground squirrel population growth rate between sites. In the forest, population growth rate was most sensitive to adult survival whereas in the alpine, it was most sensitive to juvenile survival. More importantly, average population growth rate ( $\lambda$ )

for squirrels living in the boreal forest was  $<1$ , meaning the forest was a sink habitat and may have relied on nearby grassy meadows to supply immigrants. In contrast, the average population growth rate for squirrels living in the alpine was on average  $\geq 1$ , indicating the alpine habitat maintained a ground squirrel population in the absence of immigration.

I propose that the differences in demographic rates and population dynamics between ground squirrels living in low elevation boreal forest and high elevation alpine habitats arise from phenotypic responses to different habitat structure (Chapter 2). Arctic ground squirrels rely on sight to detect predators from a safe distance, and in this context the boreal forest, with its lower visibility and higher predator density, appears to be sub-optimal habitat. The strong effect of habitat on population demography obscures any trends that may arise from differences in climate between elevations.

#### Fate of adult males that disappear (CHAPTER 3)

The annual disappearance rate of adult male arctic ground squirrels averaged 80% (Chapter 3). During the active season high levels of disappearance occurred late in the mating season, due to depredation, and from just prior to shortly after the emergence of juveniles, due to breeding dispersal. Winter mortality of adult males was also high – 57% of males that were alive at the end of the active season died during the winter.

#### Factors correlated with death and dispersal (CHAPTER 3)

Age was a useful predictor of mortality both in the mating season and during the winter (Chapter 3) but movement rate, year, and one measure of reproductive success (number of females in male's core home range) were not related to mortality. Males  $\geq 2$  years old had higher mortality rates than yearlings, possibly a result of a higher investment in reproduction that reduced both immediate and long-term survival.

I found little evidence of factors that could predict whether or not a male would disperse. Although age was the best predictor, it explained only a small portion of the variation in dispersal propensity and was not significant. Likewise, year, proximity to females, and the presence of putative daughters did not predict the probability a male would disperse.

#### Factors correlated with male reproductive effort and success (CHAPTER 4)

Age appeared to influence reproductive effort (Chapter 4). During the mating season, older males lost more weight and sustained more serious injuries than yearlings, indicating that older animals invested more effort in reproduction. Physical attributes may have contributed to the ability of older males to invest more resources to reproduction because older males were on average larger, heavier, and in better body condition than yearlings at the start of the breeding season. The higher reproductive effort of older males may have resulted in higher reproductive success as older males tended to have more females in their core breeding range than did yearling males. The relationship between age and reproductive success, however, needs to be confirmed directly through the conclusive identification of litter paternity by genetic techniques.

#### Cause of dispersal (CHAPTER 5)

High levels of natural variation and low sample sizes prevented me from detecting statistically-reliable differences between the reproductive effort and success of dispersers and non-dispersers. Persistent and strong but non-significant trends in the data suggest that yearlings did not disperse to avoid mating with their daughters, to increase their access to mates, or to increase their access to unrelated mates (Chapter 5). For older males, there was some, but not complete support, for all three of these potential explanations for why animals disperse.

#### **Implications of the effect of habitat on ground squirrel demography**

If the demographic rates measured at the boreal forest and alpine sites truly represent the demographic rates in their respective habitats, a major finding of my study is that in the boreal forest, low pregnancy rates and small litter sizes lower annual reproductive output to below replacement levels. In Chapter 2, I suggested, as have Hik (1995) and Karels (2000), that the reduced reproductive output in the forest arises from the sub-lethal effects of predators, either via chronic stress (Hik *et al.* 2001) or foraging decisions made by squirrels under a high perceived risk of predation (Lima and Dill

1990). If so, the southern limit of arctic ground squirrel distribution may be determined by the direct and indirect effect of predators.

Many ground squirrel distribution limits are associated with the edges of continuous closed habitats (Burt and Grossenheider 1980) and I believe high risk of predation in continuous low visibility habitats limits squirrel distribution through indirect effects on reproduction and possibly direct effects on survival. Visibility does influence vigilance behaviour of ground squirrels (Sharpe and Van Horne 1998), probably because ground squirrels rely on vision to detect predators at a safe distance and closed habitat increases the risk of predation (Hik 1995 and references therein). This increased predation risk may cause higher stress levels or alter foraging behaviour of populations of other species of ground squirrels living in low visibility habitat, thereby decreasing reproduction.

Predators in low visibility habitat may also directly affect ground squirrel distribution by increasing the mortality rate in closed habitat. An increased mortality rate could result from either a higher predator abundance or a decreased ability for squirrels to detect and avoid predators in closed habitat. In my study, survival was significantly lower in the forest than in the alpine area during the time period for which squirrels were available to predators (active season, Chapter 2). Hackett (1987) also found that risk of predation was related to habitat. In his study, yearling Columbian ground squirrels living within 30m of cover were significantly more likely to be killed by predators than those living in open grassland, resulting in lower squirrel densities near the edge relative to the centre of a grassland habitat.

The amount of continuous unsuitable habitat required to create a barrier is unknown, but such a barrier has significant implications for regional ground squirrel dynamics and conservation of some species (Valdez and Ceballos 1997, Gavin *et al.* 1999, Johnson and Chromomanski 1992). In the northern boreal forest, it appears that source arctic ground squirrel populations, probably in open areas, are close enough to provide immigrants to sink habitats and to permit arctic ground squirrels to persist in the forest. Presumably, a similar scenario occurs near the edges of the ranges of other ground squirrel species, although only one study has compared the demography of populations living in distinct, nearby habitats. Slade and Balph (1974) found that *S. armatus*

populations on an open lawn served as a source for a nearby sink population living in a more closed habitat of mixed grasses and shrubs. Direct genetic measures of gene flow between populations may help identify what type and width of habitat constitutes an impenetrable barrier.

### **A conceptual model relating age, reproductive effort, and dispersal in male arctic ground squirrels**

In the following section, I integrate the results, observations, and suggestions from several arctic ground squirrel studies into a conceptual model relating male size, timing of natal and breeding dispersal, male reproductive effort and success, male parental care, and infanticide by males. I start by outlining the correlations between variables that have been observed or implied, then propose potential causal relationships among variables. Finally, I outline the decision rules that males should make with respect to dispersal, reproductive effort, parental investment, and committing infanticide if the suggested causal relationships are correct.

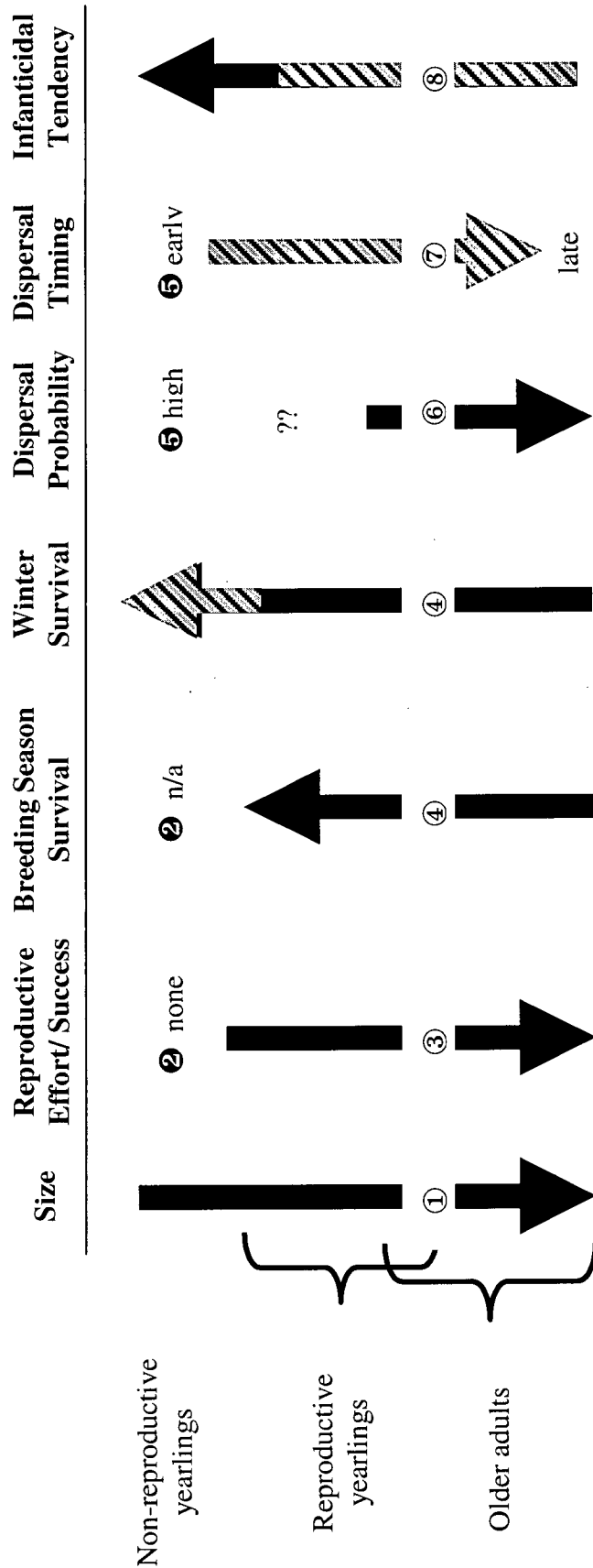
The studies I will mention all had very different objectives, and the model I propose is the first attempt at integrating the results in this manner. Thus, it should be considered a testable hypothesis for which there is some empirical evidence, and the key assumptions in the model require further testing.

#### Observed Correlations (FIGURE 6.1)

Figure 6.1 outlines observed (solid) and predicted (striped) relationships among some life-history traits of male arctic ground squirrels. Below, I summarize the evidence and sources for these associations. The number beside each association refers to the corresponding trend on Figure 6.1.

- ❶ Although there is some overlap in size between the age classes (*E. Gillis, unpublished data*), upon emergence from hibernation in the spring, non-reproductive yearlings tend to be smaller than reproductive yearlings (Green 1977, Buck and Barnes 1999a) and reproductive yearlings tend to be smaller than older reproductive males (Chapter 4, Buck and Barnes 1999a).





**Figure 6.1** Observed (solid) and predicted (striped) trends among some parameters of male arctic ground squirrel life-history traits. Direction of arrow indicates the direction of increase. Please see appropriate reference number in text for complete description of relationships and references.

② Non-reproductive yearlings delay emergence until late in the breeding season (Green 1977, McLean and Towns 1981, Buck and Barnes 1999a), and invest no resources in reproduction. Because they spend a majority of the mating season below ground, risk of depredation (the primary cause of male mortality during the mating season, Chapter 2) is very low during this time.

③ Among reproductive males, reproductive effort (as measured by mass loss) is higher for older animals than yearlings (Chapter 4, Lacey 1991, Buck and Barnes 1999a) and is correlated with male mass at spring emergence ( $r^2 = 0.55$ ,  $n = 26$ ,  $t = 5.4$ ,  $p < 0.001$ , E. Gillis *unpublished data*).

④ Both active season survival and winter survival are higher for reproductive yearlings than older males (Chapter 4). Winter survival for non-reproductive yearlings has not been considered separately from reproductive yearlings, however I predict, based on the causal relationships proposed below, that it is equal to or higher than reproductive yearlings.

⑤ Individuals that did not disperse as juveniles are non-reproductive and undergo delayed natal dispersal shortly after the mating season ends (Lacey 1991).

⑥ For reproductive males, the probability of an older male dispersing is associated with reproductive effort (non-significant trend) but the same relationship is not found in the yearling cohort (Chapter 5).

⑦ McLean (1983) predicted that males that have mated successfully with many females should delay dispersal until after juveniles emerge from natal nests.

⑧ Infanticide of male and female juveniles by immigrant adult males does occur in arctic ground squirrels (McLean 1983, Lacey 1991 and E. Gillis, *unpublished*

*data*) and is usually committed by non-reproductive yearlings that immigrate into an area before juveniles emerge (Lacey 1991).

#### Proposed Causal Relationships (FIGURE 6.2)

Figure 6.2 outlines what I believe to be the causal relationships that give rise to the correlations summarized in Figure 6.1.

**A** The probability that a juvenile male disperses in the year he is born or delays dispersal until he is a yearling depends upon whether or not he attains a critical body mass (Lacey 1991, Nunes and Holekamp 1996). The body mass a male reaches by the end of the summer is primarily determined by juvenile growth rate (food availability) because there is little variance among years in the date that juveniles are born (Chapter 2). Mating and parturition, however, span a two to three week period within a year, so young born later in the summer may have up to three weeks less time to grow and may be less likely to disperse (Lacey *et al.* 1997).

**B** Juvenile mass in the fall also determines if a male is reproductive as a yearling, either directly (if breeding condition is size dependent) or indirectly (if breeding condition depends on dispersing from the natal area).

**C** Among reproductive males, size determines dominance status (Watton and Keenleyside 1974) and reproductive effort of an individual (Chapter 4), which in turn determines his reproductive success.

**D** Reproductive effort can directly affect mating season survival by altering a males' risk of predation or his probability of being killed while fighting for females, and may also directly affect survival during the winter due to long term costs associated with mating effort (Chapter 3).



**E** Reproductive effort may indirectly affect winter survival if it influences the timing of dispersal, through the causal relationship (G) proposed below, and late dispersing males are forced to occupy territories with poorer hibernacula.

**F** Whether or not a male undergoes breeding dispersal may be related to mating success, although this is still unknown. If males disperse to avoid mating with their daughters or to increase their access to unrelated females with which to mate the following year, reproductive success determines the probability that a male disperses. It is possible, however, that some males (probably yearlings) may disperse to acquire a territory with better resources (mates or hibernacula; Chapter 5) because hibernacula and burrow quality vary among territories (Karels and Boonstra 1999, Buck and Barnes 1999b, Karels 2000). If they do, the probability of dispersal will depend upon these external resources as opposed to reproductive success.

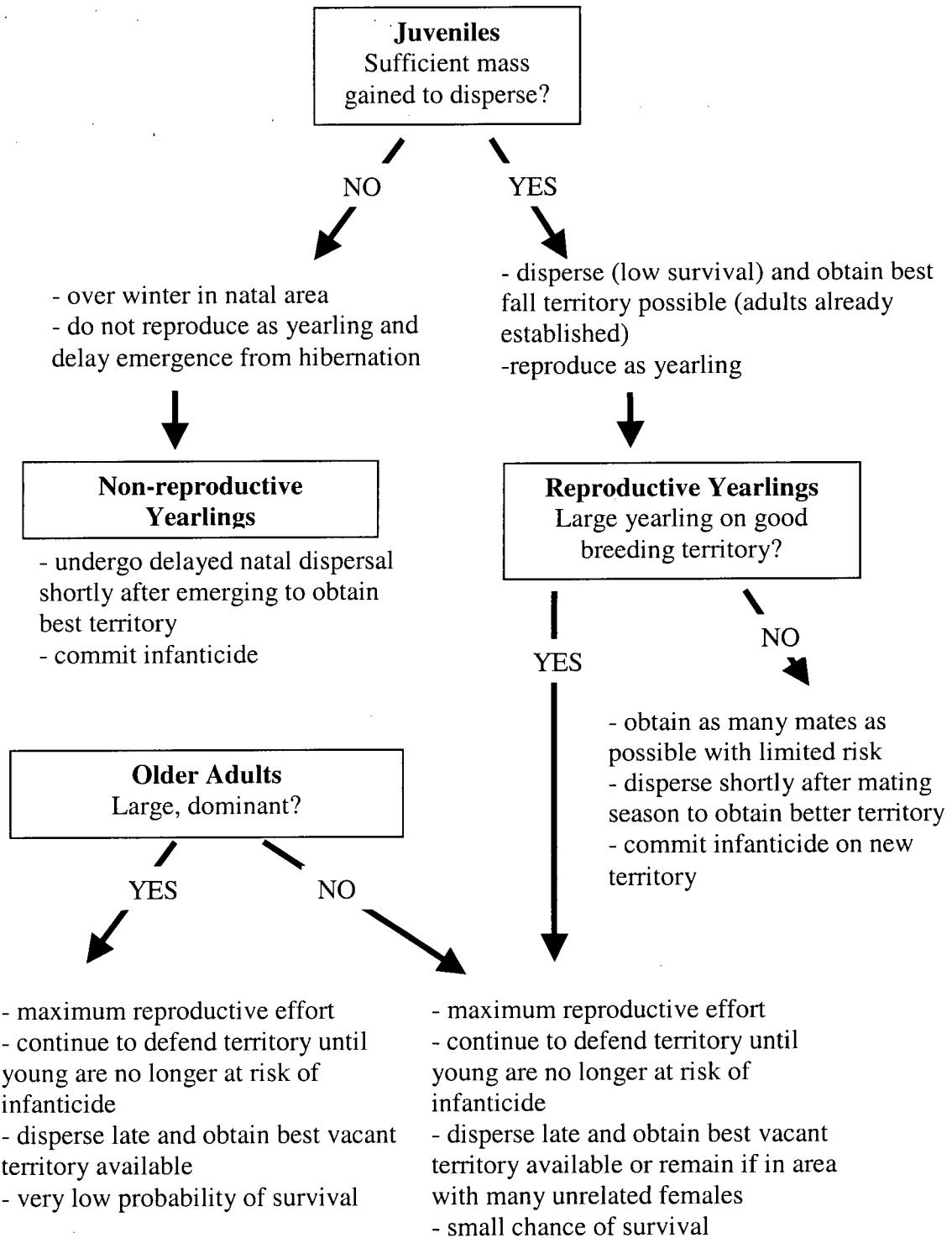
**G** Timing of male dispersal is most likely directly determined by their reproductive success. McLean (1983) proposed males should disperse as early as possible in order to secure territories with the best resources (mating and non-mating). Because infanticide occurs, however, males with many offspring should continue to defend their breeding territories until their juveniles become independent. Thus, non-reproductive yearlings should disperse before reproductive males, and males with little reproductive success should disperse before males that were very successful in obtaining mates during the breeding season. There is some evidence to support parts of McLean's hypothesis. Previous residence is associated with dominance in this species (Carl 1971, Watton and Keenleyside 1974), and males that take over new burrows between mating and the emergence of juveniles tend to be non-reproductive yearlings (Lacey 1991).

**H** Males may commit infanticide for food, to reduce future competition, or to increase the probability that females successfully reproduce in the following breeding season (McLean 1983 and references therein). Another potential hypothesis, which has not previously been considered, is that killing a female's litter increases her tolerance of unfamiliar males and allows him to immigrate more easily. If this is true, infanticide will be related to the time a male disperses, as only males that attempt to immigrate when females are most aggressive (during lactation) will benefit from killing young. In Columbian ground squirrels, females switch from being relatively subordinate to being dominant in relation to males once they start lactating (Murie and Harris 1987). In arctic ground squirrels, females chase and engage in antagonistic interactions with males during, but not before, lactation (Green 1977, E. Gillis *personal observation*). Female aggression towards unfamiliar males may stop if she loses her litter. During my study, one female was aggressive towards an immigrant male until he killed young. After this time, the male and female were often seen foraging together near the burrow where the litter had been killed.

#### Decision rules (FIGURE 6.3)

Assuming the causal relationships proposed in the previous section are correct, dispersal and mating behaviour and the consequences of these behaviours of male arctic ground squirrels should be predictable (Figure 6.3). High mortality is known to be associated with natal dispersal of juveniles (Byrom and Krebs 1999). Evidence for all other relationships has been provided in the previous two subsections.

Although the decision rules in Figure 6.3 would appear to select for males to delay sexual maturation until they have reached maximum size (presumably two years old), they do not. This is probably because arctic ground squirrels have low and very unpredictable annual survival (Chapters 2 and 3 and references therein). Such an environment selects for commencing reproduction as young as possible because the probability of surviving to the next reproductive season is uncertain (Pianka 1970). Thus, although yearlings may not have high reproductive success, in many years few animals survive until the next reproductive season, so reproductively mature yearlings will have



**Figure 6.3** Proposed life-history decision rules and consequences for male arctic ground squirrels relating size and age to reproduction, dispersal, and survival. See Figure 6.2 and description in text for explanation for potential causal relationships and references.

higher lifetime reproductive success than yearlings that delay reproduction and die before reproducing.

Theory predicts that a male's investment in paternal care should be related to degree of the certainty of paternity (Westneat and Sargent 1996), and experiments have supported this in one species of fish (Neff 2003). The timing of dispersal decision that I propose for arctic ground squirrels may not apply to all other ground squirrel species because it assumes that a male makes parental care decisions based on reproductive success. Arctic ground squirrels may be better able to evaluate their reproductive success than many other ground squirrel species because multiple paternity within a litter is rare in arctic ground squirrels (Lacey *et al.* 1997) but common in other species (Hanken and Sherman 1981, Sherman 1989, Schwagmeyer and Foltz 1990, Boellstorff *et al.* 1994). Therefore, males in most *Spermophilus* species cannot be certain of the paternity of offspring born to females with whom they have mated, although *S. citellus* males do base the amount of paternal effort (digging litter burrows for females) on their mating success. In contrast, in arctic ground squirrels the first male to mate with a female usually fathers all her offspring, and males appear to be able to tell if they were not her first mate (Lacey *et al.* 1997). Since male arctic ground squirrels can potentially evaluate their reproductive success whereas other species cannot, it may influence the amount of time males continue to defend their breeding territories and delay dispersal (McLean 1983). Once again, given the low and unpredictable survival of arctic ground squirrels, males who protect their current offspring may experience higher lifetime reproductive success than males who trade off current for future reproductive investment.

### **Future research directions**

In addition to answering many questions, my study on the arctic ground squirrel has raised many additional questions. In each chapter, I have indicated some future studies that could be carried out to answer some of the specific questions raised. Below, I highlight those that I feel will most benefit both ground squirrel research and ecological theory.



*Are sub-lethal predator effects responsible for reduced reproduction in the boreal forest?*

The current study as well as past studies (Karels 2000, Hik et al. 2001) suggest that the increased perceived and actual risk of predation in the boreal forest may indirectly affect reproduction negatively in females (Chapter 2), either through a chronic stress response (Hik et al. 2001) or predator-sensitive foraging behaviour of squirrels (Lima and Dill 1990). Whether or not predators affect reproduction and the mechanism by which they do so should be examined experimentally. Additionally, the role of habitat in mediating such a response should be explored (i.e. is the effect increased predation risk the same in areas of low visibility, where predators are less likely to be detected, and high visibility).

*Is the boreal forest really a sink habitat, and if so, is it a sink during all or only part of the snowshoe hare cycle?*

Based on results from the demographic model, the boreal forest habitat appears to be unable to maintain a stable ground squirrel population (Chapter 2). The importance of immigration into this habitat should be evaluated empirically and theoretically, along with its potential implications for regional squirrel population dynamics. Ground squirrel survival in the boreal forest fluctuates with changes in predation pressure associated with the snowshoe hare cycle in the boreal forest (Hubbs and Boonstra 1997, Boutin et al. 1995). These cyclic changes in survival may cause source-sink dynamics between the forest and adjacent open areas to cycle. Thus, any model must incorporate spatial structure, the temporal variability in survival, and potential sub-lethal effect of predators on reproduction associated with predictable changes in the predator regime.

*Is reproductive success linked with subsequent winter survival, and if so, how?*

Although older males recovered from their greater weight loss during the breeding season and had body condition similar to yearlings just prior to hibernation, they were much less likely to survive the winter (Chapter 4). The link between mating season mass loss and reproductive success still needs to be established for arctic ground squirrels, but this has been established for the European ground squirrels (Millesi et al.

1998). Additionally, the mechanism by which mating effort affects winter survival needs to be established. Two hypotheses proposed in this study are that (1) the physiological effects incurred during the mating season had a long-term survival cost which was realized under the physiological demands of hibernation (Chapter 3), and (2) high reproductive success resulting from a high reproductive effort causes males to delay dispersal to prevent infanticide, and by the time they disperse, the territories with the best hibernacula are already occupied (Chapter 6).

*How are age, size, reproductive effort and success, survival, and dispersal related?*

I have proposed a working hypothesis for the relationships among age, size, reproductive effort and success, survival, and dispersal (Chapter 6). Many of the causal relationships I suggest, however, still need to be tested empirically. In particular, it would be useful to know what determines the reproductive status of yearling males – their size or their location (i.e. presence on natal territory) – as well as whether or not females decrease their aggression to unfamiliar males if they kill her litter.

## **Conclusions**

Survival, mating effort, and dispersal behaviour differed between yearling and older arctic ground squirrel males even though all males in both age classes were reproductively mature. I suggest that differences in mating effort arise because males are unable to grow to their maximum size before they are reproductively mature, allowing older males to invest more energy in reproduction than yearling males. The differences in reproductive effort between the age cohorts may be the reason their survival and dispersal behaviours differ. Given its potential effects, further studies examining mating effort, reproductive success, and their consequences on male survival and behaviour are warranted.

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## Appendices

**Appendix 1** Summary of years and grids of data collection with sources for previously published data. Spatial arrangement of and descriptions of boreal forest grids can be found in Hubbs and Boonstra (1997) and Krebs *et al.* (2001). Unpublished boreal forest data was provided by C.J. Krebs, R. Boonstra, and T.J. Karels and data from the alpine site for 1998 and 1999 were provided by D.S. Hik.

	Boreal Forest		Alpine <sup>a</sup>	
	Years	# grids	Years	# grids
Population trends	1998 – 2002	2 <sup>b</sup>	1998 – 2002	2
Annual survival	1992/93 – 2001/02	2 – 4 <sup>c</sup>	1998/99 – 2001/02	2
Summer survival	1991 – 2002	2 – 4 <sup>d</sup>	2000 – 2002	2
Winter survival	1990/91 – 2001/02	2 – 4 <sup>e</sup>	1999/00 – 2001/02	2
Reproduction				
Detailed parameters	1991 – 1997	2 – 4 <sup>f</sup>	2000 – 2002	2
Ratio juveniles:adults	1998 – 2002	2 <sup>b</sup>	1998 – 2002	2
% yearlings lactating	1993 – 1997	2 – 4 <sup>g</sup>	2000 – 2001	2
Morphology	1991 – 2002	1 – 4 <sup>h</sup>	1999 – 2002	2

<sup>a</sup> Control grids east and west, spaced 400m apart

<sup>b</sup> Control grids A and #3

<sup>c</sup> Control grids A (1992/93 – 2001/02), B (1992/93 – 1996/97), C (1993/94 – 1995/96) and #3 (1993/94 – 2001/02)

<sup>d</sup> Control grids A (1991 – 2002), B (1991 – 1996), C (1993 – 1996), and #3 (1993 – 2002)

<sup>e</sup> 1990/91 – 1995/96 data from Karels *et al.* (2000); 1996/97 – 1997/98 data from Karels (2000); 1998/99 – 2001/02 *unpublished data* from ground squirrel control grids A and #3

<sup>f</sup> data from Hubbs and Boonstra (1997), Karels *et al.* (2000), and Karels (2000)

<sup>g</sup> Control grids A (1993 – 1997), B (1993 – 1996), C (1993 – 1997), and #3 (1993 – 1997)

<sup>h</sup> Ground squirrel control grids A (1992 – 2002), B (1991 – 1997), C (1993 – 1996) and #3 (1993 – 2002)

**Appendix 2** Difference between actual and effective trapping areas. The edge-effect distance was the mean distance moved by individuals captured more than once in a single census.

Site	Year	Trap locations	Grid dimensions (m)	Edge effect (m)	Actual grid size (ha)	Effective grid size (ha)
Forest	1998-2002	grid stakes	270 x 270	50	7.3	13.7
Alpine	1998	burrows	150 x 200	80	3	11.2
	1999-2002	grid stakes	300 x 300		9	21.2

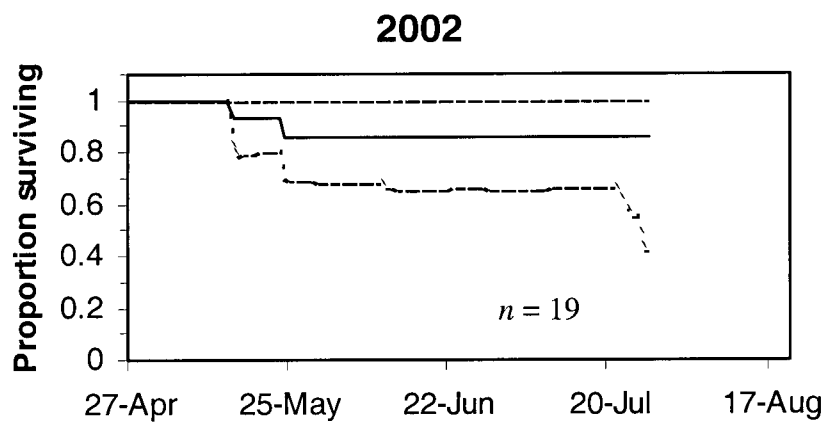
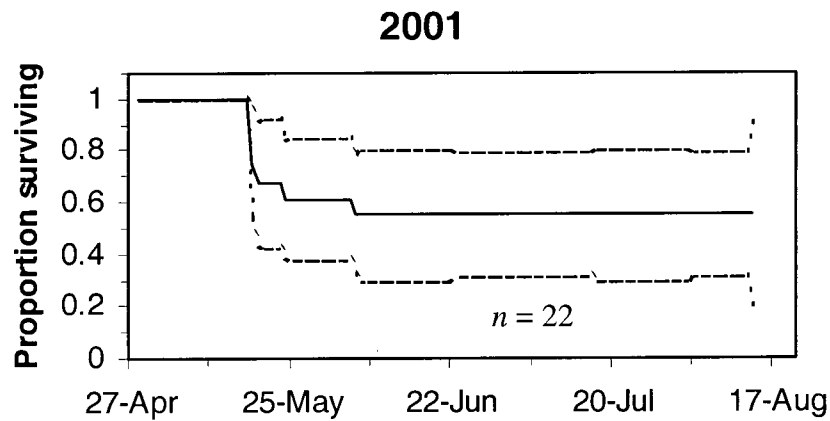
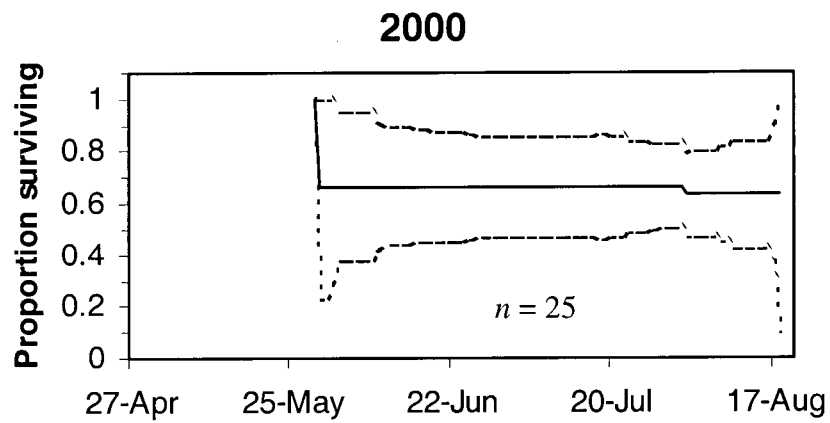
**Appendix 3** Sample sizes used to calculate yearly rates used in reproductive and survival analyses.

	Forest		Alpine	
	mean yearly <i>n</i>	range	mean yearly <i>n</i>	Range
Lactation rate	7	11 – 31	40	34 – 42
Weaning rate	13	7 – 23	20	19 – 26
Litter size	10	6 – 18	16	10 – 20
Annual survival				
Adult	7	1 – 14	8	5 – 9
Juvenile	10	1 – 27	7	1 – 14
Winter survival				
Adult	18	2 – 30	14	10 – 17
Juvenile	18	2 – 30	8	2 – 12
Summer survival	18	2 – 40	20	7 – 28

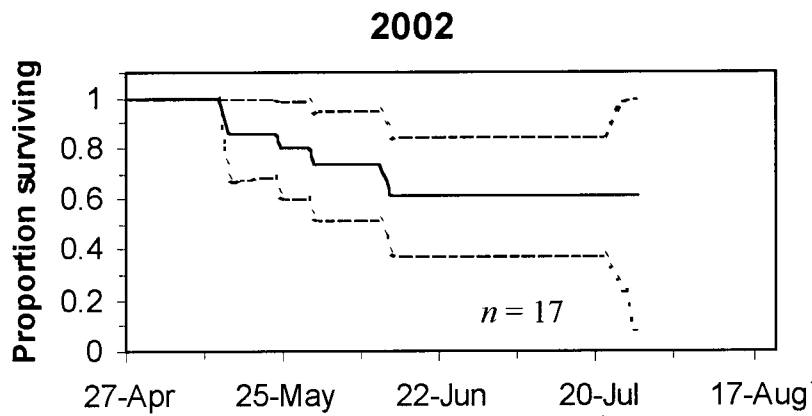
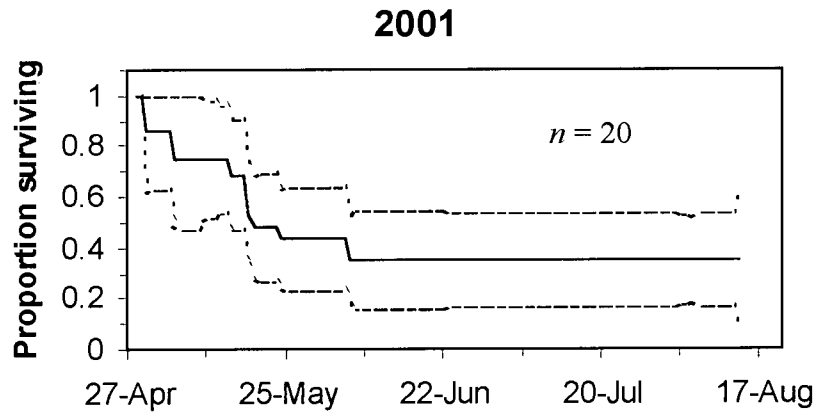
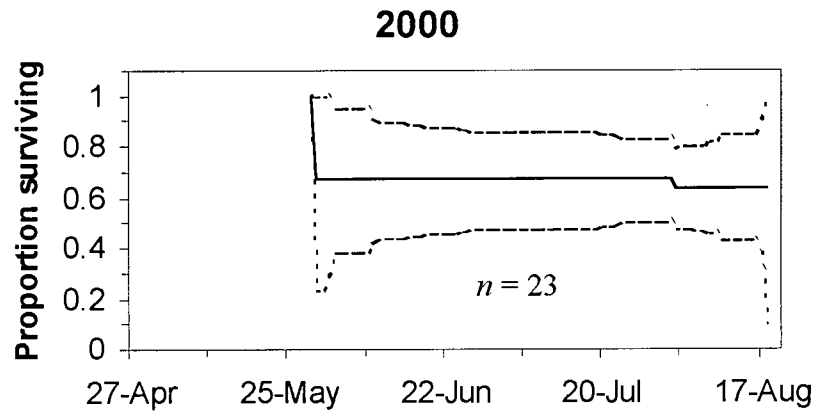
**Appendix 4** Comparison of yearly means calculated with all years weighted equally (Tables 4 and 5) and means weighted by yearly sample size (Appendix 3).

	Forest		Alpine	
	unweighted	weighted	unweighted	weighted
Lactation rate (%)	73.8	73.1	98.3	98.3
Weaning rate (%)	73.7	71.4	77.1	78.7
Litter size	3.3	2.5	3.9	4.0
Annual survival (%)				
Adult	34.1	33.6	27.1	25.6
Juvenile	31.9	24.8	40.2	24.2
Winter survival (%)				
Adult	67.8	65.4	40.4	40.5
Juvenile	67.8	65.4	54.9	29.2
Summer survival (%)	48.2	49.0	86.4	77.4

**Appendix 5** Kaplan –Meier survival curves with 95% confidence intervals for radio-collared males with animals with unknown fates censored from the analysis.



**Appendix 6** Kaplan –Meier survival curves with 95% confidence intervals for radio-collared males with animals with unknown assumed to have died.



**Appendix 7** Model selection results for male mating season survival. Independent variables considered were male age (A, yearling or  $\geq 2$  years old), year (Y), an index of male movement rate (M), and reproductive success, as measured by the number of females in a males core home range during the mating season (R). [YA] indicates the model included 2 independent variables (in this case, age and year) and the interaction while [Y][A] indicates only main effects were included in the model.  $k$  is the number of estimable parameters + 2, and  $\Delta AIC_c$  is the difference between a model's second order Akaike's information criterion ( $AIC_c$ ) and the  $AIC_c$  score and the score for the most parsimonious model.

Model	n	$K$	-log likelihood	$r^2$	$\Delta AIC_c$
[A]	23	3	10.7	0.283	0.0
[Y][A]	23	4	9.7	0.344	1.1
[A][M]	23	4	9.9	0.337	1.4
[Y][A][M]	23	5	9.0	0.394	3.0
[AM]	23	5	9.2	0.383	3.3
[YA]	23	5	9.2	0.380	3.4
[Y]	23	3	13.0	0.126	4.7
[Y][M]	23	4	12.7	0.180	7.0
[M]	23	3	14.5	0.027	7.6
[R]	23	3	14.8	0.006	8.2
[YM]	23	5	12.1	0.188	9.1
[YMA]	23	9	6.4	0.571	16.0



**Appendix 8** Model selection results for male winter survival for (a) 2000 and 2001 and (b) 2001 only. Independent variables considered for 2000 and 2001 were male age (A, yearling or  $\geq 2$  years old), fall body condition (C) and year (Y). For 2001 only, whether or not a male had dispersers (D) and reproductive success, as measured by the number of females in a males core home range during the mating season (R), were also investigated. [YA] indicates the model included 2 independent variables (in this case, age and year) and the interaction while [Y][A] indicates only main effects were included in the model. k is the number of estimable parameters + 2, and  $\Delta AIC_c$  is the difference between a model's second order Akaike's information criterion ( $AIC_c$ ) and the  $AIC_c$  score and the score for the most parsimonious model.

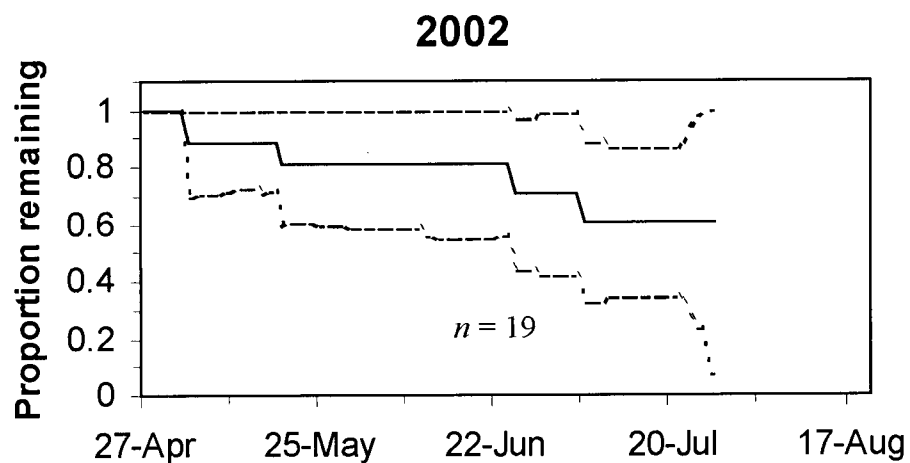
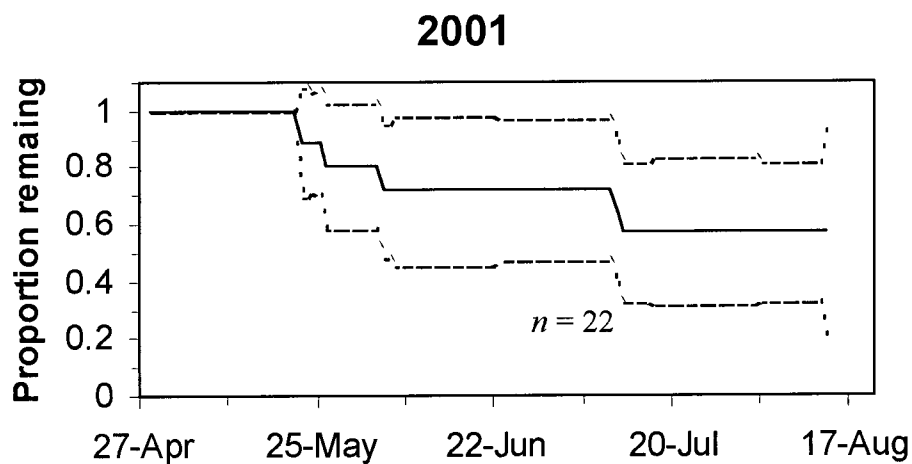
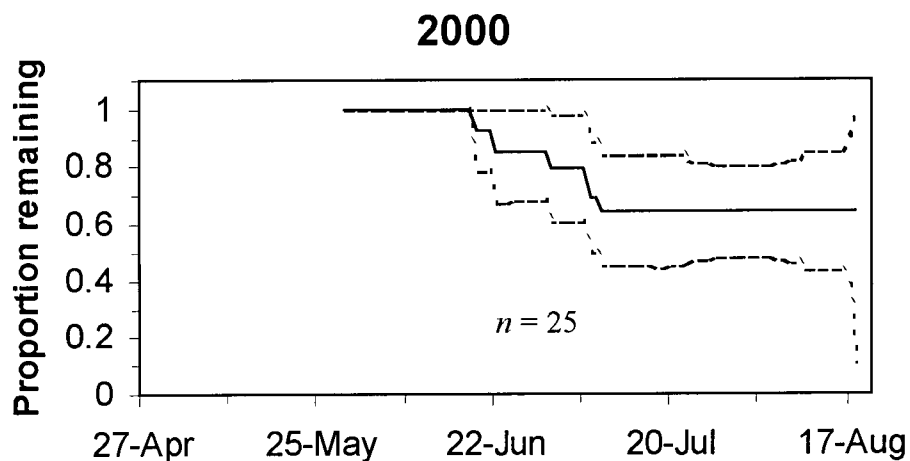
(a) 2000 and 2001

Model	n	k	-log likelihood	$r^2$	$\Delta AIC_c$
[A]	24	3	15.1	0.090	0.0
[C]	24	3	16.0	0.034	1.8
[Y]	24	3	16.4	0.010	2.6
[YA]	24	5	13.3	0.194	2.7
[Y][A]	24	4	15.1	0.090	2.9
[Y][C][A]	24	5	14.1	0.151	4.1
[CA]	24	5	14.1	0.150	4.1
[Y][C]	24	4	15.9	0.042	4.5
[C][A]	24	4	16.6	0.147	5.9
[YC]	24	5	15.9	0.042	7.7
[YCA]	24	9	9.4	0.432	12.3

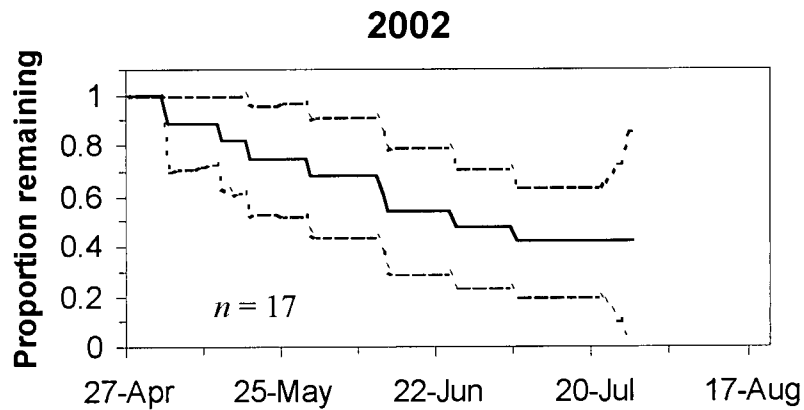
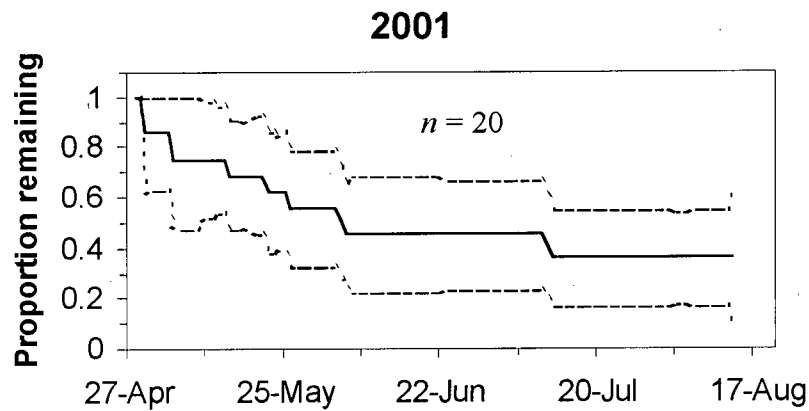
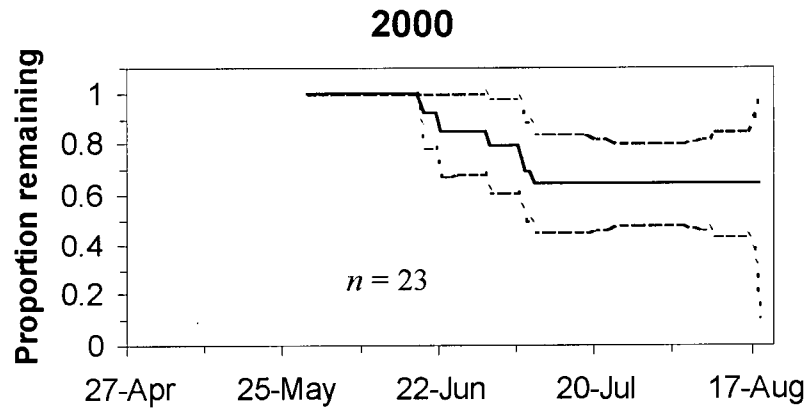
(b) 2001 only

Model	n	k	-loglikelihood	$r^2$	$\Delta AIC_c$
[A]	7	3	1.9	0.514	0.0
[D]	7	3	4.2	0.007	4.5
[R]	7	3	4.1	0.033	9.3
[A][D]	7	4	1.4	0.669	13.0
[A][R]	7	4	1.4	0.669	13.0
[R][D]	7	4	3.8	0.091	17.8
[RD]	7	5	1.0	0.413	54.2
[AD]	7	5	1.4	0.669	55.0
[AR]	7	5	1.4	0.669	55.0
[A][R][D]	7	5	n/a	n/a	n/a

**Appendix 9** Kaplan –Meier dispersal curves with 95% confidence interval for radio-collared males with animals with unknown fates censored from the analysis.



**Appendix 10** Kaplan –Meier dispersal curves with 95% confidence interval for radio-collared males with animals with unknown fates assumed to have dispersed.



**Appendix 11** Model selection results for dispersal. Independent variables considered were male age (A, yearling or >1 year old), year (Y), the number of females within 100m of a male's main sleeping burrow (F), and the presence or absence of juveniles, presumably daughters, within 100m of a male's main sleeping burrow (J). [YA] indicates the model included 2 independent variables (in this case, age and year) and the interaction while [Y][A] indicates only main effects were included in the model.  $k$  is the number of estimable parameters + 2, and  $\Delta AIC_c$  is the difference between a model's second order Akaike's information criterion ( $AIC_c$ ) and the  $AIC_c$  score and the score for the most parsimonious model.

Model	n	k	-log likelihood	$r^2$	$\Delta AIC_c$
[Y]	34	3	21.0	0.051	0.0
[A]	34	3	21.0	0.048	0.1
[Y][A]	34	4	20.1	0.091	0.8
[Y][A][J]	34	5	18.7	0.151	0.9
[Y][J]	34	4	20.2	0.086	1.0
[A][J]	34	4	20.5	0.071	1.7
[J]	34	3	21.8	0.011	1.8
[F]	34	3	21.9	0.008	1.9
[Y][F]	34	4	20.9	0.055	2.4
[Y][F][J]	34	5	19.5	0.117	2.4
[A][F]	34	4	21.0	0.050	2.6
[Y][A][F][J]	34	6	18.3	0.172	2.9
[YA]	34	5	19.8	0.104	3.0
[YJ]	34	5	19.8	0.102	3.1
[F][J]	34	4	21.3	0.033	3.4
[Y][A][F]	34	5	20.1	0.092	3.5
[A][F][J]	34	5	20.2	0.083	3.9
[AJ]	34	5	20.3	0.080	4.1
[YF]	34	5	20.7	0.063	4.8
[AF]	34	5	20.8	0.056	5.1
[FJ]	34	5	21.3	0.033	6.1

**Appendix 12** Model selection results for male mass loss during the mating season.

Independent variables considered were male age (A, yearling or  $\geq 2$  years old), year (Y), male body condition (C), and the mean distance to the nearest three females ( $F_d$ ). [YA] indicates the model included 2 independent variables (in this case, age and year) and the interaction while [Y][A] indicates only main effects were included in the model.  $k$  is the number of estimable parameters + 2, and  $\Delta AIC_c$  is the difference between a model's second order Akaike's information criterion ( $AIC_c$ ) and the  $AIC_c$  score for the most parsimonious model.

Model	n	k	log likelihood	$r^2$	$\Delta AIC_c$
[A]	24	3	120.4	0.276	0.0
[Y][A]	24	4	121.4	0.341	0.8
[A][C]	24	4	121.2	0.313	1.3
[A][ $F_d$ ]	24	4	120.4	0.281	2.9
[YA]	24	5	121.7	0.363	3.4
[Y][A][C]	24	5	121.7	0.362	3.4
[C]	24	3	118.4	0.147	3.8
[Y][A][ $F_d$ ]	24	5	121.4	0.346	4.0
[AC]	24	5	121.2	0.324	4.5
[A][C][ $F_d$ ]	24	5	121.2	0.323	4.5
[A $F_d$ ]	24	5	120.4	0.282	6.0
[Y][A][C][ $F_d$ ]	24	6	121.8	0.366	6.9
[C][ $F_d$ ]	24	4	118.3	0.147	7.0
[Y][C]	24	4	118.3	0.148	7.0
[ $F_d$ ]	24	3	116.6	0.000	7.5
[Y]	24	3	116.6	0.004	7.5
[C $F_d$ ]	24	5	118.7	0.170	9.5
[YC]	24	5	118.3	0.148	10.3
[Y][C][ $F_d$ ]	24	5	118.3	0.148	10.3
[Y][ $F_d$ ]	24	4	116.6	0.004	10.5
[Y $F_d$ ]	24	5	116.8	0.023	13.3

**Appendix 13** Model selection results for level of male wounding (2 wound classes) during the mating season. Independent variables considered were male age (A, yearling or  $\geq 2$  years old), year (Y), male body condition (C), and the mean distance to the nearest three females ( $F_d$ ). [YA] indicates the model included 2 independent variables (in this case, age and year) and the interaction while [Y][A] indicates only main effects were included in the model.  $k$  is the number of estimable parameters + 2, and  $\Delta AIC_c$  is the difference between a model's second order Akaike's information criterion ( $AIC_c$ ) and the  $AIC_c$  score and the score for the most parsimonious model.

Model	n	k	- log likelihood	$r^2$	$\Delta AIC_c$
[ $F_d$ ]	24	3	10.4	0.359	0.0
[ $CF_d$ ]	24	5	8.1	0.505	1.4
[Y][ $F_d$ ]	24	4	9.7	0.404	1.4
[Y $F_d$ ]	24	5	8.7	0.468	2.6
[C][ $F_d$ ]	24	4	10.4	0.368	2.7
[A][ $F_d$ ]	24	4	10.4	0.359	2.9
[Y][A][ $F_d$ ]	24	5	9.7	0.406	4.6
[Y][C][ $F_d$ ]	24	5	9.7	0.405	4.6
[A $F_d$ ]	24	5	10.1	0.380	5.5
[A][C][ $F_d$ ]	24	5	10.3	0.368	5.8
[Y][A][C][ $F_d$ ]	24	6	9.7	0.406	8.2
[Y]	24	3	15.1	0.073	9.3
[A]	24	3	16.0	0.021	11.0
[C]	24	3	16.3	0.002	11.6
[Y][C]	24	4	15.0	0.079	12.0
[Y][A]	24	4	15.0	0.077	12.1
[YC]	24	5	14.2	0.128	13.7
[A][C]	24	4	16.0	0.021	13.9
[YA]	24	5	14.8	0.091	14.9
[Y][A][C]	24	5	15.0	0.080	15.2
[AC]	24	5	16.0	0.021	17.1

**Appendix 14** Model selection results for male movement rate during the mating season. Independent variables considered were male age (A, yearling or  $\geq 2$  years old), year (Y), male body condition (C), and the mean distance to the nearest three females ( $F_d$ ). [YA] indicates the model included 2 independent variables (in this case, age and year) and the interaction while [Y][A] indicates only main effects were included in the model.  $k$  is the number of estimable parameters + 2, and  $\Delta AIC_c$  is the difference between a model's second order Akaike's information criterion ( $AIC_c$ ) and the  $AIC_c$  score and the score for the most parsimonious model.

Model	n	k	log likelihood	$r^2$	$\Delta AIC_c$
[ $F_d$ ]	24	3	-130.3	0.090	0.0
[C]	24	3	-131.3	0.013	2.0
[A]	24	3	-131.4	0.003	2.2
[Y]	24	3	-131.4	0.001	2.2
[C][ $F_d$ ]	24	4	-130.1	0.106	2.5
[A][ $F_d$ ]	24	4	-130.2	0.100	2.6
[Y][ $F_d$ ]	24	4	-130.3	0.093	2.8
[Y][C]	24	4	-131.3	0.015	4.8
[A][C]	24	4	-131.3	0.013	4.9
[Y][A]	24	4	-131.4	0.003	5.1
[C] $F_d$ ]	24	5	-129.9	0.124	5.2
[A] $F_d$ ]	24	5	-129.9	0.124	5.2
[Y][C][ $F_d$ ]	24	5	-130.1	0.111	5.6
[A][C][ $F_d$ ]	24	5	-130.1	0.110	5.6
[Y][A][ $F_d$ ]	24	5	-130.2	0.101	5.8
[Y][ $F_d$ ]	24	5	-130.2	0.098	5.9
[Y][ $F_d$ ]	24	5	-130.4	0.081	6.4
[AC]	24	5	-130.6	0.070	6.7
[YC]	24	5	-130.6	0.067	6.7
[Y][A][C]	24	5	-131.3	0.015	8.0
[Y][A][C][ $F_d$ ]	24	6	-130.0	0.112	9.2