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FEMALE REPRODUCTIVE SUCCESS IN THE NORTH AMERICAN RED SQUIRREL, *TAMIASCIURUS HUDSONICUS*

BY

KARL W. LARSEN

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
SPRING 1993

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Karl W. Larsen

Karl W. Larsen

Department of Zoology
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January 12, 1993

If you're going to do battle with squirrels, you're going to lose every time - unless you know as much about them as you possibly can. Intelligence is frequently 90 percent of any war - and the war against squirrels in no exception. The Japanese knew all about Pearl Harbor in 1941. Israel's victory in 1967 was due in large measure to superior Israeli intelligence. The Soviet bugging of the U.S. Embassy in Moscow rendered our embassy virtually useless for confidential work. Mata Hari was famous only because she gathered facts. Regular soldiers may be interned in prisoner of war camps during wartime, but spies are shot because one scrap of useful information about the enemy can be worth a thousand soldiers.

I repeat: you have to know everything about squirrels. Because they know everything about you.

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled FEMALE REPRODUCTIVE SUCCESS IN THE NORTH AMERICAN RED SQUIRREL, *TAMIASCIURUS HUDSONICUS* submitted by KARL W. LARSEN in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Stan Boutin

Stan A. Boutin

Jan O Murie

Jan O. Murie

A. Richard Palmer

Mark R.T. Dale

Mark R.T. Dale

Peter M Wa

Peter M. Waser

November 6, 1992

DEDICATION

This thesis is dedicated to Mr. George W. Mansoff (1909 -), who has trapped in the Athabasca River Sandhills area near Fort Assiniboine for over fifty years. His genuine concern, respect and admiration for wildlife are traits that have become far too exceptional.

ABSTRACT

The reproductive success of female red squirrels (*Tamiasciurus hudsonicus preblei* Howell) was studied from Spring 1988 to Spring 1991 in a jack pine (*Pinus banksiana*) forest in central Alberta, Canada (54.20°N, 114.45°W). There were two major objectives: (1) document the natural variation and potential correlates of reproductive success within each year, and (2) conduct experimental manipulations to test the relative importance of several potential factors in affecting reproductive success. Using a combination of live-trapping, visual observations, and radio telemetry, the reproductive success of mother squirrels was measured by documenting the fates of individual offspring, starting from birth.

Factors such as parturition date, previous breeding experience and territory area were relatively unimportant in determining a female's reproductive success, whereas litter size (range 1 - 4) had a significant influence. Also, the mean diameter of trees on the territory (inversely related to tree density) was related to offspring survival to weaning and beyond. Females allowed their offspring to reside on the natal territory until offspring were able to obtain their own territory. However, approximately half of dispersing offspring acquired territories on or adjacent to the mother's territory, with no sex-biased patterns being evident. This suggests that females suffer little from the close settlement of progeny and/or that long-distance emigration away from the natal area is too costly.

Manipulations of the overwinter food hoard of females were conducted using natural food items (pine cones) and artificial, high-energy items (sunflower seeds).

Females with hoard additions produced significantly higher litter sizes than control animals. A census of the cones cropped by squirrels during the autumn hoarding period suggested that individuals were not limited in their hoard size by the absolute number of cones.

The importance of territory quality to reproductive success was explored through a series of removal experiments. These experiments indicated that (1) neither non-breeding or breeding females responded to habitat vacancy by relocating their entire territory, (2) squirrels did not preferentially visit or settle on vacant territories that originally belonged to males, breeding females or non-breeding females, and (3) females with previous breeding experience shifted their territories in order to encompass neighbouring, vacant areas. These new areas were then allocated to offspring in the following year.

ACKNOWLEDGEMENTS

Although it has been said many times before, virtually all research projects depend on financial support, and this study was no exception. Grants were provided by The Canadian Circumpolar Institute (formerly The Boreal Institute for Northern Studies) and The Recreation, Parks and Wildlife Foundation of Alberta. An operating grant to Stan Boutin from the Natural Science and Engineering Research Council of Canada (N.S.E.R.C.) also helped with the funding. Critical manpower (see the long list below) and additional funding were provided through contracts with Employment and Immigration Canada, under the Unemployment Insurace Section 25 job creation program. Research permits were supplied by the Fish and Wildlife Division of the Alberta Ministry of Forestry, Lands and Wildlife. My financial support came from an N.S.E.R.C. Postgraduate Scholarship, an Izaak Walton Killam Doctoral Scholarship, and Teaching Assistant contracts with the Department of Zoology, University of Alberta.

Now comes the difficult part: recognizing *all* of the people who in some way, shape or form helped me complete this research and dissertation. I shall foresake the interests of brevity, in order to provide a detailed account of those who provided assistance over the years. I do this not so much for the sake of the reader, or for those whose names I will cite, but rather to ensure I will never forget the contribution of even one person who helped me achieve my goals during the past few years.

First off, I want to thank my summer research assistants. To someone undoctrinated in the trials and tribulations of field ecology, being put in charge of following ten radio-collared, juvenile red squirrels around the boreal forest may sound like a joyous occasion. It definitely has its good points, but along with those come mosquitos, horseflies, deerflies, inclement weather, bogs, spruce thickets, wet feet, more deerflies, very long days and empty stomachs. Here are the dedicated people (in no particular order) who took all of these things in stride: Sally Adomitus (*nee* Turner), Linda Appleton, Michael Blower, Zena Tooze, Cobey Langille, Todd Zimmerling, Richard Cotter, Linda Boonstra (now Linda Zimmerling!), Colleen Jevne, Thomas Boag, Heather Dundas, Iwona Pawlina, Anthony "Toner" Bösecke, Bill Turko, Al "Beeker" Verbeek (who is **not** related to the N.H.L. player), Lisa Takats, Christopher Yeremiy, Brett Leoppky, and Tarquin Caraher. Although most of the information collected by the 1992 Field Crew was not used in the preparation of this thesis, they also must be acknowledged for the role they played in filling certain gaps in both the database and my slide collection. The 1992 crew was composed of Lisa McDonald, Ron Maunder, Christie Johnson, Darren Linn, Jeff 'J.P.' Buck and Claude LeFebre. Lisa McDonald helped me immensely in finishing this thesis by doing a lot of the last-minute 'running around'.

Two of the aforementioned people need to be singled out: Michael Blower worked with me throughout the first two years of the study. He was there when the very first and last grid stakes were driven into the ground. He helped perfect the radio-collars we used, and between us we learnt the fine art of nest raiding (both arboreal and subterranean). Mike assisted me in hauling buckets of cones to what seemed to be the most distant points on the study area, and he accompanied me on many pitch-black, mid-winter mornings when we left Edmonton to go radio-tracking juvenile squirrels. He also helped me dig the horseshoe pits and fabricate the moose story, and together we brewed some mighty-fine batches of Trapper George's Spring Ale and Mayor Ernie's Pilsner. Thanks, Mike.

Anthony Bösecke came to Fort Assiniboine as a research assistant in 1990. He spent the summer getting me addicted to sunflower seeds and strange little black candies imported from the Netherlands. He also displayed an incredible amount of enthusiasm and dedication, so much so that I rehired him the following year to oversee the field operation. Anthony ran "a tight ship", and helped me immensely in completing the data collection. Thanks, Anthony.

The residents of Fort Assiniboine were instrumental in helping me complete my studies, and in making our stay in the area very enjoyable. George Mansoff, to whom this thesis is dedicated, graciously allowed me to conduct my research on a portion of his trapline, while simultaneously terminating his trapping operations in all of the neighbouring areas. Chris, Lynn and Paul at Redi-Fast Fixit, Ltd. managed to keep my field vehicle operating, despite overwhelming odds. Walter and Ansgaard Thomson provided us with delightful and inexpensive accomodation at Roscarrock, and each year they welcomed the field crew to Fort Assiniboine and into their own home. The proprietors of the Sportsman's Inn, Sigmund and Ramona, were always hospitable towards the Squirrel People, and the presence of their establishment made those sweltering, $+30^{o}$C days much more tolerable. In the same vein, the waitresses out at Big Al's Cafe usually kept pecan pie and hot chocolate in reserve for cold, wet, miserable days. Finally, Ernie Charman (Village Mayor/Councilman) supplied us with a colour TV during the N.H.L. playoffs.

When I sat down in 1987 to draw up a list of potential members for my thesis committee, I selected Drs. Palmer, Murie and Dale because I thought they would provide rigorous evaluations of my progress. Boy, was I right. But, I know I have emerged from all this in much better shape than if I had selected people with less of a professional or demanding approach to science, and therefore I extend my gratitude to these three gentlemen. Out in the field, Dusty Becker and I proved that two people can work on the same organism, in the same place, at the same time, and still come out talking to one another. Dusty supplied me with many important data through her winter and early spring trapping seesions, and our food addition experiments (see Chapter 4) complemented one another quite nicely.

One can discuss squirrels and research most of the time, but not all of the time. For helping to fill that void, I have to thank the good friends I have made through the Department of Zoology. Jim 'Bocephus' Hare, Richard 'Bulb' Cotter, Dennis Murray and I banded together when we first arrived, and had many, many good times together (some I can't remember all too well). Then there were my office mates: Mrinal Das, John Clay Bruner, and Ierecê de Lucena Rosa. Despite the fact these three people were ichthyologists and MacIntosh users, I still found them to be wonderfully unconventional and caring people that I enjoyed having around. I tolerated Mrinal's weird music, John's never-ending parade of curios, and Ierecê's incredibly long phone calls, and in return they tolerated my wall-to-wall pet collection and leaky aquariums. I definitely will miss seeing them on a regular basis, and I can only hope my next group of co-workers also will appreciate the philosophical virtures of Star Trek.

Other people at the University of Alberta offered me help when I needed it (which was quite often...). I lost count long ago of the number of times Lorne LeClair solved one of my computer problems. Don Paradis, in the Zoology main office, was equally adept at explaining to me the contractual rigmarole which accompanied my research grants and contracts. The secretaries, Sandy, Wilma, Cheryl, Sandra, and Elaine never seemed to get tired of my accounting dilemmas or inability to operate the photocopiers. Similarly, Dean and Dennis in Zoology Stores were always accomodating, and always seemed to have a back-up copy of some crucial invoice that I had misplaced. The chairman of the department, Dick Peter, was also supportive and helpful throughout the years. Dushanti Pinnaduwage in the Department of Statistics and Mathematics helped me determine the proper statistical approaches to several statistical nightmares, and Terry Taerum, Statistical Consultant with University Computing Systems spent many hours working with me to produce and then decipher SAS output. Finally, Barb Thomas from Forest Science was my own personal ANOVA consultant, and I owe her many beers for her time and effort.

I have been incredibly fortunate in my graduate career to have had not one, but two excellent thesis supervisors. Patrick Gregory of the University of Victoria first encouraged me to undertake a Master's degree, and then he inspired me to pursue a Ph.D. During the past years, Pat and I have kept in contact, through a series of enjoyable but intense snake-paper production meetings. I hope my association and friendship with Pat will continue into the future.

After having Pat Gregory as a supervisor for my Master's degree, I prepared myself to experience a less-rewarding, more distant relationship with my Ph.D. supervisor. As it turned out, I need not have worried. Stan Boutin has been a fantastic Ph.D. supervisor, in every way possible. I have gained so much from my association with him over the past few years, that I really don't know where to start. Despite my empirical stubbornness, Stan managed to lure me into the realm of experimental, manipulative field ecology ("the Dark Side of The Force"). Perhaps one story will serve to illustrate Stan's approach to thesis supervision: I believe there was one or two times, in the past five years, that I asked Stan for a few minutes of his time and he didn't immediately pull out the chair for me. At least one of those times was about ten minutes before one of his lectures. All I can say is, thanks Stan, for being meticulous, supportive, highly critical, and a good friend (thanks also for being openminded about coffee tables, sombreros and leopard frogs).

Finally, I would like to discuss some of the more important things that have happened since I came to Edmonton. I have already mentioned the good friends I have made, so I won't repeat that. Wayne Gretzky was traded to Los Angeles in 1988 (thus paralyzing Edmonton) and, much more importantly, the Calgary Flames won the Stanley Cup in 1989. Miraculously, not one single research assistant at Fort Assiniboine fell out of a tree (at least, no one was seriously hurt from falling), and my 1978 Courier kept running until I sold it in 1990. But by far the most important thing that has happened to me in my life, much less the last few years, was my marriage to Cindy James. She really deserves co-authorship on this thesis, since she helped with its completion in so many ways. She put up with my five-month stints at Fort Assiniboine and the distinct smell of stale peanut butter that accompanied me whenever I did return to Edmonton. Through the years she has endured turtles in the closets, flying squirrels in the kitchen cupboards, and salamanders under the heat registers. She also allowed our spare bedroom to resemble a messy office most of the time, and she tolerated my self-imposed periods of isolation during the writing of this thesis. Through all of this, she quietly and efficiently went about doing all of the day-to-day chores that normally would have occupied much of my time. I hope I will be able to repay her for all of the support. Thank you, Cindy.

October 12, 1992

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CHAPTER 1

GENERAL INTRODUCTION TO THE STUDY AND THE AREA

THE STUDY OF REPRODUCTIVE SUCCESS

"Reproductive success" is not easily defined. It may mean number of matings, number of zygotes, number of propagules produced, number of offspring weaned, and even fitness *per se* (see reviews by Clutton-Brock 1988a and Newton 1989a). To evaluate reproductive success requires some form of comparison, such as the differences in reproductive success between individuals within the same population. Regardless of the precise working definitions, studies of reproductive success are of obvious importance to our understanding of population biology, autecology, life history and evolution (Newton 1989b).

Studies of reproductive success in animal populations recently have garnered much attention. Long-term investigations into lifetime reproductive success (LRS) are becoming more common, and they have proven useful in documenting variation in the contribution of individuals to succeeding generations during their life spans (see major reviews by Newton 1989a and Clutton-Brock 1988a). However, the need for shorter-term or 'cross-sectional' studies, which focus on certain components of LRS, such as mating success, fecundity, offspring survival, etc., remains (Clutton-Brock 1988b). Although long-term research may reveal if fitness shows low heritability (as predicted by Fisher in 1930), short-term studies can provide answers to some very important questions, including: To what extent is variation in certain components of reproductive success caused by an individual's attributes (e.g. phenotypic differences, behaviour, etc.), by short-term environmental variations, or by chance (Boyce 1988, Clutton-Brock 1988b). Measuring the relative effects of these situations and traits is also necessary to assess their adaptive significance (Grafen 1988).

Examining the relative reproductive success of individuals, even over a brief time, requires two things: (1) an adequate sample base and (2) the ability to follow the fate of offspring as well as parents. Most species do not satisfy both of these conditions. For example, microtine rodents and small birds are prolific and locally abundant, but they (particulary offspring) are not easily followed. For this reason, most studies of reproductive success have focused on larger animals (see Clutton-Brock 1988a), but these species pose other problems. Both adults and offspring are relatively more conspicuous, but they often do not occur in large numbers. They also are relatively less fecund, making it harder to detect differences between individuals except over long periods of time (e.g. Clutton-Brock 1982). One approach to dealing with these problems is to truncate the measurement of 'success'. For example, one may forego measuring the ultimate fate of offspring, and instead rely simply on the total number of offspring produced at parturition, the number of offspring fledged or weaned, etc. This approach, of course, does not take into account differential success of independent offspring, which is the criticism normally leveled at short-term studies. Indeed, Clutton-Brock (1988b), after reviewing a large number of studies involving reproductive success, made the following statement:

> "One of the most obvious generalizations arising from the analysis of fitness componenents in females is that individual differences in offspring survival are one of the most important components of variation in lifetime reproductive success among breeding females in many birds and mammals. In particular, differences in offspring survival *after* fledging or weaning were the principal source of variation in reproductive success among breeding adults in several species".

In studying reproductive success, I wanted to choose a relatively small animal, in order to correct the taxonomic imbalance in the literature. This would also allow me to collect a reasonable amount of information within the normal duration of a Ph.D. study. I also wanted to include in my measurements of reproductive success an assessment of offspring survival *after* independence from the parent(s). Red squirrels, *Tamiasciurus hudsonicus* (Family Sciuridae), constituted a good choice of study organisms. They are abundant locally, and like most sciurids, they are easily observable. Also, techniques established by Stan Boutin indicated that both adults *and* offspring may be followed well-past the parental care stage.

The reprodutive life-span of red squirrels is too long to have made a study on LRS feasible as a Ph.D. thesis. Also, the promiscuous mating system of red squirrels made it logistically difficult to evaluate male (sire) reproductive success. Therefore, I focussed on variation in female reproductive success within the single annual breeding episode. Within any given year, the ability of an individual female squirrel to reproduce 'successfully' (relative to other females) may be influenced by **(1)** the quality of the female herself (or "maternal selection" - Kirkpatrick and Lande 1989) and **(2)** external or environmental conditions. To date, very few studies have sought to decouple these two influences, likely because of the difficulty involved (see introduction to Chapter 5). One of my goals, therefore, was to investigate the potential influence on reproductive success by characteristics of both the mother *and* her territory. I attempted to do this using two main approaches, empirical observations and experimental manipulations.

Chapter 2 of this thesis concentrates on the natural variation and patterns of female reproductive success observed in a red squirrel population. These data were collected by monitoring the success of reproducing females from parturition until the offspring were at least one year of age. The mother's previous breeding experience, body mass, territory quality, and litter size are al[illegible]ned as possible correlates of reproductive success.

Chapters 3 and 4 represent my efforts to experimentally manipulate the environmental resources available to adult females, in order to examine their possible influence on reproductive success. Squirrels are well known for their hoarding behaviour, so to answer the question, "Does the level of hoarded, overwinter food affect the reproductive success of mothers?", I manipulated the contents of winter hoards. In addition to these hoard manipulations, I also performed a series of removal experiments, in which individual, adult females were given the opportunity to relocate or re-establish the boundaries of their territories.

Squirrels in northern regions must possess a territory in order to survive the winter (C.C. Smith 1968). Thus, a female's reproductive success must depend to some extent on the ability of her offspring to acquire their own territories, prior to the onset of winter. Potentially, this success also may be influenced by *where* the offspring settle, relative to her own location. For this reason, mothers may be expected to affect the dispersal patterns of offspring. In Chapter 5, I investigate settlement tactics and survival from the perspective of dispersing offspring. I address the questions (1) what are the mechanisms by which offspring acquire vacant territories? and (2) what patterns of settlement are present?

In writing this thesis, I have tried to minimize the repetition of information, so there are numerous cross-chapter references to methodology and results. Pertinent details on the study site are provided in each chapter, but following is a more detailed overview of the research area and the environmental conditions which existed during the study years.

NATURAL HISTORY OF THE POPULATION AND STUDY AREA

This study was conducted in the Athabasca Sand Hills at Fort Assiniboine, Alberta (54.20°N, 114.45°W, see Fig 1.1 and Appendix 1), from April 1988 to October 1992. The predominant habitat in this area is jack pine (*Pinus banksiana*) forest, with occasional, smaller stands of white spruce (*Picea glauca*). Interspersed in this forest are sporadic patches of aspen (*Populus*) and birch (*Betula*) parks, or tamarack (*Larix*) and black spruce (*Picea mariana*) bogs. These patches of apparently suboptimal habitat are devoid of resident red squirrels, except during late summer and early fall, when juveniles may occupy them. During the study, annual adult survivorship ranged from 67-71 % (Larsen unpubl.). Survivorship estimates reported from other studies of *Tamisciurus* are approximately 48% (Kemp and Keith 1970), 47% (Rusch and Reeder) and 40% (Wood 1967).

Red squirrels in the jack pine forest maintain individual, non-overlapping territories year-round. Mean territory size during the study was 0.65 h (Chapter 2). Most territories in the study area resemble convex polygons, with some exceptions (e.g. elongate territories alongside clearings) (Chapter 2). The activity center of each squirrel's territory is conspicuously marked by the presence of a midden (*v.* Gurnell 1984, Obbard 1987), where the winter hoard is stored. Midden sites are traditional, and when a territory owner is replaced, the new squirrel continues to use the established midden.

In central Canada, female red squirrels rarely breed as yearlings (Rusch and Reeder 1978; Wood 1967; Davis 1969; Becker 1992), and during my study females were usually at least two years of age before bearing their first litters. Males develop scrotal testes in their first spring (pers. observ., Becker 1992, Rusch and Reeder 1978) but it is not known if they breed. At Fort Assiniboine, the ratio of adult males to reproducing females during the spring breeding periods of 1989 and 1990 was approximately 2.2:1. During the five-week or longer breeding season (Becker 1992), adult females tolerate the presence of males on their territory during the brief one-day estrous period (Lair 1985). Mothers bear and raise their litters within the confines of their territories, and offspring have little if any direct contact with other conspecifics until they leave the mother's territory (>8 weeks after parturition).

During this study females produced one litter per year, except in very rare cases (approximately 4% of all mothers) when an entire litter was lost early enough permit a second successful mating. Data obtained from these abnormally late litters were not used in this study (Chapter 2). Litter sizes ranged from 1 to 4 during the study. Sex ratio of offspring at birth did not differ significantly from a 1:1 ratio within each year, nor within the pooled sample (heterogeneity chi^2 test following Zar 1984, all $Ps > 0.08$). Similarly, litter size and other measurements of female reproductive success did not differ significantly from year to year (Chapter 2). Offspring emerged from the nest at approximately 50 days of age, but nursing continued for up to three additional weeks.

The weather at Fort Assiniboine is typical of a continental, temperate zone area, with long cold winters and warm and relatively dry summers. During the study the average temperatures did not deviate considerably from long-term averages (Fig. 1.2). The spring periods of 1988 and 1991 were somewhat warmer than usual, and Spring 1989 was slightly colder.

Jack pines are unlike many coniferous trees in that major fluctations in cone crop availability are rare (Owens and Molder 1984). However, because pine cones constituted the major food source for the Fort Assiniboine squirrel population, it was important to monitor the cone production during the study years. Twenty branches (one on each tree) were haphazardly selected from within 1 km^2 of the study area, and the production of mature cones was recorded in early August of each year. Changes were not significant at $\alpha=0.05$ ($G=24.04$, $df=16$, $P=0.089$; Fig. 1.3). The fluctuations that did occur were not on the magnitude reported in other studies of red squirrels living in spruce forests (e.g. M.C. Smith 1968, Rusch and Reeder 1978).

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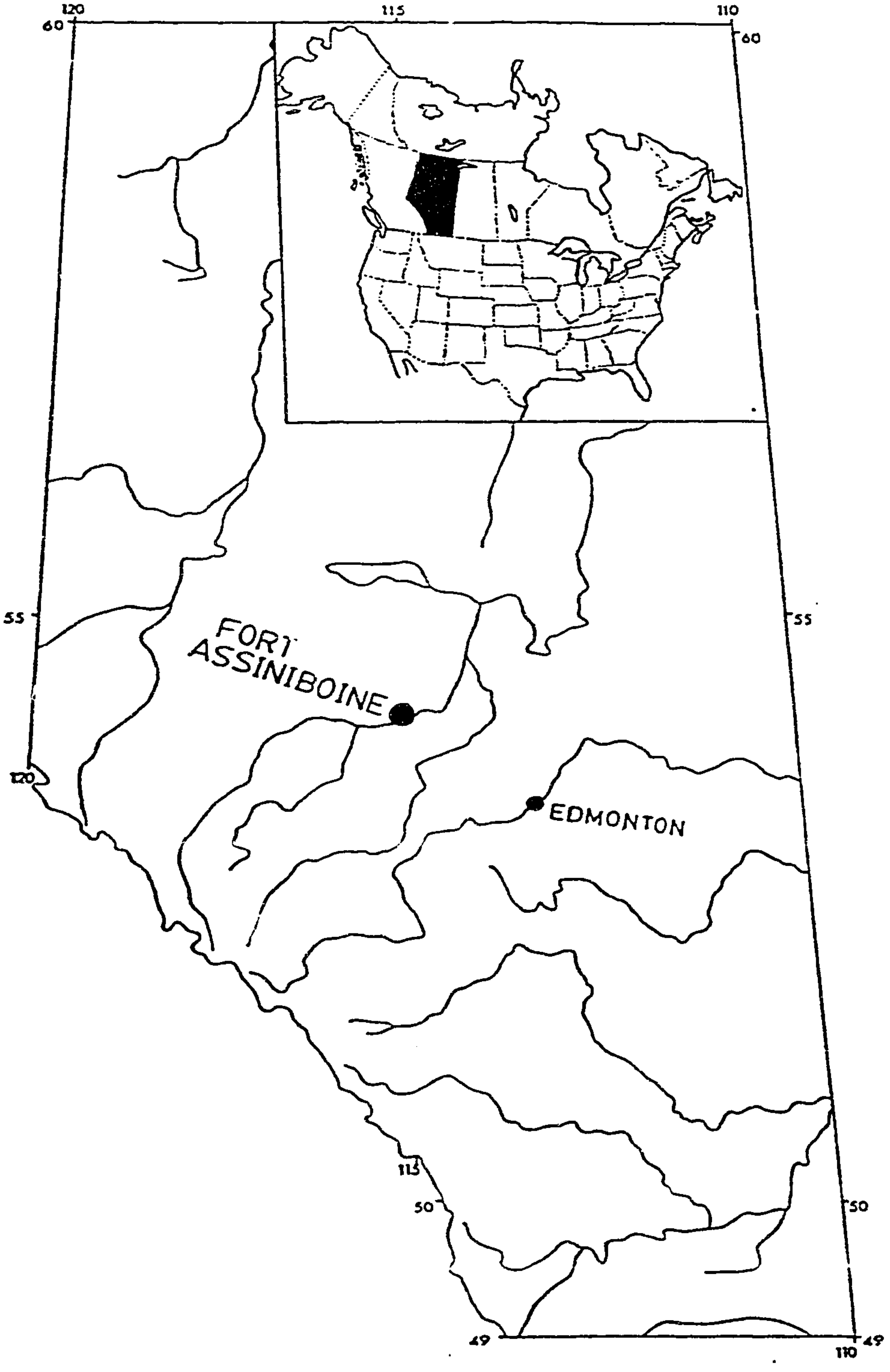

FIGURE 1.1. Location of study site, Fort Assiniboine, Alberta (54.20°N, 114.45°).

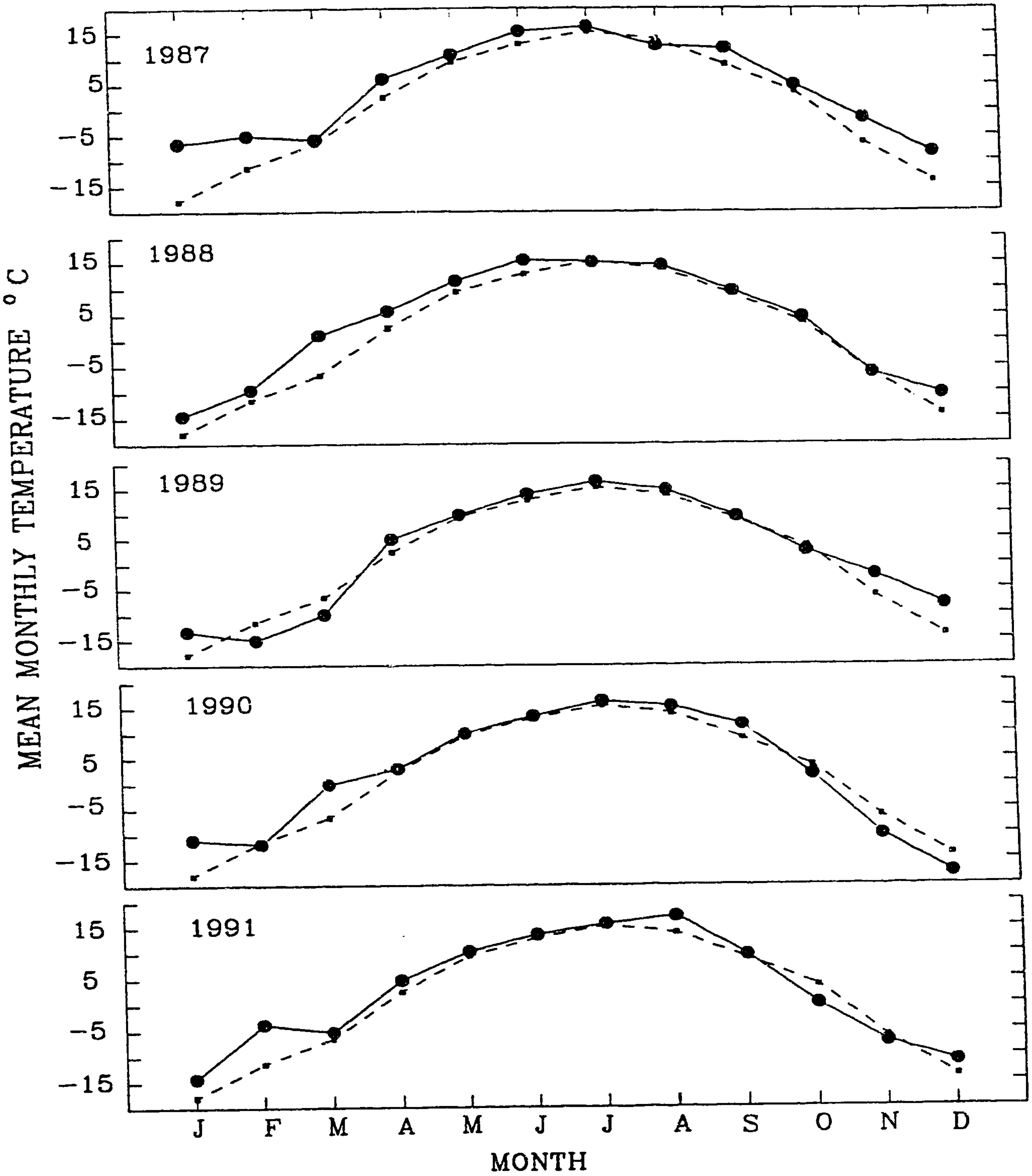

FIGURE 1.2. Mean monthly temperatures for Fort Assiniboine, Alberta, during the years 1987 to 1991, inclusive. Dotted line represents 30-year norms. (source: Atmospheric and Environmental Weather Service, Environment Canada, Edmonton, Alberta).

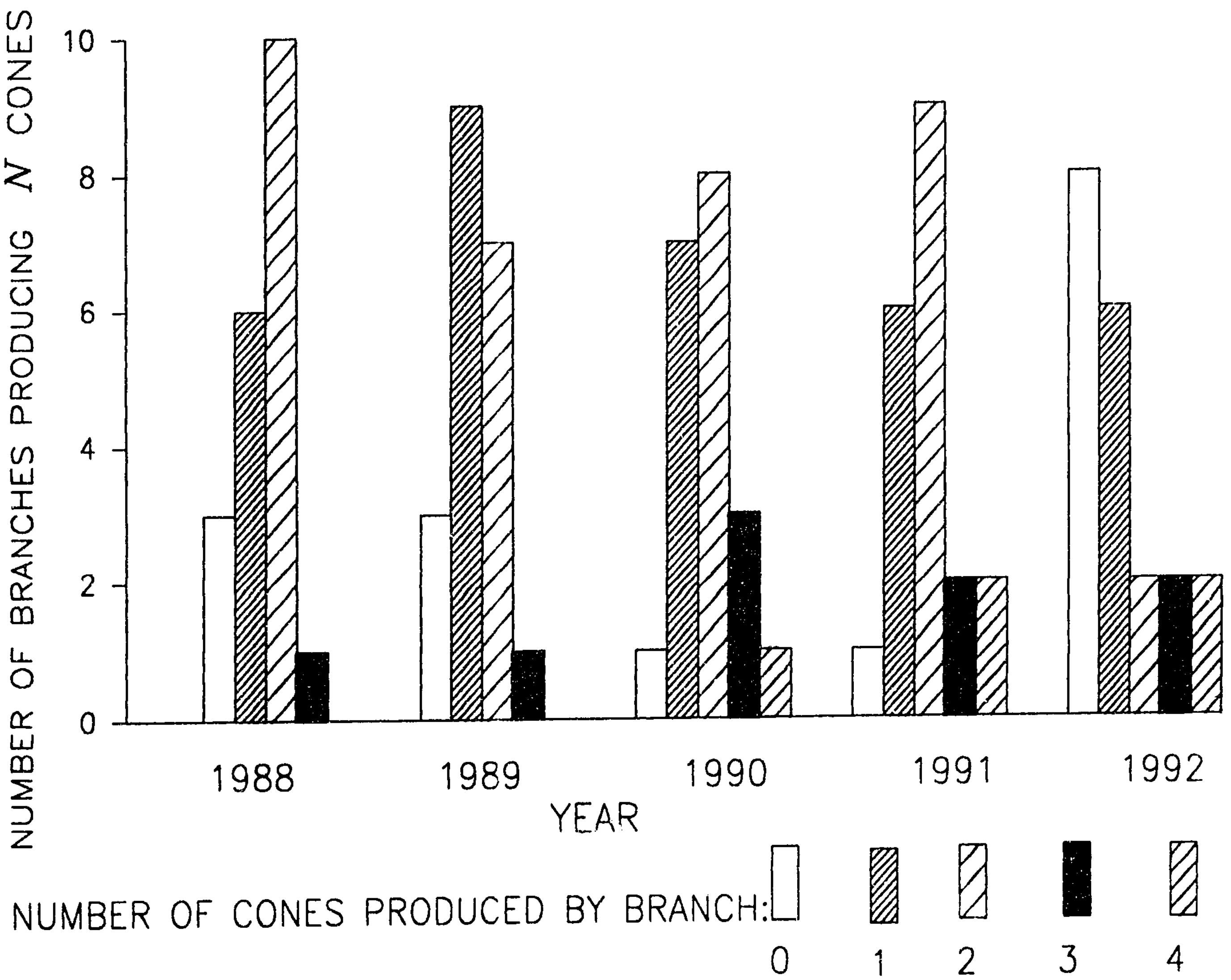

FIGURE 1.3. Relative numbers of jack pine branches producing 0,1,2,3 or 4 mature cones during the years 1988-1992. Data was collected each August from 20 branches (each on a different tree) that were haphazardly selected at the start of the study. As shown, highest production was in 1991, when an average of 1.9 cones/branch were produced.

CHAPTER 2

CORRELATES OF REPRODUCTIVE SUCCESS IN FEMALE RED SQUIRRELS

INTRODUCTION

Most studies of individual variation in reproductive success of vertebrates have focused on birds and large mammals (see reviews by Clutton-Brock 1988 and Newton 1989), for good reasons. It is relatively easy to locate and observe individuals of these species, and to follow the survival of offspring, at least to the end of the parental care stage. However, in recent years reports on the reproductive success of smaller mammals have become more common (e.g. Sheridan and Tamarin 1988, Ostfeld *et al.* 1988, Boyce and Boyce 1988, Wauters and Dhondt 1989, Waser and Jones 1991, Ribble 1992).

Squirrels (Family Sciuridae) are good model organisms for studying individual life-histories and traits, because they are often abundant locally and, compared to many small mammals, they are very tractable (e.g. Boag and Murie 1981, Murie and Harris 1984, Michener 1989, Wauters and Dhondt 1989, Festa-Bianchet and King 1991, McWhirter 1991, etc.). One potential problem in studying reproductive success of sciurids is that many species bear their litters underground, and male offspring often undertake interpopulation dispersal (Holekamp 1984). These two factors make it relatively difficult to assess initial litter size and subsequent offspring survival. To date, variation in individual reproductive success has been studied in three species of squirrels, yellow-bellied marmots (*Marmota flaviventris*, Andersen *et al.* 1976, Armitage and Johns 1982, Armitage 1986, 1987, 1991, etc.), Columbian ground squirrels (*Spermophilus columbianus*, King *et al.* 1991) and European red squirrels (*Sciurus vulgaris*, Wauters and Dhondt 1989). Yellow-bellied marmots are social, and reproductive success is subject to group and habitat effects (Armitage 1991). In Columbian ground squirrels, weight of adult females at emergence from hiberation is correlated with annual reproductive success, but the greatest source of variation in life-time success is due simply to offspring survival (King *et al.* 1991). In the polygynous European red squirrel, reproductive success of breeding females has been shown to be influenced by body mass and social rank (Wauters and Dhondt 1989).

Unlike the European red squirrel, the North American red squirrel (*Tamiasciurus hudsonicus*) exhibits a promiscuous mating system, with individuals maintaining individual, non-overlapping territories. Females allow males onto their territory during the one-day estrous period (Lair 1985, Becker 1991), and are solely responsible for raising the offspring. Because it is possible to follow the survival of individual offspring from birth, this species presents good conditions for studying the role of maternal and environmental characteristics in determining reproductive success.

The first major objective of this study was to learn what variation existed in within-year reproductive success of female *Tamiasciurus* bearing litters. I also conducted a preliminary examination of the costs of reproduction, by determining whether relatively successful mothers allocated more effort to parturition and/or suffered higher mortality. An ultimate goal of any study of reproductive success, however, is to identify the factors causing individual differences. A fundamental step in achieving this goal is identifying correlates of reproductive success, so that observational or manipulative experiments may be designed to support inferences of causation. Thus, my third objective was to determine what factors were correlated with variation in female reproductive success. The potential correlates I examined were previous experience and success, body mass, parturition date and attributes of the maternal territory.

Age and/or experience effects have been shown to influence reproductive success in many animal populations, through both increases in initial litter size and increased survival of offspring (Festa-Bianchet 1988, Nol and Smith 1987, Sæther 1990, Forslund and Larsson 1992, see reviews by Clutton-Brock 1988 and Newton 1989). Maternal body mass has also been linked to success at raising offspring, both through increased litter size and the ability to provision offspring (Sauer and Slade 1986, Clutton-Brock 1982, Wauters and Dhondt 1989). Hence, I expected body mass of mothers and their reproductive success to be directly correlated. I considered parturition date as another possible correlate of reproductive success, as studies have shown that timing of birth (or hatching, or fledging) may affect offspring survival (Bekoff, Scott and Conner 1989, Newton and Marquiss 1984, Nilsson and Smith 1988, Clutton-Brock 1982, Reiter *et al.* 1978, Nowasad 1975).

Territory or home range effects, including food supply, have also been shown to influence reproductive success (Weatherhead and Robertson 1977, Hogstedt 1980, McCleery and Perrins 1985, Jackson 1989, Elmberg 1991, etc.). Larger territories may reflect increased access to food (positive effect on reproductive success) or, conversely, poorer quality habitat with concomitant increases in foraging and defense times (negative effect). I also considered attributes of the forest surrounding the midden as potential correlates of each female's success.

SITE DESCRIPTION AND NATURAL HISTORY OF RED SQUIRRELS

I conducted this study in a jack pine (*Pinus banksiana*) forest near Fort Assiniboine, Alberta (54.20°N, 114.45°W), from Spring 1988 to Spring 1992. Red squirrels at Fort Assiniboine maintain individual, non-overlapping territories, and larderhoard their winter food supply (pine cones) on traditional middens (*v*. Gurnell, 1984). Females are normally two or three years of age before they bear their first litter, and then they give birth to one litter per year. Rare exceptions occur when females (approximately 4% of all mothers) lose their first litter early enough to permit a second mating. Data obtained from these few breeding attempts were not used in this study (see METHODS). Gestation period is 30 days, and parturition usually occurs between late April and late May. Offspring emerge from the nests at approximately 50 days of age, and shortly thereafter begin making forays off of their mother's territory as they search for a vacant territory (Chapter 5). Weaning occurs at 70-80 days of age, although offspring that have not yet acquired their own territory continue to use the mother's territory as a home base for much longer. Females usually produce two litters over their lifetime, but instances of successive parturition over four consecutive years has been recorded.

METHODS

MEASURING THE REPRODUCTIVE SUCCESS OF MOTHERS

I measured the reproductive success of breeding females by following the survival of their respective offspring, from parturition to at least their first spring (≈11 months of age). One hundred nineteen litters were located by using telemetry to locate postpartum females in their nests. Newborn offspring (<12 g) were removed temporarily from the nest, and their sex and weight were recorded. Each litter was relocated approximately three weeks later, using the same procedure, and the nestlings received metal and colored eartags. Numbers of offspring emerging from litters handled once during the nesting stage were not significantly different from litters handled twice (*G*-tests, each year tested separately, all *P*s > 0.14). In 1990 I monitored the emergence of 11 litters (from outside the study area) which were not visited during the nesting stage. The numbers of offspring emerging from these litters did not differ significantly from those litters which had been handled at least once during nesting (G=0.754, df=4, P=0.94).

Upon emergence from the nests, the fates of the individual offspring were determined through a combination of visual observations, live-trapping (see below) and telemetry. Offspring emerged at approximately 50 days of age, and were monitored intensively until they were at least 80 days of age (approximate age of weaning).

Major trapping censuses were conducted each year in the spring (on and after 1 May) and in early autumn (on and after 23 August). The spring and fall trapping censuses were close to 100% accurate at determining which individuals of the study population remained alive on the grids. Of the 909 individual squirrels tagged on the grids during the three years of the study (adults, nestings, juveniles), I had only 17 cases (<2%) where an animal was observed after being undetected during a previous major census. Moreover, fifteen of these 17 individuals likely held territories off of the study area, as they were captured rarely, and then only on the periphery of the grid. Relatively short dispersal distances (Chapter 5) resulted in the majority of the offspring settling within the study area.

The survival data of offspring were used to measure the reproductive success of mothers. Five different measurements of reproductive success were considered: (1) number of offspring at parturition [=litter size], (2) number of offspring emerging from the nest, (3) number of offspring reaching 80 days of age, (4) number of offspring surviving to autumn and (5) to spring.

Litter sizes were obtained for some females living off the study grids, but in some of these cases logistical constraints prevented us from obtaining further estimates of reproductive success. During the study there were four cases where a female lost her litter, and gave birth to a second litter within the same summer. None of the offspring from these three 'second' litters survived for more than a few days past emergence. Because of the rarity of this event, these four second attempts at reproduction were omitted from the analyses.

MEASURING POTENTIAL CORRELATES OF REPRODUCTIVE SUCCESS

Previous breeding history and reproductive success: Red squirrels cannot be aged by any absolute body measurements (Obbard 1988). Thus, I could not estimate the age of squirrels that were born prior to the start of my study. This problem, together with high adult survivorship (Chapter 1) and delayed reproductive maturity of females (Becker 1992), made it difficult for me to analyze relationships between age and reproductive success. However, once females bear their first litter they continue to bear litters in all subsequent years, without interruption (pers. obs.). Thus, after the first year (1988), I could classify females by whether they were bearing their *first* litters (uniparous) or at least their second litters (multiparous). Survival data also allowed me to look at the success of females during their last breeding attempt.

Towards the end of the study, my longitudinal data on individuals allowed me to determine if females were bearing their first or second litters.

Female body mass and parturition date: Live-trapping permitted us to obtain body mass measurements of most reproducing females at least every second day. In these cases (≈85% of all mothers), parturition dates could be determined within ±1 day, because of the sudden decrease in body mass. When sufficient female body mass data were unavailable, and when the mean body mass of the nestlings exceeded 10 g (maximum mass of known-age neonates), a growth curve based on the mean body mass of the nestlings was used to estimate parturition date (Boutin and Larsen *in press*). Because breeding periods in the population vary from year to year (Becker 1992), it was necessary to standardize parturition dates. To do this, parturition dates were converted to ranks within each year prior to pooling across years.

Territory characteristics: The areas of squirrel territories were measured during the years 1988 to 1990, using the methods outlined by Price *et al.* 1986. Time and manpower constraints made it impossible to map all territories during a standardized time of the year. I measured the areas of 22 female squirrel territories in autumn (1 August - 2 September), and again in the following spring (15 May - 7 June). No significant changes in size of areas existed between the two sets of measurements (Wilcoxon paired-sample test, T=102, P>0.20. Eight of the territories measured in Autumn 1989 and Spring 1990 were also measured in the ensuing summer and autumn, giving a total of four measurements. Again, no significant changes occured in the size of the individual territories (repeated measures ANOVA, F=0.47, df=3,6, P=0.716). None of these females had offspring residing on part of their territory during any of the mapping periods. Further, there were no significant differences between years in the mean size of all measured territories in the population (all measurements pooled, regardless of season and owner's sex and reproductive status, F=0.19, df=2,158, P=0.828). Because of this consistency in territory size across seasons and years, I felt valid measurements of territory size of reproducing females were those taken during the preceding autumn, or during the spring and early summer that the female gave birth. I did not measure territories during the period when females had emergent offspring, as territorial defence by the mothers, and territory perimeters, may have been influenced by the presence of her emergent offspring (as reported by Price and Boutin *in press*, Boutin *et al. in press*).

Measurements of vegetation characteristics were taken on the territories of females using four 50 m^2 quadrats. The centre of each quadrat was located 20 m N, S, W and E (respectively) of the midden. Data collected from these quadrats included numbers of each tree species present and the DBH (diameter at breast height) of Jack Pine trees.

STATISTICAL ANALYSES

Logistic regression was used to test for the effects of reproductive success in year x (independent variable) on reproductive success in year $x+1$ (dependent variable). In measurements where the observed frequency of one success class was small (<4, i.e. number of offspring alive at weaning, and number of offspring alive at autumn), I pooled the small frequency with that in the next largest category. For example, when comparing litter size of females from one year to the next, I pooled those females with litters of 1 and 2 offspring.

Contingency table analyses (*G* tests) were used to determine whether the degree of reproductive success a female exhibited in one year influenced her likelihood of surviving to the following spring. Separate tests were conducted within each of the five measurements of success.

Relative mass loss (RML) was used as a measure of reproductive effort. Two measurements of RML were calculated, that due to parturition (RML_P) and that experienced during the nursing period of nestlings (RML_N). The former was calculated using the maximum prepartum body mass measured (≤3 days before parturition), and the minimum postpartum body mass measured (≤3 days following parturition). Relative mass loss due to nursing was based on the postpartum body mass, and the mass of the female at the time of offspring emergence. To avoid problems stemming from the use of ratio data (Shine 1980), I obtained residuals from the regressions of absolute body mass loss due to parturition (prepartum body mass - postpartum body mass) versus postpartum body mass. Differences in the residuals between litter sizes and years were then compared using ANOVA. Logistic regression and ANOVA were used to test if survival (Yes or No) was influenced by reproductive effort at parturition (residuals).

Pearson's correlation coefficients were first used to investigate relationships between reproductive success and the potential correlates. Because the values of reproductive success ranged over a small number of discrete integers (0 - 4), Spearman's rank correlation was used to verify the results of the Pearson's correlation. I also used logistic regression and ANOVA (parametric and non-parametric) to corroborate these initial analyses. To determine if success (dependent variable) was influenced by the potential correlates (independent variables), simple logistic regressions were first run, using only one of the potential correlates at a time.

If an independent variable was found to have a significant effect, other significant independent variables and interactions were then added to the model to test their significance. In situations where strong correlation existed between two variables (e.g. prepartum and postpartum body masses), I entered only one of the two variables into the logistic regression model. If this variable was found to make a significant contribution to the model the second variable was added to test if it increased the overall significance.

RESULTS

GENERAL TRENDS

Year effects: Litter sizes at parturition ranged from one to four offspring during each year of the study (X=2.81, SE=0.069, n=119); the mode of three was consistent across years. The frequency distributions of litter sizes was not significantly different between years (G=12.28, df=9, P=0.198, n=119). Further, the relative proportions of mothers having zero, one, two, three or four offspring alive at time of emergence, age 80 days, autumn and spring did not differ between years (G tests, all P>0.16). By weaning, most females had ≤1 offspring alive, and only 18 of 106 females (all years combined) had offspring survive to the following spring (Fig. 2.1).

Previous breeding history and reproductive success: A female's reproductive success in year x did not influence her success in year $x + 1$, in all five measurements of success (logistic regressions, all P>0.20, n=48). When a female's success did change from one year to the next, there was no tendency for the change to be in a positive or negative direction (Wilcoxon signed-paired tests, all P>0.13). This pattern also was seen within the subset of females in which I was certain that it was the first and second litters that were produced (all P>0.625, n=20). Similar tests comparing the success of 9 mothers in their third and last year of breeding (prior to death during winter) to their success in their first year also revealed no significant changes (Wilcoxon tests, all $P>0.65$). Because of the lack of year, experience and individual effects on reproductive success, I pooled my measurements of the reproductive success of all females from all years (*seq*. Waser and Jones, 1991).

LITTER SIZE AND SUBSEQUENT REPRODUCTIVE SUCCESS

Approximately 25% of all mothers failed to have any offspring emerge from their nests, while 36% had only a portion of their initial litter survive to emergence. The remaining 39% of the mothers managed to have all of their young emerge from the nest. The relative proportions of mothers in these three categories did not differ between litter size classes ($G=6.27$, $df=4$, $P=0.179$, litter sizes of 1 removed from analysis - Fig. 2.2).

Litter size at parturition and year had no significant effect on age of litter mates at emergence (ANOVA, all Ps > 0.57, $n=68$). The relationship between offspring body mass and age changes between years (Boutin and Larsen *in press*), but within years, litter size at parturition had no effect on mean body mass of litter mates at time of emergence (ANOVA: all Ps > 0.35).

Litter size was directly correlated with the number of offspring reaching emergence, age 80 days and autumn (Table 2.1). Nonparametric ANOVA (Kruskal-Wallace) also indicated highly significant differences between litter size classes in the number of offspring emerging ($chi^2=6.29$, $df=3$, $P<0.001$), but differences in the number of offspring reaching age 80, autumn and spring were increasing less significant (Ps = 0.098, 0.139, 0.678, respectively). Regardless of statistical significance, trends towards females in the larger litter size classes having greater mean reproductive success were present in all years (Fig. 2.3).

The reproductive success of females in year *x* did not have affect the likelihood of females surviving to the following spring (year $x+1$) (all measurements of success, all *P*s > 0.11, $n \geq 106$).

RELATIONSHIPS AMONG POTENTIAL CORRELATES

Not surprisingly, measurements of prepartum body mass, postpartum body mass, and mass at offspring emergence were all significantly correlated (Table 2.2). Parturition date (rank) was significantly correlated with both prepartum body mass, RML_p, and mass at offspring emergence (Table 2.2). This correlation indicates that heavier mothers gave birth relatively earlier in the year.

The mean area of 50 territories belonging to mothers was 0.65 ha (*SE*=0.044, *range*= 0.27 - 2.36). Territory area was inversely correlated with measurements of female body mass, suggesting females with larger territories may have had relatively lower body mass. A strong indirect correlation also occured between mean DBH and number of trees surrounding the middens (Table 2.2). This relationship was expected, as natural spacing patterns of trees generally result in trees with larger DBH being less crowded (Davis and Johnson 1987).

REPRODUCTIVE EFFORT AND SURVIVAL

Females averaged a 14.2% loss of their body mass at parturition (*SD*=0.041, *n*=84). Measurements of RML_p did not differ between litter size classes or year (Table 2.3).

Further, RML_P did not influence mothers' survival to autumn or spring (logistic regression, both Ps > 0.15; similar results achieved with ANOVA).

Following parturition, females on average gained 3.2% of their postpartum body mass by the time their offspring emerged (SD=0.059, n=77). Measurements of RML_N did not differ between litter size classes, although there was a year effect (Table 2.3). However, this effect was due to one 'outlier' female in the relatively small 1988 dataset (N=7, compared to 19, 24 and 27 for the following years). This female lost 41 g (16% of her body mass) during the time her offspring were in the nest and did not survive to autumn. When this female was omitted from the dataset the year effect was nonsignificant.

The relationship between a mother's own survival and her litter size was unclear during the study. Whether or not a mother survived to autumn was related only to her litter size during 1991 (G=11.22, df=2, P=0.004; Ps in all other years > 0.18), when mothers bearing three offspring had disproportionately lower survival. Survival to spring was related to litter size in 1989 (G=6.16, df=2, P=0.046) and 1991 (G=10.10, df=2, P=0.006, [illegible] other years >0.19). In 1989 mothers with litters of one and two offspring had relatively higher survival to spring, while in 1991 mothers bearing three offspring incurred the greatest proportional mortality.

REPRODUCTIVE SUCCESS AND POTENTIAL CORRELATES

Litter size: Litter size was not significantly correlated with the prepartum and postpartum body mass of the mother, but it was directly related to RML_P and to body mass at offspring emergence (Table 2.4). i.e. litter size was higher in females with relatively low RML_P, and in females that weighed more at the time of offspring emergence. Mean body mass of mothers at time of offspring emergence was 231.6 g (*SE*=1.77, *n*=92).

Logistic regression also indicated a significant relationship between litter size, $\mathrm{RML_P}$ and body mass at offspring emergence (*G*=11.87, *df*=2, *P*=0.003). ANOVA (nonparametric and parametric) also indicated that these measurements were significantly different between litter size classes ($\mathrm{RML_P}$: chi^2=11.92, *df*=2, *P*=0.003; body mass at emergence: *F*=2.44, *df*=3,88, *P*=0.069)

Number of emergent offspring: Simple correlation analysis revealed no strong relationships between the number of offspring emerging from a female's nest, and any of the potential correlates (Table 2.4). Body mass of mothers at offspring emergence appeared to be the variable best correlated with success at this level, but only at *P*=0.07 (Table 2.4). Logistic regression analysis indicated that the number of pine trees was the variable which best explained the number of emergent offspring, but the relationship also was not statistically significant (*G*=2.96, *df*=1, *P*=0.085). The only statistically significant relationship was that indicated by ANOVA, where the number of emergent offspring was related to prepartum body mass (*F*=2.87, *df*=4,79, *P*=0.028).

Number of offspring surviving to age 80 days: Both mean pine DBH and body mass at offspring emergence were correlated (positively and negatively, respectively) with the number of offspring surviving to age 80 days (Table 2.4). Logistic regression also indicated that these two variables were significantly related to this measurement of reproductive success (*G*=14.08, *df*=2, *P*<0.001 and *F*). ANOVA suggested mean pine DBH was important (*F*=3.53, *df*3,72, *P*=0.019, *n*=75) more so than body mass (*F*=2.22, *df*=3,88, *P*=0.092, *n*=92).

These statistical analyses indicated that mothers that weighed relatively more at offspring emergence tended to have more offspring surviving to age 80, as did females with relatively smaller trees on their territories.

Number of offspring surviving to autumn and spring: The number of offspring a female had surviving to autumn was not significantly related to any of the potential correlates (Table 2.4). However, logistic regression did suggest mean pine DBH was related to the number of offspring surviving to autumn ($G=5.41$, $df=1$, $P=0.020$); again, a lower mean DBH seemed to confer increased survival of offspring. Nonparametric ANOVA showed no significant relationship between the number of offspring surviving to fall and pine DBH ($chi^2=2.87$, $df=2$, $P=0.238$).

A similar pattern was seen when considering the number of offspring each female had surviving to spring. Pine DBH was again found to be a significant covariate in the logistic regression ($G=4.55$, $df=1$, $P=0.032$). This model correctly predicted 33 of 76 observations. Nonparametric ANOVA did not corroborate this relationship ($chi^2=1.38$, $df=2$, $P=0.502$).

Summary: Table 2.5 summarizes the aforementioned cases where one or more measurements were found to be significantly associated with a change in the reproductive success of the mothers.

DISCUSSION

I found no evidence to suggest year or experience had a bearing on the reproductive success of the mothers. On average, success of mothers within a given year appeared primarily dependent on initial litter size, with the largest litters being the most successful. Further, my correlational tests revealed no costs of reproduction associated with changes in litter size: mothers bearing relatively larger litters did not exhibit greater relative mass loss at parturition, and there was no significant differences in nestling mortality, or the age and size of offspring at emergence. Reproductive effort and success did not appear to influence the survival of the mothers, nor postpartum reproductive success.

My results support the experimental tests of Lack's (1947) hypothesis regarding the evolution of clutch (litter) size. These tests have suggested that the mean number of offspring seen in a population may be less than the most productive number (see review by Lessells 1991). Although controversy over the costs of reproduction exist (see Reznick 1992), theory and evidence indicates that individual parents produce an optimum number of offspring; this number is influenced by the costs of reproduction (both immediate and future) to the parent(s), and the fitness of the individual offspring (Partridge 1989, Lessels 1991). In this red squirrel population, litter sizes of four appeared to present the best opportunity for reproductive success in the population, yet most mother squirrels produced three or fewer offspring. Observed litter sizes likely represent the optimum number for each particular mother in each particular reproductive episode, as suggested by manipulative studies on clutch sizes in birds (e.g. Pettifor *et al.*).

Correlational tests using sparrow hawks (Newton 1988) and collared flycatchers (Gustaffson and Sutherland 1988) found no relationship between reproductive effort/success and future costs, as did a study of bighorn sheep (Festa-Bianchet 1989). However, most correlational studies of avian reproduction have shown costs are directly related to increased clutch sizes (Partridge 1989). Recently, Waser and Jones (1991) found no evidence of a cost to reproduction in kangaroo rats, both in terms of survival and future fecundity. Hare and Murie (1992) also failed to show a cost of reproduction through litter size manipulations of Columbian ground squirrels. Price (1989) studied a population of red squirrels in the Yukon, and showed that females reproducing relatively early in the year exhibited greater weight loss, and suggested this increased the risk of losing the territory. Murie and Dobson (1987) and Michener and Locklear (1990) found no relationship between costs of reproduction and litter size in two species of ground squirrels. Michener (1989) also found age and maternal mass to be poor correlates of litter size (and litter mass). Festa-Bianchet and King (1991) found maternal survival in a ground squirrel population to be indirectly related to litter size only during a period of population decline.

Even if the individual mother red squirrels were optimizing their litter sizes, one or more factors must have been responsible for the variation in litter sizes I observed. In other words, why do reproductive optima differ between individual mothers? Although I observed no instances of litters greater than four during this study, there are cases where females from the Fort Assiniboine population have produced five offspring (see Discussion in Chapter 4). Clearly, most if not all of the litters born to mothers in this study were limited in some fashion. Body mass of mothers, particularly at offspring emergence, appeared to be the variable best correlated with reproductive success to the point where offspring reached 80 days of age (≈weaning). Body mass at offspring emergence may have been a good indication of relative body condition, more so than the prepartum or postpartum measurements. Body mass early in the spring is a good indication of whether female red squirrels enter estrous (Becker 1992), and litter size may also be determined then.

Body mass at emergence likely reflected a mother's ability to nurse offspring during the nesting stage. Kenagy *et al.* 1990 found that female golden-mantled ground squirrels with larger litter sizes had higher energy expenditure, and because growth of juveniles prior to weaning was independent of litter size, they suggested milk production must increase in relation to litter size. Although I did not directly measure energy expenditure, the data on the body mass of mothers and the similar growth rates of nestlings does suggest all of the mothers were allocating similar relative proportions of energy to offspring rearing. Interestingly, *Tamiasciurus* females have an extremely high body mass to litter size ratio, especially when compared to other temperate zone mammals (May and Rubenstein 1984), and arboreal squirrels are known to be able to nurse two litters simultaneously (Gilbert 1986). Thus, lactational demands would not be expected to be overly high relative to energy intake. Experimental work will be required to address this question.

Once offspring emerged from the nest, their survival would have been influenced less by maternal phenotype. Emergent offspring used the natal territory as a base from which to conduct forays for vacant territories (Chapter 5). Risk of predation increased significantly when offspring were off of the natal territory, and approximately half of all offspring were killed by predators, usually raptors, before they were able to acquire a territory (Chapter 5). When offspring did obtain a territory, it was usually located on or next to the mother's territory, but predation continued to be the major source of mortality among these offspring (Chapter 5). Mean DBH measurements of trees is a good index of tree density not only around the natal midden, but also in the general vicinity of the natal territory. Higher tree density may impart lower risk of predation, making mean DBH inversely related to reproductive success of mothers following offspring emergence. Patton (1975) reported that tree characteristics (density, diameter and grouped distribution) were important components of nest cover for the Abert squirrel.

Ostfeld *et al.* (1988) and Ribble (1992) found no relationship between home range size and reproductive success in two species of small mammals. In avian studies, larger territories have been shown to be directly correlated with parental success. However, in these studies, increases in offspring numbers occured through increased hatching and fledging success, and greater likelihood of laying a second clutch, rather than increases in clutch size (e.g. McCleery and Perrins 1985). Oring *et al.* (1991) found that territory size of female sandpipers varied with breeder density, and probably habitat quality, making it difficult to interpret its direct correlation with reproductive success. Vehrencamp *et al.* (1988) found a correlation existed between territory size and reproductive success in groove-billed anis, but they felt territory quality (i.e. tree cover) was the important underlying factor, because of the protection it afforded. A similar situation appears to exist in the Fort Assiniboine squirrel population, where territory size *per se* is not correlated with the reproductive success of mothers. Territory area, unlike tree density and DBH, was remarkably consistent throughout the study area, and it appeared regulated by some factor other than tree density, and perhaps food availability (see Chapter 3). Female red squirrels, including unsuccessful mothers, do not change the size of their territory area in response to neighbour removals (Boutin and Schweiger 1988; Chapter 5). In fact, inclusion of wintering and hoarding sites, rather than size, may be a more important determinant of reproductive success, because mothers will adjust the perimeter of their territory to encompass middens from neighbouring territories (Smith 1968, Chapter 5).

Parturition date was not significantly correlated with reproductive success. However, it was correlated with female body mass at offspring emergence, which was in turn related to reproductive success. King *et al.* (1991) found that annual reproductive success of female Columbian ground squirrels was related to their body weight at emergence from hibernation. In red squirrels, larger females come into estrous earlier (Becker 1992) and have greater reproductive success, at least up to offspring emergence (this study). Hence, failure of early litters would not likely be due to an inability to nurse the offspring. Nests (arboreal and subterranean) likely provide suitable protection from the relatively short bouts of inclement weather in the early spring. In birds, late clutches are often relatively small, with lower hatching and fledging success (see Hochachka 1990 and Perdeck and Cave 1992 for examples). Some of this effect is due to younger individuals laying later and producing fewer offspring. Many bird species re-establish territories prior to each breeding period, so inferior/younger individuals may obtain inferior territories, relatively late in the season. Thus, differential territory quality and/or individual quality may contribute to a seasonal decline in these species, but that is not clear (Hochachka 1990). Analogous effects, if they exist, would not have been accentuated in the Fort Assiniboine squirrel population, because individuals maintained territories year round, and because age and experience had no apparent influence on reproductive success. Clutton-Brock (1982) found red deer calves born relatively late suffered greater winter mortality, likely due to their lighter body mass at the beginning of winter. Even those red squirrel offspring born late in each year's cohort are able to reach near-adult body mass by early winter (Boutin and Larsen *in press*), making parturition date an unlikely correlate of survival.

Sciurids demonstrate a wide range of social and mating systems, and the territoriality and promiscuity of northern populations of *Tamiasciurus* represent one extreme (Heaney 1984). Therefore, it may be expected that an equally wide range of factors influencing reproductive success may exist. Armitage (1991) demonstrated that in the group-living yellow-bellied marmot, individual female success decreased as group size increased, a phenomenon also reported in prairie dogs (Hoogland 1981) and voles (Boyce and Boyce 1988) (but see Festa-Bianchet and King 1991). Habitat and year also affected the success of the female marmots. Still, Armitage (1991) concluded that the principal causes of variation in female reproductive success were unexplained differences among individuals. These differences may have been caused by social behavior, such as reproductive inhibition (Armitage 1989). Obviously, group effects will be relatively unimportant in non-gregarious species such as *Tamiasciurus*, particularly in areas where only one litter is produced per year.

Wauters and Dhondt (1989) studied female reproductive success in two populations of the European red squirrel (genus *Sciurus*). In both coniferous and deciduous habitats, body mass during lactation was a good predictor of the number of offspring emerging from the females' nests. This result is comparable to my finding that body mass at offspring emergence was related to early measures of reproductive success in female *Tamiasciurus*. However, females in Wauters and Dhondt's study populations maintained overlapping home ranges, and females with high dominance rank weighed significantly more than low-rank females. Higher ranking females were able to use areas with better food reserves, hence their heavier body masses. This relationship was not as obvious in this study: while on their respective territories, female *Tamiasciurus* are not subordinate to other conspecifics, male or female. Females tend to remain on essentially the same territory throughout life, and if differential habitat quality did affect reproductive success, then one may expect to see differences in territory area, or unsuccessful females moving to new territories when given the opportunity. Neither of these expectations have been seen (this study and Chapter 5).

Although my measurements of habitat quality in this study were not correlated with reproductive success prior to offspring emergence, food manipulations do affect litter size (Chapter 4). It will be difficult to separate effects stemming from habitat quality and individual foraging efficiency.

Identifying the correlates of reproductive success (or lack thereof) is only the first step in understanding individual variation. Experiments, particularly manipulations, are necessary to determine causation. Phenotypic effects of body mass can be tested through food addition and deprivation, at varying points in the reproductive cycle (Boutin and Larsen, in press). Unfortunately, controlling other factors, such as tree densities or size, will prove more difficult. Moreover, isolating the causes of variation in reproductive success (assuming they exist) may prove very difficult, if not impossible, in a system where predation is a major and perhaps unpredictable source of both adult and offspring survival. Any potential effect on reproductive success by parental or environmental characteristics likely will be masked, if not nullified, by the extremely high rate of offspring mortality due to predation (Chapter 5).

It may also be unlikely that patterns in lifetime reproductive success will become evident in animals, such as red squirrels, which have very short breeding histories. In long-lived species which breed more frequently, parental and environmental effects on reproductive success should be more obvious over the prolonged period of time (e.g. Clutton-Brock 1988, Newton 1989). In those cases, unpredictable events such as predation or inclement weather will play a minor role. Conversely, the most significant contributor to variation in individual reproductive success in animals such as red squirrels may be perturbations in the environment, such as severe weather conditions or large-scale changes in resource availability (e.g. Festa-Bianchet and

King 1991, King *et al.* 1991). These major events may suppress or magnify reproductive success in one particular breeding episode. During the four years of this study, the high adult survival may have made it abnormally difficult for offspring to obtain territories, and seasonal weather patterns were not unusually harsh (Chapter 1). Squirrel populations in forests more prone to dramatic fluctuations in mast crop (e.g. spruce - Rusch and Reeder 1978) may be expected to show more drastic fluctuation in reproductive success.

What the results of this study indicate is that the measured characteristics of the females had little long-term effect on reproductive success. Body mass near or at the time of parturition is correlated with litter size, but the ultimate factors responsible for variation in litter size is not clear. Further, larger litter sizes alone do not ensure relatively higher numbers of surviving offspring, suggesting factors that influence the survival of offspring after parturition may play a major role in determining reproductive success.

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	LITTER SIZE	NO. EMERGE	NO. AGE 80	NO. AUTUMN
NO. EMERGE	0.48* <0.001 106			
NO. AGE 80	0.27* 0.006 106	0.59* <0.001 106		
NO. AUTUMN	0.23* 0.017 106	0.53* <0.001 106	0.86* <0.001 106	
NO. SPRING	0.09 0.344 106	0.28* 0.003 106	0.54* <0.001 106	0.55* <0.001 106

TABLE 2.1. Correlation matrix showing relationships among measurements of reproductive success. For each pair combination, Pearson correlation coefficients are given, with their respective probability values and sample sizes appearing below them. Statistical significance at $P \leq 0.05$ is indicated by an asterisk (*). Litter size at parturition was correlated with number of offspring emerging from nest (NO. EMERGE), reaching 80 days of age (NO. AGE 80) and surviving to autumn (NO. AUTUMN). By spring (NO. SPRING) the relationship was no longer evident.

	PART RANK	PRE MASS	POST MASS	RML_P	EMER MASS	RML_N	AREA	NO. PINE
PRE MASS	-0.09 0.425 84							
POST MASS	0.03 0.809 84	0.88* <0.001 84						
RML_P	-0.23* 0.036 84	0.56* <0.001 84	0.09 0.412 84					
EMER MASS	-0.14 0.175 92	0.51* <0.001 77	0.63* <0.001 77	-0.01 0.957 77				
RML_N	-0.12 0.301 77	-0.70* <0.001 77	-0.76* <0.001 77	-0.16 0.154 77	0.02 0.876 77			
AREA	0.34* 0.009 57	-0.31* 0.018 57	-0.32* 0.014 57	-0.03 0.813 57	-0.32 0.021 53	0.14 0.299 53		
NO. PINE	0.13 0.244 79	0.24* 0.05 63	0.09 0.482 63	0.37* 0.003 63	-0.01 0.965 68	-0.12 0.356 58	0.14 0.372 45	
DBH PINE	0.05 0.639 76	-0.29* 0.023 60	-0.16 0.222 60	-0.35* 0.007 60	<-0.01 0.998 65	0.19 0.166 55	-0.15 0.330 43	-0.68* <0.001 76

TABLE 2.2. Correlation matrix showing relationships among potential correlates of reproductive success in female squirrels. Pearson correlation coefficients are given, with their respective probability values and sample sizes appearing below them. Statistical significance at $P \leq 0.05$ is indicated by an asterisk (*). Abbreviations: PART RANK - rank of parturition date within year, PRE MASS - prepartum body mass, POST MASS - postpartum body mass, RML_P - relative mass loss due to parturition, EMER MASS - body mass at time of offspring emergence, RML_N - relative mass loss due to lactation, AREA - area of territory (h), NO. PINE - number of pine with sample quadrats, DBH PINE - mean DBH of pine tree sampled.

RML_P

Source	*DF*	Type III SS	*F*	*P*
LITSIZE	3	868.62	3.04	0.093
YEAR	3	255.08	0.89	0.487
LITSIZE*YEAR	8	761.97	1.39	0.216
ERROR	69	4723.82		

RML_N

Source	*DF*	Type III SS	*F*	*P*
LITSIZE	3	527.17	2.28	0.156
YEAR	3	1031.63	4.46	0.040
LITSIZE*YEAR	8	616.37	0.56	0.803
ERROR	62	8450.06		

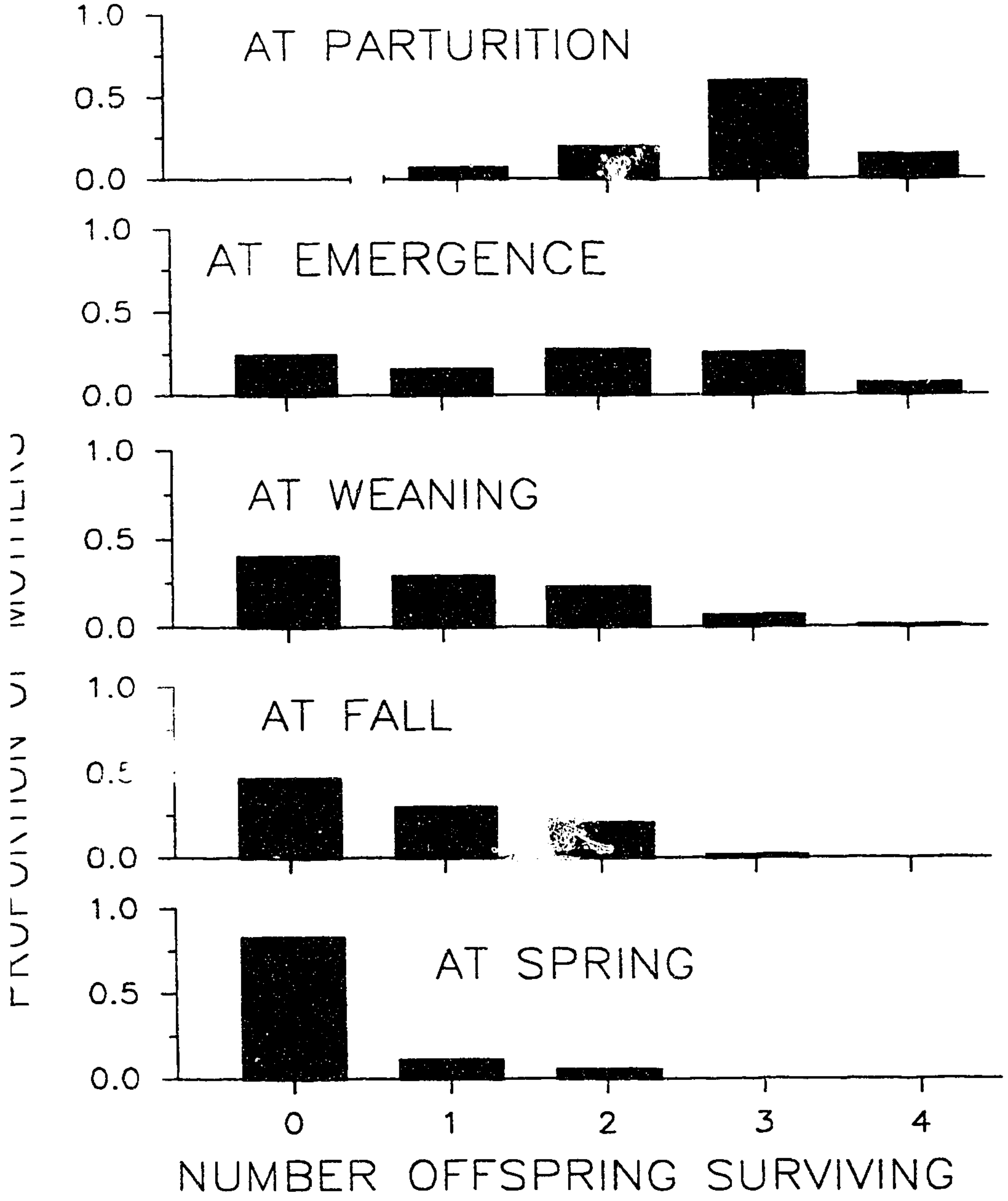
TABLE 2.3. ANOVA (Model II) summary tables for tests of year and litter size effects on reproductive effort in female red squirrels. Two measurements of reproductive effort were used, RML_P (weight loss due to parturition) and RML_N (weight gained during the time offspring were in the nest). See text for details on methods of calculations. Year effects were apparent in measurements of RML_N, otherwise no significant effects were observed.

	LITTER SIZE	NO. EMER	NO. AGE 80	NO. AUTUMN	NO. SPRING
PART RANK	0.05	-0.14	-0.13	<0.01	-0.05
	0.615	0.150	0.189	0.975	0.617
	106	106	106	106	106
PRE MASS	0.16	0.19	0.074	-0.03	0.10
	0.143	0.084	0.505	0.782	0.361
	84	84	84	84	84
POST MASS	0.04	0.13	0.07	-0.01	0.05
	0.691	0.249	0.552	0.949	0.645
	84	84	84	84	84
RML_P	0.26*	0.17	0.04	-0.05	0.12
	0.018	0.115	0.724	0.643	0.273
	84	84	84	84	84
EMER MASS	0.24*	0.19	0.25*	0.17	0.06
	0.019	0.071	0.019	0.114	0.545
	92	92	92	92	92
RML_N	0.17	<-0.01	0.04	0.07	<0.01
	0.140	0.985	0.714	0.538	0.953
	77	77	77	77	77
AREA	-0.01	-0.08	-0.05	-0.05	-0.04
	0.939	0.564	0.719	0.722	0.768
	57	57	57	57	57
NO. PINE	0.018	0.19	0.12	0.04	-0.03
	0.875	0.083	0.306	0.723	0.821
	79	79	79	79	79
DBH PINE	-0.09	-0.17	-0.35*	-0.19	-0.13
	0.419	0.150	0.002	0.109	0.282
	76	76	76	76	76

TABLE 2.4. Correlation matrix showing relationships between measurements of reproductive success in female squirrels (top row) and potential correlates (column on left). Pearson correlation coefficients are given, with their respective probability values and sample sizes appearing below them. Statistical significance at $P \leq 0.05$ is indicated by an asterisk (*). For key to abbreviations of reproductive success measurements and potential correlates, see captions for Figures 2.1 and 2.2, respectively.

MEASUREMENT OF RS (number offspring surviving to...)	CORRELATES		
	Pearson's *R*	logistic regression	ANOVA
parturition (litter size)	emerge. mass (+) RML_P (+)	emerge. mass (+) RML_P (+)	emerge. mass (+) RML_P (+)
emergence	*none*	*none*	prepart. mass (+)
age 80 days (≈weaning)	emerge. mass (+) pine DBH (-)	emerge. mass (+) pine DBH (-)	emerge. mass (+) pine DBH (-)
autumn	*none*	pine DBH (-)	*none*
spring	*none*	pine DBH (-)	*none*

TABLE 2.5. Summary of correlates ($P \leq 0.05$) in five measurements of reproductive success measured in female red squirrels, as determined by three different statistical tests. Direct and indirect relationships are indicated by + and - signs, respectively. Nonparametric ANOVA was used if data did not satisfy assumptions of parametric test. Precise *P* values and description of statistical tests appear in text.



E 2.1 Relative proportions of mother red squirrels having various numbers of ng alive at five measurements of reproductive success: parturition (initial litter offspring emergence from nest, age 80 days of offspring (≈weaning), autumn gust) and spring (15 April). N=119 for parturition data; n=106 for all other ements of success.

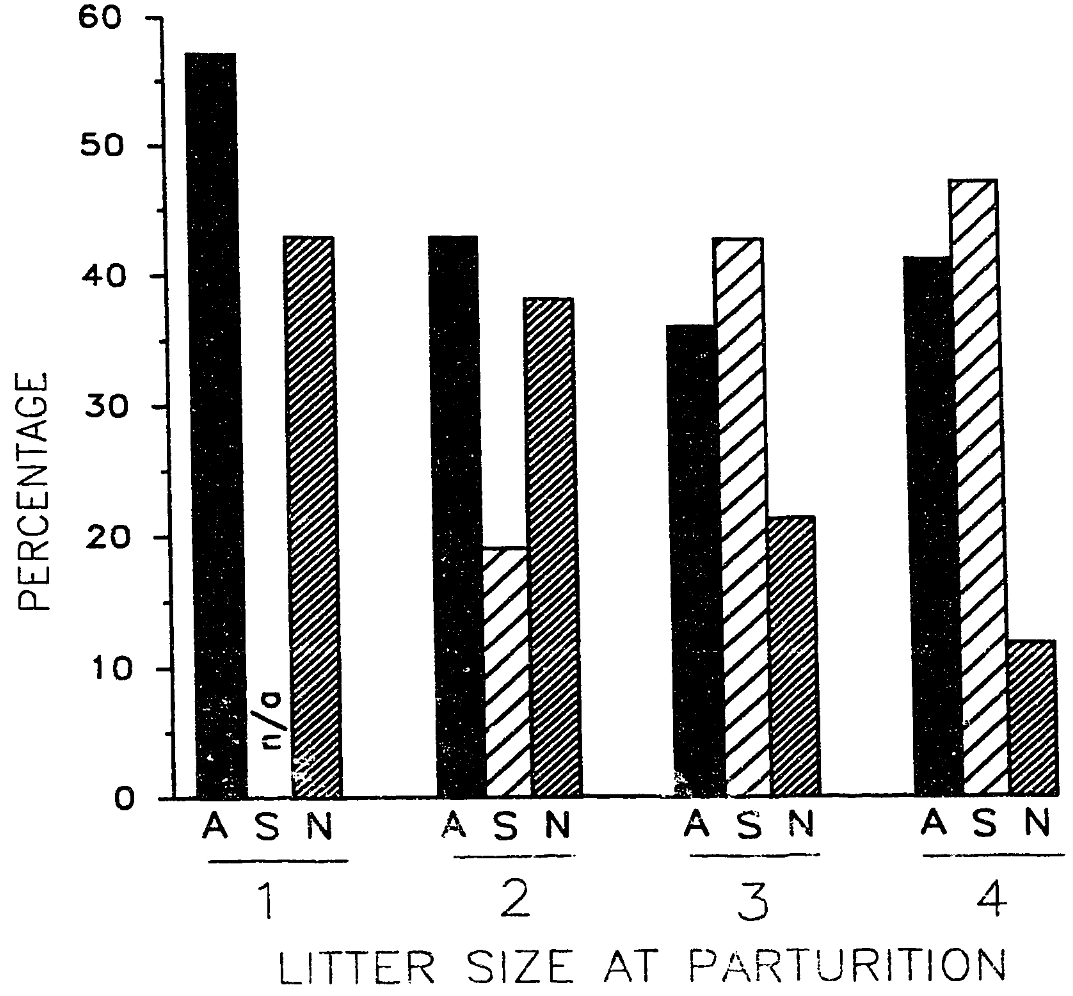


FIGURE 2.2. Proportions of offspring emerging from nests of mothers with different initial litter sizes. Categories shown for each litter size class are All offspring emerging, Some offspring emerging, and No offspring emerging. Note that litter sizes of one (1) can only be placed into A and N categories. Sample sizes for litter sizes 1 to 4 are 7, 21, 61 and 17, respectively.

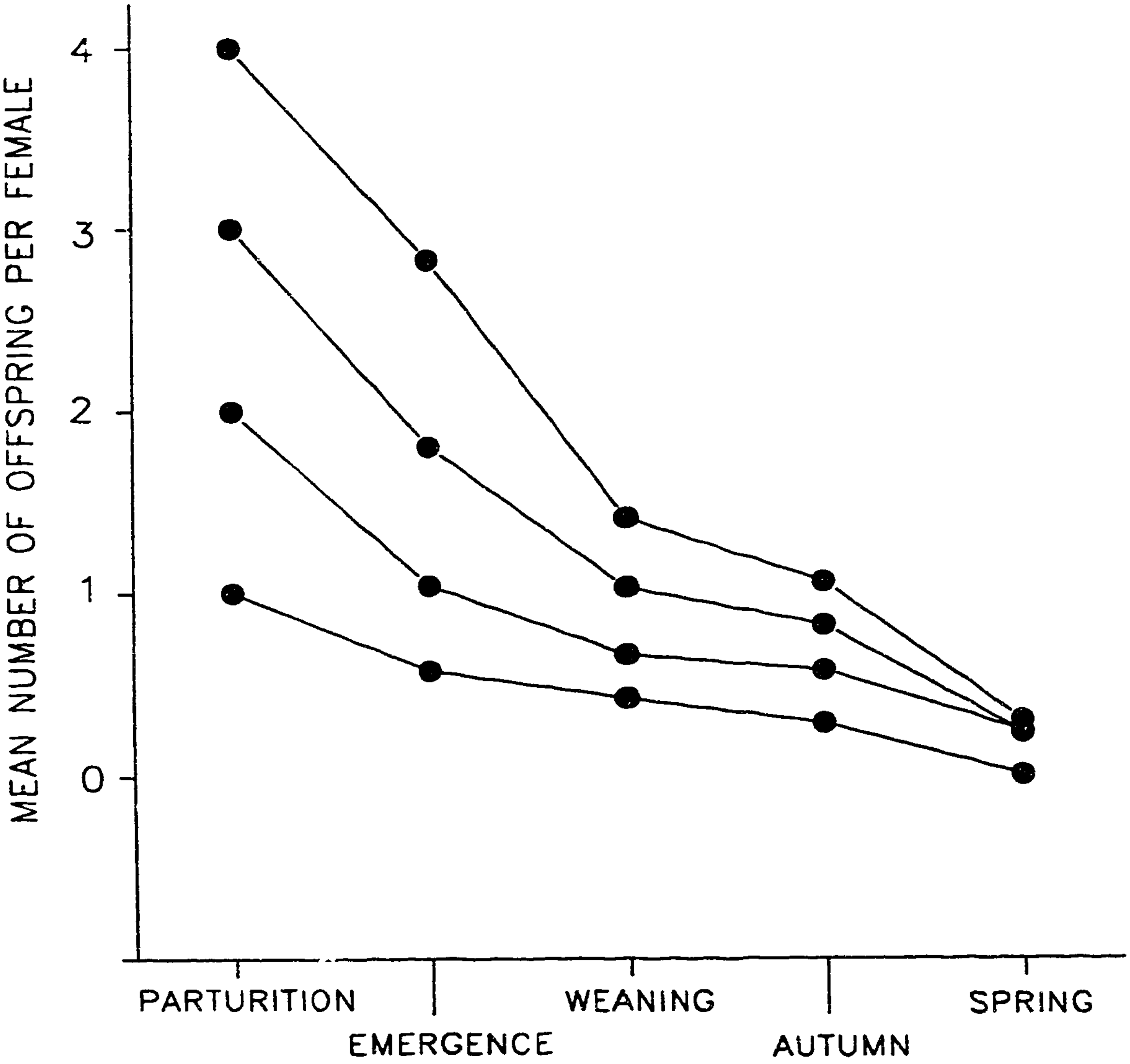


FIGURE 2.3. Relative reproductive success of females bearing different litter sizes, measured at five different stages. Mean reproductive success is given as average number of offspring alive per mother in each litter size class. The four lines represent mothers bearing the four different litter sizes. Sample sizes for the litter sizes 1 to 4 are 7, 21, 61 and 17, respectively.

CHAPTER 3

EFFECTS OF WINTER HOARD MANIPULATION ON THE REPRODUCTIVE SUCCESS OF FEMALE RED SQUIRRELS

INTRODUCTION

The relationship between food abundance and reproductive success has long been of interest to reproductive ecologists (see review by Martin 1987). Although traditional thinking has been that food limits reproductive success, the data supporting this contention are equivocal. For example, Boutin (1990) reviewed the food-addition literature and found that only 4 of 13 avian studies recorded an increase in clutch size following food addition (see also Marjakangas and Aspegren 1991, Hiom *et al.* 1991). Although studies involving mammals were, Boutin found that five of eight such studies reported an increase in litter size following food addition. Boutin alluded to the greater difficulty in determining litter sizes in mammals than, say, measuring clutch size in birds. Even more difficult is documenting the survival of offspring after they become independent of the parents (a problem also faced in studies of birds - Martin 1987). These obstacles contribute to the general shortage of studies on the reproductive success of mammals (see Chapter 1), much less those seeking to examine the effects of supplemental food.

The difficulty in targeting specific individuals with food additions has meant that most such studies have operated at the population level (see Table 1 in Boutin 1990). One way to circumvent this problem is to focus on species that maintain individual food caches, or hoards. Many vertebrates, particularly mammals, depend on cached food to sustain them through periods of resource shortages (Vander Wall 1990). Potentially, such caches could act as a proximate influence on the reproductive success of females, but this will vary with life-history attributes and timing of reproduction. In species where mating and conception take place during or shortly after a [illegible] of resource shortage (e.g. winter, or a dry season), the degree to which females can maintain critical or optimal body mass (and fertility - see Bronson 1989) may depend to a large extent on the food cache. Koenig and Mumme (1987) found that woodpeckers that had not exhausted their cached food (acorns) by spring had relatively larger clutches. Korpimäki (1989) demonstrated that owls with supplemented caches laid more eggs, and Yosef and Pinshow (1989) found that male shrikes with artificially increased caches appeared to father more clutches.

Arboreal squirrels afford good opportunity to investigate the influence of cached food on the reproductive success of females. First, the reproductive success of individual females, including litter size and offspring survival, may be readily ascertained (Chapter 2). Second, many populations of squirrels larderhoard their food in large, obvious piles, making the cache quite tractable. In Alberta, red squirrels (*Tamiasciurus hudsonicus*) maintain individual, non-overlapping territories year-round, and in autumn each individual larderhoards conifer cones at a central location on its territory, the midden. Midden sites are highly traditional, being used without interruption by successive territory occupants, which in turn generates sizable accumulations of cone bracts and rachii (pers. obs.). During winter, the squirrels spend proportionately more time in nests in the midden, emerging to forage in nearby trees only when relatively mild temperatures occur (*v. et.* Pruitt and Lucier 1958, Zirul 1970). Lair (1985) and Becker (1992) determined that spring body mass of female squirrels influenced several aspects of reproduction, including probability and onset of estrous. Abundant food stores during winter may influence spring body mass, by enabling individuals to spend proportionately more time underground, where thermoregulation is less costly (Pauls 1978, Knee 1983). Spring food levels, including cached items, may also be important in maintaining female body condition during early spring when breeding commences (Lair 1985).

The accessibility of the larderhoard, combined with the solitary, territorial nature of *Tamiasciurus*, makes it possible to manipulate the food resources of *individual* females. This study sought to determine if the reproductive success of individual female red squirrels was limited by the amount of food present in their winter hoard. Both natural (pine cones) and artificial (sunflower seed) food were used to experimentally increase the amount of food available to females during the winter preceding the breeding season. Depletion of hoards were also conducted in one year of the study to test for reverse effects. I also collected information on the proportions of cones cropped by females during the autumn harvest from trees on their respective territories. Finally, I attempted to correlate natural variation in winter hoards with subsequent reproductive success.

METHODS

CONE HOARD ADDITIONS

In late October, 1988, 24 squirrels from the adult female population on the study site (see Chapter 2) were randomly selected to receive additions of cones to their winter hoard. This sample consisted of 20 females (83%) which had given birth to offspring during Summer 1988, and four females (17%) which had not yet reproduced. Jack pine cones were collected from the hoards of squirrels living off the study site, with no more than approximately 2200 cones (two 20-liter buckets) being taken from any one midden. The only cones collected were those on the surface of the middens, or those easily reached in existing tunnels. Cones used for the addition experiments were also obtained from the middens of females selected for cone depletions (see below). On 8 and 9 November, 1988, approximately 4400 cones were added to each of the existing hoards on the middens of the 24 females. Excavated hoards at Fort Assiniboine normally contain 2000 - 4000 cones (Becker 1992, Zimmerling unpubl.), so these manipulations represented at least a 100% increase in hoard size.

On 18 October, 1989, cone additions were conducted on 25 females (14 and 11 reproducing and non-reproducing females, respectively). None of the females selected for cone-additions during this year had experienced hoard manipulations in 1988. Cone additions were conducted earlier in 1989 than in 1988, because the hoarding activity of squirrels in the population commenced and ended earlier in the former (Larsen unpubl.).

CONE HOARD DEPLETIONS

Cone depletions were carried out in conjunction with the 1988 cone additions. Eighteen individuals (15 and 3 previously parous and non-parous females, respectively) had approximately 1100 cones removed from their individual hoards. I set this limit for two reasons, (1) the effect of cone depletions on the overwinter survival of the females was unknown, and (2) collecting more that 1100 cones would have, in some instances, necessitated destruction of the midden and overwintering nests constructed by the squirrels.

SUNFLOWER SEED ADDITIONS

A concurrent study (Becker 1992) on the effect of food availability on the onset and timing of estrous in squirrels provided an opportunity to study the effects of a high net-energy food source on litter size. During Winter 1988/89, and early Spring 1989, sunflower seeds were supplied to 21 individual females by placing a 20-liter bucket containing seeds above or on each midden of the targeted squirrels. The seeds in each bucket were continually replenished as they became depleted until the parturition date of the targeted female, at which point the bucket was removed. Seed additions also were conducted on a different sample of females through Winter 1989/90 and into Spring 1990 (Becker 1992).

The dates at which seed additions commenced, as well as the reproductive status of targeted females, varied both within and between years. For details, see Becker (1992). For the purposes of this study, I consider all seed-addition females to be one experimental group, as effecting this manipulation for even part of a winter provided the targeted females with a food (and energy source) far in excess of that normally experienced (Becker 1992).

Seed addition experiments were conducted in the Athabaska Sand Hills, but at locations separate from my main study site (see Becker 1992).

SURVIVAL AND REPRODUCTIVE SUCCESS OF FEMALES

The winter and summer survival of experimental females was monitored through intensive live-trapping. Prepartum and postpartum body mass, litter size and subsequent reproductive success was determined following the procedures and techniques outlined in Chapter 2.

Winter survival for seed-addition females was available for only 1989-1990 (Becker 1992). Similarly, time and logistical constraints allowed litter sizes to be determined for the seed-addition females, but not subsequent measures of reproductive success.

QUALITATIVE ASSESSMENT OF UNMANIPULATED CONE HOARDS

Zimmerling (unpubl.) has shown that the number of surface cones appearing on a midden in the Fort Assiniboine population could be used to approximate the total number of cones contained in the hoard (surface+subsurface). Thus, an attempt was made to relate unmanipulated hoard sizes to the litter sizes of females in the following spring. On 1 and 2 November, 1988, the middens of all females with unmanipulated cone hoards were visited twice by each of two observers. A score ranging from 0 to 5 was assigned to each cone hoard, based on a qualitative assessment of the number of cones visible (0=no cones visible, 5=a large number of cones visible), and the mean of the four values was used as a qualitative assessment of the hoard size.

The same procedure was conducted in Autumn 1989, but the earlier caching period (Larsen unpubl.) which occured in that year allowed the hoards to be evaluated on 5 and 6 October.

CONE CROP HARVESTING

I attempted to determine the relative number of cones harvested from jack pine trees by squirrels. In early August 1989, prior to harvesting, the territories of five control females (all having reproduced in 1989) were selected randomly, and on these territories, a number of trees were chosen for study. Although an effort was made to randomize tree selection in terms of size (diameter, height, proximity to midden), some trees were chosen over others because they were more suitable for climbing.

When possible, trees unsuitable for climbing (i.e. small diameter, absence of low branches, etc.) were reached from neighbouring trees.

Once trees were scaled, branches (including crown leaders) that were accessible were tagged and numbered for future reference. The cones on each branch were enumerated and classified as being either from the current year's crop (bright green), the previous year's crop (bronze-yellow), or older (grey). In total, 2055 cones were recorded on 220 branches, on 73 trees.

In November 1989, after harvesting by the squirrels had ceased, each tree was reclimbed and the presence or absence of each enumerated cone was determined.

RESULTS

UTILIZATION OF CONE ADDITIONS

Most if not all of the cones supplied to the hoards of females were used by the following spring, as evidenced by the unusually large piles of cone bracts at the precise location of the addition.

WINTER SURVIVAL

Fifteen of the 24 cone-addition females survived the winter of 1988/89 (≈63%), which was not significantly different from either cone-depletion (15/18≈83%) or control (27/34≈79%) females (*G*=2.93, *df*=2, *P*=0.232).

In the following year, 18 of the 25 cone-addition females survived the winter of 1989/90 (=72%). Again, this was not significantly different from survival in the control (31/42=74%) or seed-addition (18/20=90%) groups (*G*=2.86, *df*=2, *P*=0.240).

PROPORTION BEARING OFFSPRING

Although adult females at Fort Assiniboine were not sacrificed for reproductive data, the intense monitoring and repeated recaptures of individual females at Fort Assiniboine did not show any examples of uniparous or multiparous females failing to become impregnated (N=47 control females). Data on changes in body mass and nipple appearance indicated that all uni/multiparous females carried developing offspring through some or all of the 30-day gestation period, although some appeared to abort, or lose their offspring during or immediately after parturition.

Because of this strong trend in the population, it was not surprising that all surviving uniparous and multiparous females in the cone-addition and seed-addition groups bore offspring in the ensuing spring following treatment. The cone-depletion treatment did not have a negative effect in this regard, as all surviving multiparous and uniparous females in that group also produced offspring.

There was no indication that the treatments affected the proportions of nulliparous females which bore offspring, but sample sizes were small in the first year. In Spring 1989, 3 out of 8 nulliparous, control females produced offspring (38%). In the same year, the relative proportions of nulliparous females producing offspring in the treatment groups were 2/3 (cone-addition), 2/3 (cone-depletion), and 7/11 (seed addition) (*G*=3.87, *df*=3, *P*=0.276). In Spring 1990, the relative proportions were 23/39 (control), 7/10 (cone-addition) and 4/8 (seed-addition) (*G*=0.77, *df*=2, *P*=0.680).

PREPARTUM/POSTPARTUM BODY MASS, AND PARTURITION DATE

Prepartum and postpartum body masses of reproducing females did not differ between the control, cone-addition and cone-depletion treatment groups, in both Spring 1989 and Spring 1990 (ANOVAs, all *P*s >0.25 - data in Appendix 2).

Similarly, there was no difference in parturition dates between control, cone-addition and cone-depletion females in 1989 (*Kruskal Wallace* chi^2=1.34, *df*=2, *P*=0.512), nor between control and cone-addition females in 1990 (*normal approximation to Mann-Whitney U*, *Z*=-0.86, *P*=0.389 - data in Appendix 2). Becker (1992) showed that the seed-additions resulted in significantly earlier estrous dates, and consequently earlier parturition (*P*<0.001).

REPRODUCTIVE SUCCESS

Litter sizes

Figures 3.1 and 3.2 illustrate the frequency of litter sizes in the treatment groups, for Spring 1989 and 1990, respectively. Both the cone-addition and seed-addition experiments produced proportionally more litters in the larger size classes (3 and 4) than in the control groups (**1989**: *G*=13.509, *df*=6, *P*=0.036; **1990**: *G*=12.20, *df*=6, *P*=0.058). There was no significant difference between the cone-addition and seed-addition groups themselves (**1989**: *G*=2.64, *df*=2, *P*=0.267; **1990**: *G*=1.58, *df*=2, *P*=0.454). Mean litter sizes for the groups are given in Table 3.1.

No females in the 1989 cone-depletion group produced litters in the largest litter size class (Fig. 3.1). However, the overall distribution of litter sizes in this group was not significantly different from that seen in the 1989 control females (*G*=3.26, *df*=3, *P*=0.353).

Individual females that bore young both before and after a treatment could be classified by whether their respective litter sizes had decreased, remained constant, or increased. Seventy-five percent of the females in the 1988 cone-addition group experienced an increase in their individual litter sizes, as compared to 30% and 33% in the cone-depletion and control groups, but the difference was not statistically significant (*G*=8.34, *df*=4, *P*=0.08, Fig. 3.3). The difference was more marked in the 1989 cone-addition group, where ≈88% of the individuals experienced an increase in litter size, as compared to ≈12% in the control group (*G*=16.87, *df*=2, *P*<0.001, Fig. 3.4).

Other measures of reproductive success

Success at raising a litter can be measured by whether all, some or none of the offspring emerged from the nest (see Fig. 2.2). The relative proportions of females in these three categories was not significantly different between the female groups (**1989** cone-additions, cone-depletions and controls: *G*=1.13, *df*=4, *P*=0.889; **1990** cone-additions and controls: *G*=1.61, *df*=2, *P*=0.447).

Differences in reproductive success between the treatment and control groups were tested more directly, by comparing the relative numbers of offspring alive at various levels of success, namely emergence, age 80 days (≈weaning), autumn and the following spring (see Chapter 2 Methods, and Fig. 2.1). No significant differences were detected between the female groups at any of these four levels of reproductive success (*G* tests, all *P*s >0.11).

SUMMER SURVIVAL OF FEMALES FOLLOWING WEANING

There was no significant difference in the summer survival of females in the experimental and control groups. In 1989, females in the cone-depletion group experienced greater summer survival than the cone-addition or control groups, but the difference was not statistically significant (83%, 71% and 58%, respectively; $G=2.74$, $df=2$, $P=0.255$). During 1990 7/13 cone-addition females survived to autumn, compared to 20/38 control females ($G=0.006$, $df=1$, $P=0.940$).

QUALITATIVE ASSESSMENT OF UNMANIPULATED CONE HOARDS

In 1989, litter size of control females was weakly correlated to the previous autumn's qualitative assessment of the hoard (Pearson's $R=0.42$, $n=19$, $P=0.070$). In 1990, there was no relationship ($R=0.18$, $n=23$, $P=0.404$).

CONE CROPPING

Only 160 of the 2055 cones enumerated in 1989 were harvested by the time the trees were reclimbed, with a strong preference shown for cones from the current year's crop (Fig. 3.5). There was also a significant difference in the proportion of current year's cones cropped between the five territories sampled ($G=18.65$, $df=4$, $P<0.001$). The proportion of current year's cones cropped on any one tree ranged from 6 to 80% (using only trees with >10 cones initially counted), and on three of the territories this variation was significantly different between trees (G tests, all $Ps\leq 0.003$). These data suggest that female squirrels in the Fort Assiniboine population harvest less than half of the year's cone crop available on their territories.

DISCUSSION

The results of this experiment suggest that litter size in the study population may be limited by the size of the mother's cached hoard. However, the effect does not appear to be strong. Although the food additions produced noticeable changes in litter sizes (*P*s=0.036 and 0.058), the increase in average litter size was small. Moreover, the food additions did not seem to confer any other advantages, such as increased survival of the targeted female and/or her offspring. Apparently, females take only a small proportion of the cones available on their territories, which suggests that the size of the hoard is not limited by the number of available cones *per se*, and other factors may be more responsible in determining litter size in this population.

It is not surprising that neither the food addition or depletion experiments produced changes in winter and summer survival. Squirrel populations in spruce habitat (*Picea*) have been observed to remain at normal densities following complete cone crop failures, by relying in some part on cones cached in previous years (Smith 1968, Boutin unpubl.). Pine trees are less susceptible to cone crop fluctuations than spruce, so although population densities in pine habitat may be relatively lower (see Rusch and Reeder 1978), the squirrels inhabiting pine habitat may experience a more consistent food supply. The variation in pine cone production recorded during this study (Fig. 1.2) was minor compared to crop fluctuations seen in spruce, and there was no significant change in litter sizes in control animals from year to year (Chapter 2). Lower population densities in pine are associated with larger individual territories (Obbard 1988). Unlike spruce trees, jack pines retain their cones and seeds indefinitely, providing squirrels with at least some opportunity to feed on older cones, either in the midden or on the trees. Klenner and Krebs (1991) found that the widespread addition of food to a red squirrel population in British Columbia produced a density increase, but did not influence survival. Similarly, Koprowski (1991) found survival of adults squirrels (*Sciurus* spp.) in Kansas to be unaffected by a shortage of staple dietary items. Extremely adverse or prolonged winter conditions would be expected to amplify the effects of food addition or depletion, yet the additions conducted in the first year of the study did not produce strikingly different results from that observed in the second year, despite the fact that the late winter/early Spring of 1989 was colder than in the following year (see Fig. 1.1). In general, it appears that the survival of squirrels (at least adults) is not strongly influenced by normal fluctuations in food, although major crop failures may have a profound effect (Sullivan 1990).

Female squirrels at Fort Assiniboine normally do not begin to breed until at least their second spring, but Becker (1992) showed that the sunflower seed additions described above significantly increased the proportion of juveniles (yearlings) that experienced estrous, as well as the timing of estrous and parturition of all females within the treatment group (*cf.* Loy 1988). Becker's results apparently resulted from the significantly higher spring body weights caused by the seed additions, and mimicked the empirical observations made by Lair (1985). Sullivan and Sullivan (1982) also noted a proportional increase in breeding females following a population-wide food addition, but they lacked data on individual life histories. However, conception, and ultimately parturition, may not occur despite the onset of estrous (Becker 1992). Apparently, the seed and cone treatments did not affect the probability of parturition in nulliparous females, although the sample sizes were small in 1989. If that is true, than body mass *per se* appears to play a role in early spring in determining the incidence and timing of estrous, but does not ensure that the female will develop and carry offspring to parturition.

The high-energy seed addition resulted in earlier estrous and parturition dates (Becker 1992), but neither the seed-additions nor the cone-addition produced large changes in litter size. A similar situation has been reported in many other food addition studies (see review by Boutin 1990, also Marjakangas and Aspegren 1991, Dhindsa and Boag 1990). A long-term food addition to a red squirrel population in British Columbia extended the breeding season, and may have enabled some females to produce a second litter (Sullivan 1990). Why should parturition date be more responsive than litter/clutch size to food availability? Several researchers have equated relatively early parturition dates with increased reproductive success (red squirrels, Price 1989, Gurnell 1983, Rusch and Reeder 1978; birds, Perrins 1970 and Yom-Tov and Hilborn 1981). One may hypothesize that in the Fort Assiniboine population, females with early estrous, parturition and offspring emergence dates should enjoy greater success, because (1) their offspring are more likely to obtain a vacant territory and/or (2) the female will have more time after weaning to regain body condition prior to the autumn harvest. However, I found no relationship between date of parturition and reproductive success (including female survival) within a given year, except that extremely early or late litters often experience zero success due to inclement weather.

If no direct correlation exists between parturition date and reproductive success, it becomes more difficult to invoke an adaptive explanation in this study for why earlier parturition dates resulted from the addition of food (seeds). The timing of parturition for the population as a whole varies considerably from year to year (Chapter 2), so perhaps females respond to yearly differences in spring food availability, lest they give birth too early or late in that particular year. The response in timing of estrous and parturition due to the seed-additions seen in this and Becker's (1992) study may be better explained in terms of an adaptive response to spring food levels in general, rather than an adaptive response to individual hoard size, which would be a produ the previous year. Other studies have shown that different cache levels within populations may have a strong influence on timing of breeding (jays - Balda and Bateman 1973, Ligon 1978 ;owls - Korpimäki 1987, 1989; woodpeckers - Koenig and Mumme 1987; honeybees - Seeley and Visscher 1985). These studies, however, all involved species that initiate breeding and offspring production prior to the availability of non-cached food items. In the red squirrel population at Fort Assiniboine, buds <u>and</u> cones still on the pine trees are available as forage in early spring, which may negate the importance of hoard size in timing of reproduction.

The problem of why the food additions affected the timing of reproduction more than litter size becomes more complex when one considers that, since completion of this study, litters of five offspring have been recorded in the Fort Assiniboine population, under unmanipulated conditions (1992 data, Larsen unpubl.). Also, a pregnant control female which died in 1989 during handling was found to be carrying five well-developed fetuses (Larsen, unpubl.), and one pregnant female brought into captivity gave birth to five live offspring (Becker unpubl.). These observations suggest that during this study, the females at Fort Assiniboine were not producing litters of maximum size, even with the cone and seed additions. Obviously, some factor(s) is more important than simple food abundance in dictating litter size.

Several studies have reported that reproductive performance (age at first reproduction, proportions of breeding females, litter sizes, etc.) increases in the spring preceding a high spruce cone crop (Smith 1968, Kemp and Keith 1970, Kelly 1978). These litter size increases are often of the level of more than 1 offspring/female, a more significant change than that prompted by the food additions in this study.

Because squirrel populations in spruce feed heavily on cone buds in the spring, it was suggested by Kemp and Keith that the females 'anticipated' the forthcoming mast production, and increased their reproductive output accordingly. Obbard (1988) felt that such a response may not represent a true anticipatory mechanism, as the females may simply be responding to increased food supply in the spring. If food levels *per se* dictate litter size, then one would have expected the food addition females (particularly the seed additions) to have demonstrated larger litter sizes than that observed. But, if the anticipatory mechanism relies specifically on some cues unique to buds (be it chemical or otherwise), than the cone and seed additions could not be expected to produce a major response. Becker (1992) considered the potential dietary components of jack pine buds (phytoestrogens, extra protein and extra energy), and how they might cause "anticipatory fertility" (estrous). She concluded that either jack pine buds were considerably different from spruce buds, or something other than a dietary cue was prompting the anticipatory response reported in other studies. Perhaps the relatively low variation in cone crops experienced by females living in jack pine habitat removes the usefulness of an 'anticipatory' mechanism. What is needed to solve this dilemma is simultaneous study of parapatric populations of squirrels in pine and spruce habitat. The research done at Rochester (Kemp and Keith 1970, Rusch and Reeder 1978) involved both types of habitat, but the size of the two areas (5.3 and 7.3 h) may have been too small for habitat-specific tactics to be evident.

Compared to litter size, the postpartum levels of reproductive success measured in this study were even less affected by the hoard manipulations. However, other data suggests that there is no trade-off between litter size and offspring survival in this population (Chapter 2), and although the cone additions did not result in markedly higher litter sizes, they did cause most females to produce one offspring more than in the previous year. Given these conditions, selection in the past should have favoured individuals that hoarded more cones. Why then do individuals still fail to hoard enough cones to 'move' themselves into the next litter size bracket, especially when it appears a surplus of new cones are available each autumn? Age and previous reproductive experience do not influence litter size in this population (Chapter 2), and Zimmerling (unpubl.) excavated a small number of middens, and found no differences in hoard size between multiparous and nulliparous females, also indicating that hoard sizes *per se* do not influence reproductive maturity. These observations suggest there are no ontogenetic changes in individual hoarding capability that might influence reproductive success, but Zimmerling's samples were small (4 and 3, respectively). Similarly, the significant correlation he found between cones on the surface and subsurface of middens was also based on a small sample; this may be part of the reason why this study failed to detect a relationship between surface cone levels and future litter size. Unfortunately, quantifying natural hoard sizes require excavation of the middens in autumn, an activity which jeopardizes the survival and reproductive success of the occupants.

If age and previous experience do not play critical roles in determining the amount of cones hoarded by individuals, then some other constraints must be present. These constraints may also vary in the degree to which they influence individuals, thus contributing to the variation in reproductive success seen in the population. Two such possible constraints are as follows:

(1) The criteria used by squirrels in selecting cones to hoard actually limits the amount of cones that are harvested, and variation in cone quality varies from territory to territory. Smith (1970) studied the discriminatory feeding behaviour of red squirrels in a lodgepole pine (*P. contorta*) stand, and described how squirrels altered their choice of cone in relation to its hardness and usage. Because cones from the current year were softer (as in jack pine), squirrels could increase their feeding rate by preferentially selecting them. However, Smith argued that cones cropped and cached for several weeks soon dried and became as hard as older cones, which explained why the squirrels in his study population were not as discerning in which cones were cut for caching. Elliot (1974) worked in the same area as Smith and also found that squirrels preferred certain cone phenotypes, based on width, number of viable seeds/cone, ratio of total seed to cone weight, and overall cone morphology. Like Smith's study, squirrels at Fort Assiniboine prefer to feed on cones from the current year's crop, as they will continually select them if given a choice (Larsen unpubl.). However, new cones also constitute the largest proportion of hoarded items in the Fort Assiniboine population (Zimmerling unpubl.), which is consistent with the harvesting data collected in this study. Despite this predilection for new cones, the harvest data still suggests that the squirrels crop only a small fraction of the total number available on their respective territories. The fact that jack pine trees in the Fort Assiniboine area remain covered with older cones also attests to the fact that the squirrel population only removes a small proportion of each year's crop. More detailed analyses of the properties of cones left on trees, versus those hoarded (*v.* Elliot 1974), will be necessary to test whether squirrels are constrained in the number of cones they may select from.

(2) Squirrels are not limited in the number of cones present on their territories, but the cost of harvesting enough cones to positively affect litter size is prohibitive. To achieve an increase in litter size equivalent to that created by the cone-additions, an individual squirrel may have to double its hoarding effort, which may be beyond its capacity. We lack precise data on the time and energetic costs of hoarding , as well as the risk of predation during that period. Also unknown is the relative effort involved in cropping and feeding on cones in both warm (autumn) and sub-zero (winter) temperatures. If any of these constraints exist, variations in individuals and/or territory quality could still be responsible for differences in reproductive success between individuals.

Several notable contrasts exist between the data reported herein and in other studies that have no direct bearing on the effects of the hoard manipulations. For example, the failure of some proportion of uniparous and multiparous red squirrels to reproduce has been suggested in other studies. Wood (1967) reported that only 84% of "old" (=previously reproducing) females in a population in extreme northern Alberta produced offspring, based on mid-summer nipple condition and the presence of corporea lutea and placental scars. Rusch and Reeder (1978) used similar techniques and concluded that in Rochester, Alberta (≈ 85 km W of Fort Assiniboine), less than 100% of mothers from the previous year became impregnated. These observations contrast with those from Fort Assiniboine, where all uni/multiparous females became pregnant each year. The maximum litter size observed in this study (four) is also lower than that reported elsewhere (see Table 1 in Obbard 1988). At Rochester, both Kemp and Keith (1970) and Rusch and Reeder (1978) reported maximum litters sizes of five and eight, respectively.

The differences reported between this and other studies of *Tamiasciurus* may be attributable to variation in research techniques, or the temporal and spatial differences in studies. Other studies have not used multiple recaptures and intense monitoring of individual females to infer reproductive condition, nor have they ascertained litter size directly, relying instead on placental scars or observations of emergent offspring. Boutin (unpubl.) has used techniques identical to that used in this study (see Chapter 2) at a study site near Kluane Lake, Yukon ($>6^{0}$ lat further north, and in spruce habitat), and has reported similar results. Females in populations likely experience very different conditions in different years, a notable example being complete cone crop failures in spruce habitat. As mentioned above, maximum litter sizes of five were recorded in 1992, but not in the four previous years. Also, compared to other studies, annual adult survival at Fort Assiniboine during this study was high (>60%), and juvenile survival was extremely low (Chapters 2 and 5), probably due to a shortage of vacant territories (see Obbard 1988). The high adult survivorship may indicate that females were experiencing relatively good conditions during this study. That may explain why the cone depletion experiment did not cause a decrease in the pregnancy rate of uniparous and multiparous females (but it also may be that the high density of adults would have a deleterious effect on female success - Larsen unpubl.).

Many questions remain unanswered, but what this experiment suggests is that the size and energy content of the hoard may be a subtle, but not a major constraint of reproductive success in female red squirrels. Further long-term monitoring of food levels and reproductive patterns (e.g. Korpimäki 1992) coupled with experimental manipulations such as more punctuated food additions (e.g. Richner 1992), will be necessary to understand what factors are responsible for the variation seen within and between populations.

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YEAR	TREATMENT	N	$\bar{X}$
1989	CONTROL	26	2.88
1989	CONE-ADDITION	14	3.36
1989	SEED-ADDITION	16	3.19
1989	CONE-DEPLETION	12	2.83
1990	CONTROL	42	2.62
1990	CONE-ADDITION	15	3.20
1990	SEED-ADDITION	13	3.00

TABLE 3.1. Mean litter sizes for control, hoard addition and hoard depletion groups. YEAR=year of litter, following application of TREATMENT in preceding autumn and winter. Because the range of litter sizes was very limited (see Figs. 3.1 and 3.2), the distribution of values in each treatment category were abnormal, hence standard error figures are not presented.

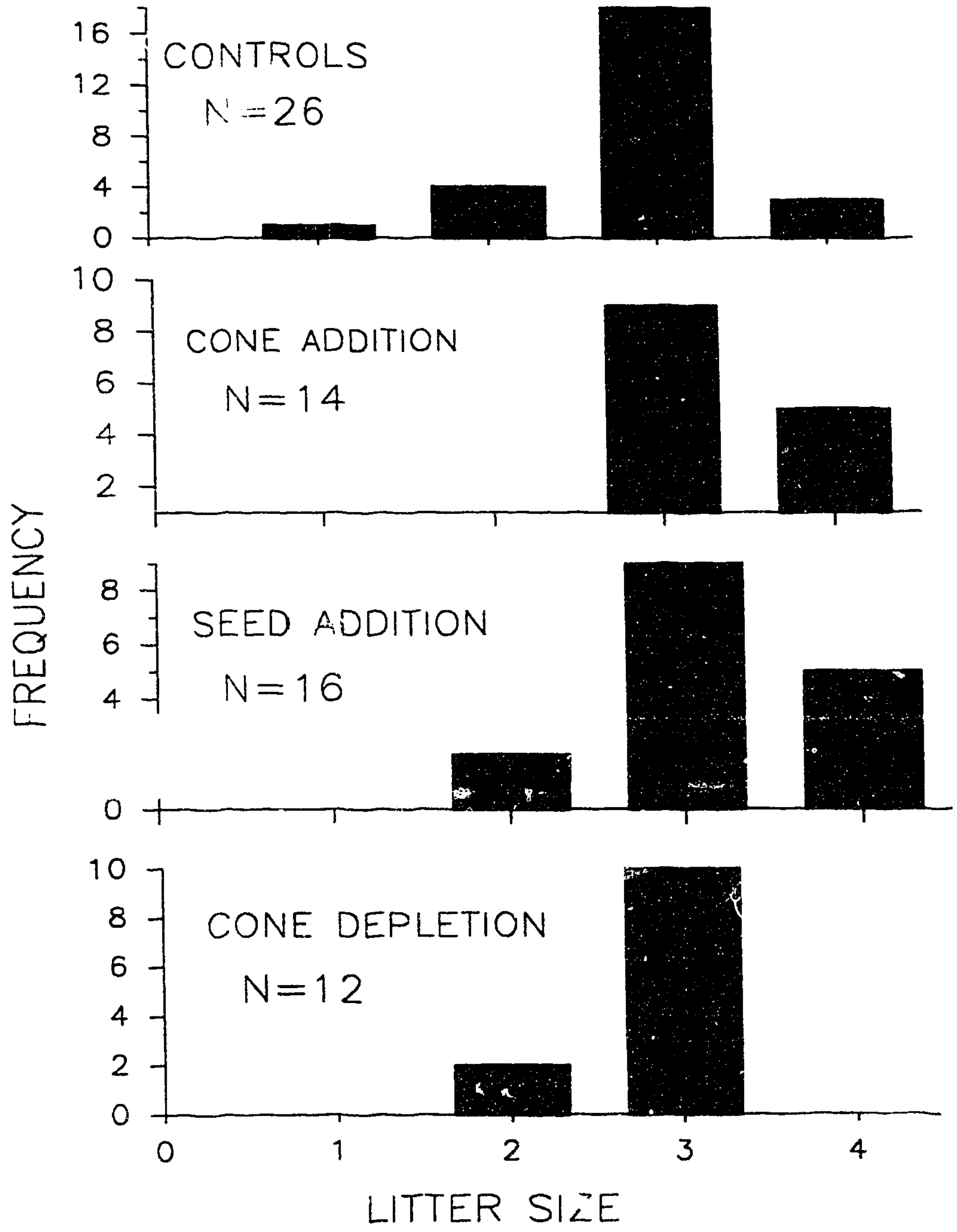

FIGURE 3.1 Frequency of litter size classes in the control and treatment groups, 1989 (treatments effected Autumn 1988). Cone-addition and seed-addition treatments resulted in proportionately higher numbers of larger sized litters than in the control and cone-depletion groups. Although no females in the cone-depletion treatment produced a litter of four offspring, the overall difference between this group and the control females was not statistically significant (P=0.454, see text).

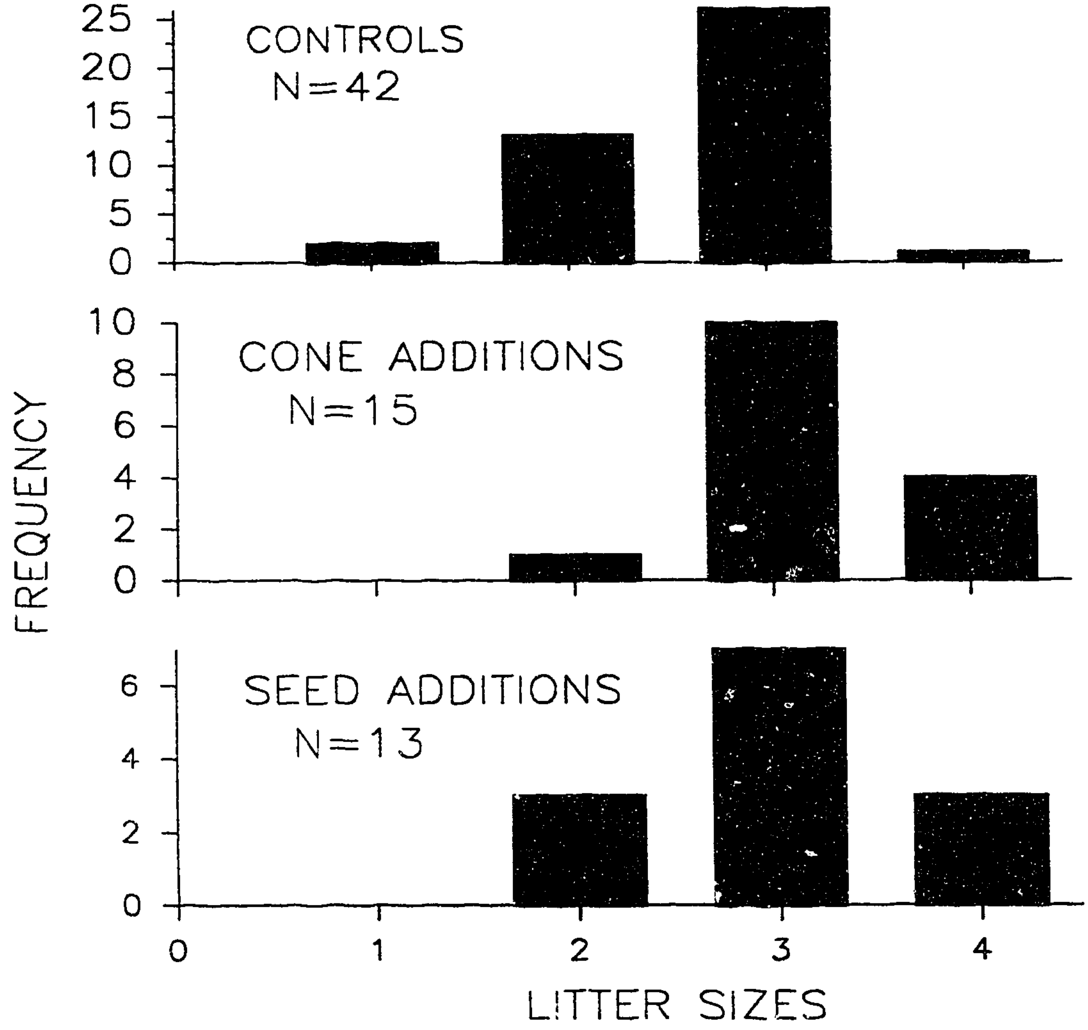

FIGURE 3.2 Frequency of litter size classes in the control and treatment groups, 1990 (treatments effected Autumn 1989). As in the previous year (see Fig. 3.1) the cone-addition and seed-addition treatments resulted in proportionately higher numbers of larger sized litters than in the control group.

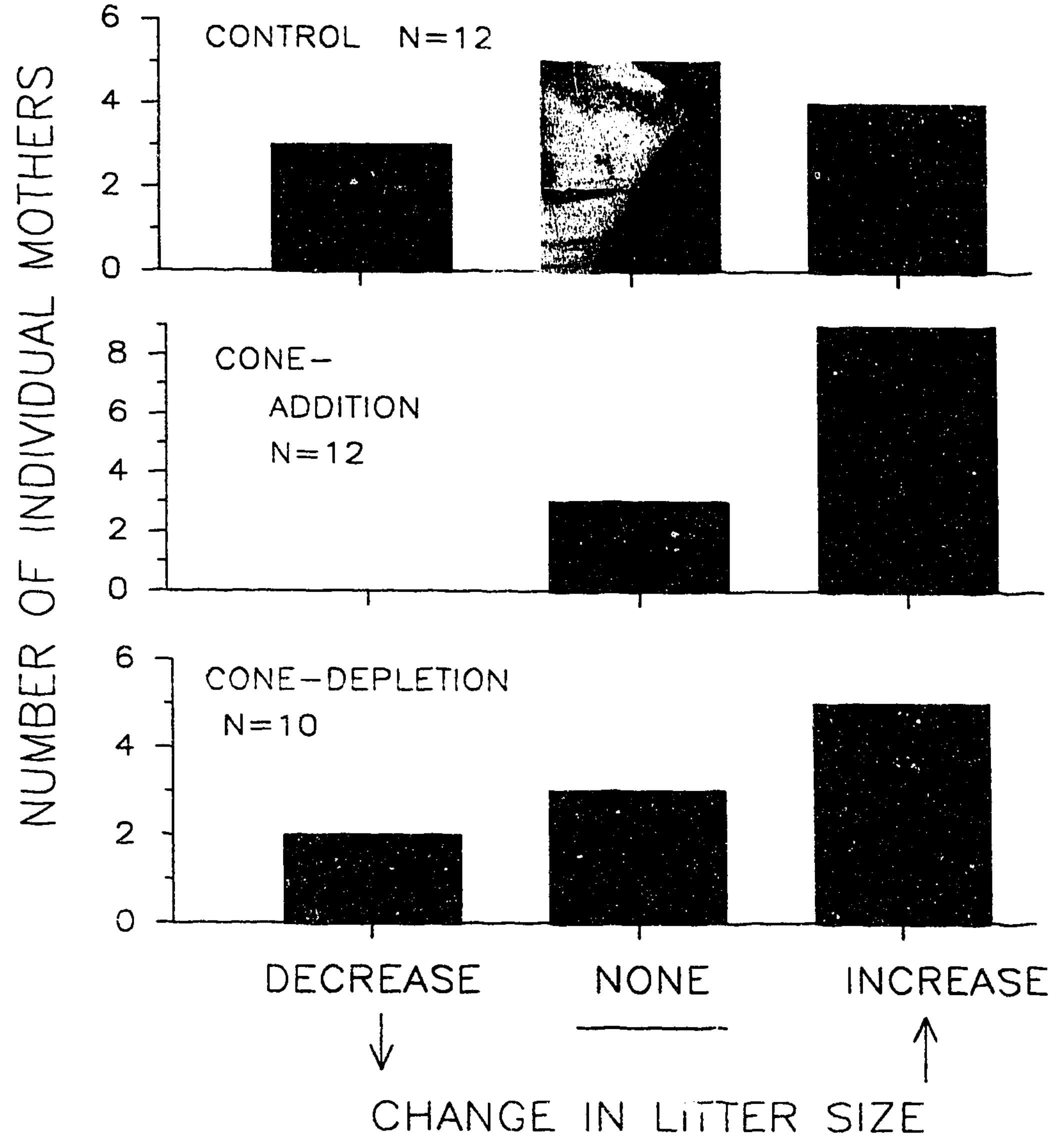

FIGURE 3.3. Changes in the size of individual females' litters from Spring 1988 to Spring 1989. Degree of change (abscissa) is expressed as a decrease of one offspring, no change, or an increase of one offspring. In contrast with the control and cone-depletion groups, most (75%) of the females given cone-additions in Autumn 1989 experienced an increase in litter size (P=0.08, see text).

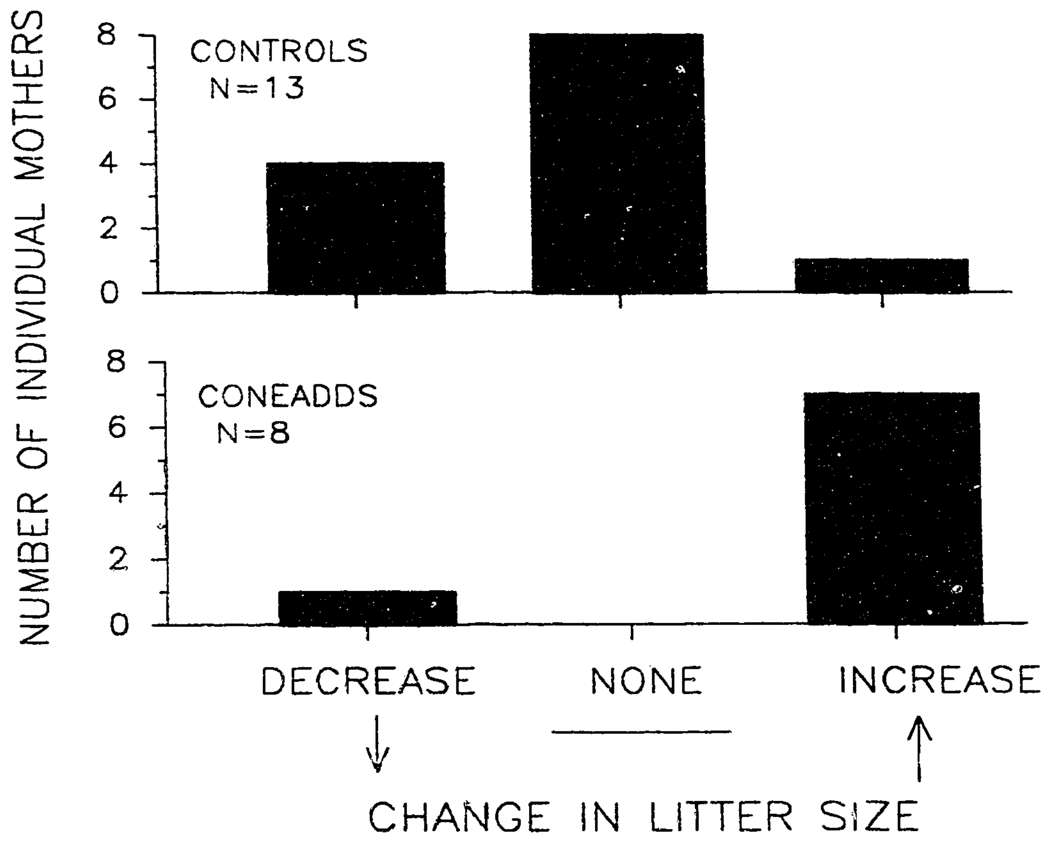

FIGURE 3.4. Changes in the size of individual female's litters from Spring 1989 to Spring 1990. Degree of change (abscissa) is expressed as a decrease of one offspring, no change, or an increase of one offspring. Relatively more females (88%) in the cone-addition group experienced an increase in litter size, compared to the control females (12%, differences statistically significant, $P<0.001$, see text).

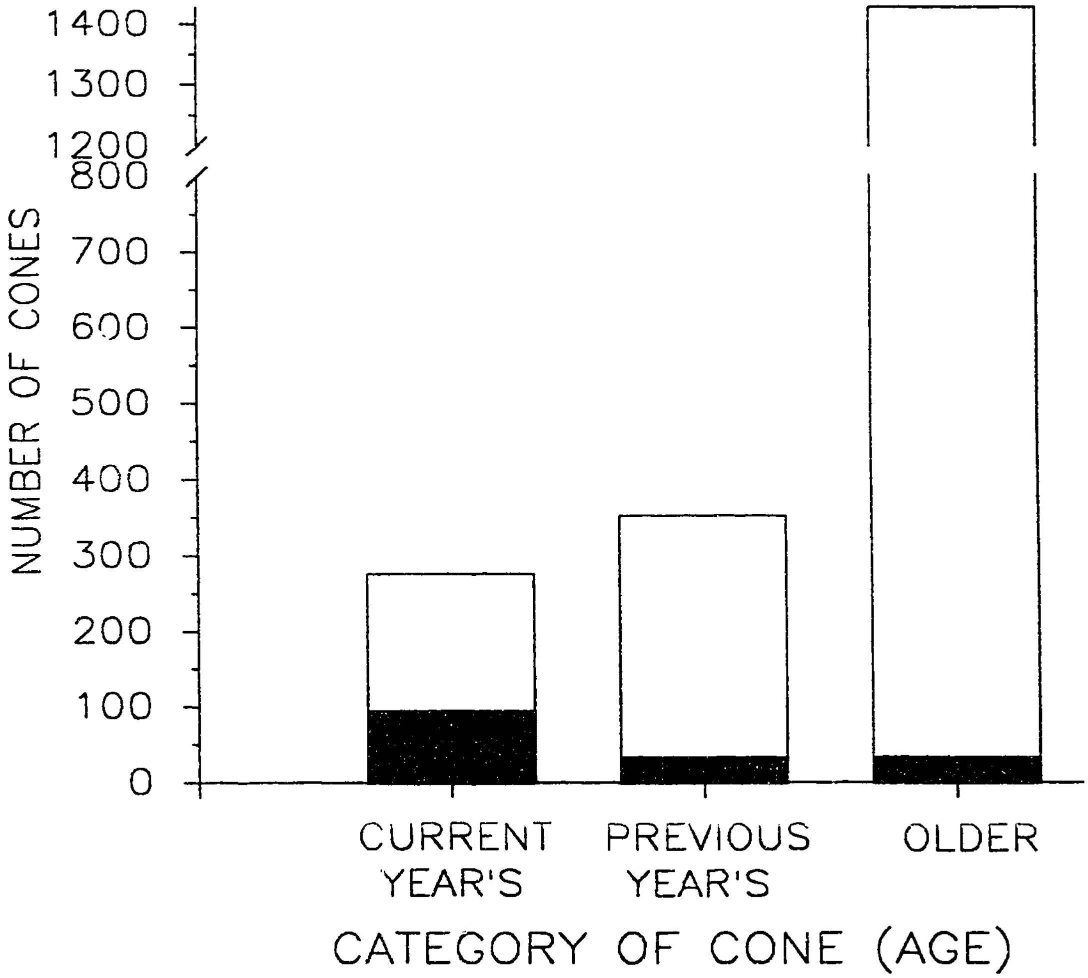

FIGURE 3.5. Numbers of cones enumerated on trees prior to harvesting by female squirrels in 1989. Cones were categorized as belonging to either the current year's crop, the previous year's (1988), or an older crop. Solid black subset within each bar indicates the number of cones which had been removed (cropped) during the autumn harvest period. Squirrels favoured cones from the current year, taking approx. 34% (94/276) of those originally recorded. In contrast, squirrel harvested only approx. 9% (33/352) and approx. 2% (94/1427) of the one-year old and older cones, respectively.

CHAPTER 4

TERRITORY FIDELITY IN FEMALE RED SQUIRRELS

INTRODUCTION

The reproductive status or success of a territorial individual may be determined by two proximate factors: (1) the quality of the individual itself, and (2) the quality of the environment. Decoupling the relative effects of these two potential factors is not easily done. Is the degree of success exhibited by an individual due to its own characteristics or the characteristics of its territory? How does one determine if high quality individuals acquire or create high quality territories, or vice versa?

One of the more direct and powerful approaches to answering these question is to determine the breeding success of individuals (or mated pairs) on one territory, and then repeat the procedure with the individuals on a different territory. After correcting for temporal effects, this analysis should reveal how individuals do relative to one another, regardless of what territory they hold (e.g. Perrins and Jones 1974). Conversely, the relative 'performance' of territories may be compared, regardless of what individuals are occupying them. An elegant test of this nature was conducted by Hogstedt (1980), who documented the clutch size of magpies that occupied different territories through time. His analysis indicated that approcimately 85% of within-year variation in the clutch size of female magpies was due to territory effects.

Obviously, not all mating and breeding systems will facilitate such an approach. Individuals in many animal species maintain the same territory throughout their life (Kaufmann 1983), making it more difficult to separate the effects of territory and individual. Unfortunately, it is in these species that the effects of territory quality on the reproductive success of the inhabitants may be most profound. Relatively low lifetime reproductive success may result from individuals (or groups) spending their adult lifespan on relatively inferior territories (e.g. Fitzpatrick and Woolfenden 1989). Individuals faced with this situation should attempt to acquire better quality territories (e.g. Newton 1989a), but such options may be unavailable due to conditions such as habitat saturation (e.g. Saurola 1989). Naturally occuring temporal and spatial variation may provide an opportunity to test such predictions (e.g. Weatherhead and Robertson 1977, Korpimäki 1988, Dhindsa and Boag 1992). However, a more direct approach is to manipulate environmental conditions and monitor the response and subsequent reproductive success of individuals, yet studies of this nature are rare.

Individuals in northern populations of the North American red squirrel (*Tamiasciurus hudsonicus*) maintain individual territories (Heaney 1984). At Fort Assiniboine, Alberta (54.20°N, 114.45°W), individuals disperse from their mothers' territories by making forays until a vacant territory is located (Chapter 5). These territories normally contain established middens, which are traditional sites used for cone hoarding and overwintering. Once females in the population acquire a territory and midden, they rarely relocate, spending virtually all of their reproductive lifespan on the same territory. Territory abandonment and relocation by adult females has been reported in other populations of red squirrels (Boutin *et al* in press, Price and Boutin *in press*) and in other species (see review by Waser and Jones 1983), although in most of these cases the act of relocation has been considered a tactic to increase the survival of current offspring rather than future reproductive success.

Becker (1992) studied red squirrels at Fort Assiniboine and found that territory area *per se* had no influence on the likelihood of resident females experiencing estrous. However, she found that females with territories containing relatively few trees (with large diameters) did not reach reproductive maturity as early as females inhabiting territories with large numbers of small trees (jack pine density and DBH are negatively correlated in the Fort Assiniboine area (Chapter 2). She hypothesized that the energetic costs of foraging may differ in relation to tree characteristics, and this in turn may influence a female's ability to reach critical body mass. I found that territory area and tree density did not influence the litter size of mother squirrels, but offspring survival after nest emergence appeared higher in territories with larger numbers of smaller trees, perhaps because they afforded more protection from predators (Chapter 2). Since reproductive lifespan and offspring survival obviously are important components of reproductive success (Newton 1989b, Clutton-Brock 1988), variation in territory quality may have an enormous impact on the fitness of female red squirrels (as reported for muskrats - Hjälten 1991). However, even if females are able to assess territories of different quality (either by tree density or some other criteria), the importance of securing and holding the first available territory (Chapter 2 and Appendix 5) may prevent a more discriminating selection process. Subsequent relocation theoretically would be possible after initial settlement, but as mentioned above, high survivorship and density may prevent such a behaviour from being observed.

In this study, I performed a series of removal experiments, designed to provide opportunities for relocation to both females that had produced offspring, and females not yet reproducing. Similar removal experiments involving red squirrels have been conducted (Boutin *et al* in press, Boutin and Schweiger 1988, Price *et al.* 1986), but those studies differed in that the females exposed to territory vacancies had concurrent offspring which were attempting to disperse. They also were conducted in an area where maternal abandonment of natal middens was observed under natural conditions (Kluane, Yukon - Price and Boutin in press). The experiments described herein were conducted at times when breeding females' decisions to relocate could not be influenced by the presence of their respective offspring.

METHODS

The reproductive histories and success, territory ownership and survival of individuals were determined following the protocol outlined in Chapter 2 and Chapter 3. Analysis of 2x2 contingency tables were done using William's correction for the *G* test (Sokal and Rohlf 1981).

PERMANENT REMOVAL EXPERIMENT 1989

During 23-25 August 1989, I tested the territory fidelity of female squirrels by permanently removing 53 resident, adult squirrels from an experimental grid (0.75 km^2). The only squirrels remaining on their individual territories were 24 adult females, twelve of which had produced offspring earlier in the summer ('Breeders'), and twelve that were greater than one year old, but had not yet reproduced ('Non-Breeders'). The midden occupied by each of the original 24 females was determined prior to the removals through repeated live-trapping and behavioural observations (see Chapter 2).

Removal of squirrels immigrating into the study area continued for another five days, bringing the total number of individuals removed to 71. Grids were re-trapped in mid-September and Spring 1990 to determine if any females had changed locations.

TEMPORARY REMOVAL EXPERIMENT 1990

From 16 - 28 August 1990, I tested whether there were intrinsic differences in quality between territories belonging to Males, Breeders (females which had previously produced offspring) and Non-Breeders (nulliparous females). To accomplish this, individuals from each of the three groups were temporarily removed from their respective territories, and the degree to which the individual territories were challenged for was then monitored. The central premise of this experiment was that if individual squirrels could detect differences in territory quality related to reproductive success, then Non-Breeders and dispersing juvenile females should prefer territories that belonged to Breeders, or territories that possessed higher densities of trees near the midden.

At less than 30 minutes prior to sunset, two males, two breeders and two nonbreeders were live-trapped and removed from their respective territories. Territories destined for removals were selected such that *(1)* no immediate neighbouring females had offspring currently attempting to disperse (see Chapter 5) and *(2)* at least one adult male and one nonbreeding female had bordering territories.

Starting at sunrise the next morning, three observers rotated between the six vacant territories, with each territory being observed for 20 minutes per hour (10 minutes allowed for the observers to relocate from territory to territory). This gave a total of 140 minutes of observation time per territory, occuring over a 7 hour span.

This procedure was repeated for seven days, producing data on the response of other squirrels to the vacancy of 42 different territories (14 which belonged to males, 14 which belonged to breeders, and 14 which belonged to nonbreeders). This provided a total of 5880 minutes, or 98 hours of observations. Information recorded while territories were being observed included the number and identity of all squirrels observed 'intruding' onto the vacant territory. In the case of adult females and juveniles (members of the 1990 cohort), an individual's identity could be quickly ascertained by the presence of colour-coded eartags (see Methods, Chapter 2). Several adult males were also identified in this fashion, because they retained coloured eartags from when they were first tagged as offspring. Identifying the other adult males required more indirect methods: in most cases, males vocalized from their own territory, either before or after making the intrusion onto the vacant territory. This provided one means of identifying the individual. When this failed, different individuals could be identified by the presence or absence of ripped ears, missing eartags, scars, different tail characteristics, etc. Through all of these methods, it was possible to enumerate the number of *different* individual squirrels that 'visited' each vacant territory, and group them into the following five categories:

- Males - all male squirrels that held territories at the time of the removals (including juveniles that held territories).
- Breeders - all females that produced litters during the summer of 1990 (all held territories)
- Non-Breeders - all nulliparous females that held territories at the time of the removals (including juveniles that held territories).
- Dispersing Males - males from the 1990 cohort that had not yet acquired a territory
- Dispersing Females - females from the 1990 cohort that had not yet acquired a territory

Also recorded was the number of chases and number of aggressive and territorial vocalizations occuring on the vacant territories. Vocalizations were categorized as follows:

- Rattles (territorial call, used for self-advertisement)
- Screech (loud aggressive call, used to signal a resident's intention to confront an intruder)
- Bark (alarm call, used to induce a change in the recipient's behaviour)

A record also was kept of the number of rattles originating on territories bordering the vacant territories. For a detailed analysis of the significance of these and other types of squirrel vocalizations, see Lair (1990).

Following the final observation at the end of each day, any intruder that had assumed control of a vacant territory was live-trapped to verify its identity. Finally, the original owners were released on their respective middens, at which time they all (42/42) reclaimed their respective territory.

Prior to conducting the first removal, the entire study area was live-trapped for two days to determine the relative proportions of Males, Breeders and Non-Breeders in the population. The dispersal of the 1990 cohort was also being monitored at the time, so it was also possible to determine the relative proportions of Juvenile Males and Juvenile Females (see above criteria) alive at the time. These data allowed me to test the relative proportions of intruders and settlers observed against the number predicted if intrusion and settlement was random with respect to the five categories of squirrels.

Territory quality (density and mean DBH of jack pines) around the vacated middens was measured following the procedure outlined in Chapter 2.

CHOICE EXPERIMENT 1990

Later in 1990, an experiment was conducted in which adult females were given the opportunity to relocate or re-establish the boundaries of their respective territories, by the permanent removal of two neighbours. This study differed from the Permanent Removal Experiment of 1989 in that (1) only a small subsection of the population was removed, (2) I attempted to influence the females' perceptions of the vacated territories by manipulating the winter hoards accumulated by the original owner, and (3) more attention was focused on the boundary shifts of the targeted females.

All adult females greater than two years of age and living in the study area were grouped into categories similar to those described above: 'Breeders' were those females that had produced offspring in the summer of 1990, and 'Non-Breeders' were females at least one year old that had not yet reproduced (nulliparous). Eight Breeders and eight Non-Breeders were randomly selected from these groups, and the boundaries and areas of their respective territories were determined during late June to October 13, using behavioural and location data (see Price *et al.* 1986). Territory boundaries and areas were also determined for the remaining Breeders and Non-Breeders who acted as controls. Territory sizes of individual squirrels do not shift appreciably over time, making it possible to pool measurements taken over several months (see Methods, Chapter 2). Territory sizes were calculated using minimum convex polygons (MCPAAL software).

On 15 and 16 October, each of the sixteen experimental females had two neighbouring males permanently removed. A coin toss was used to determine which territory in each vacated pair would receive a hoard addition, and which would undergo a hoard depletion. Approximately 2200 cones which had been collected from middens off of the study area (see Methods, Chapter 4) were supplied to the hoard addition midden. All cones which were accessible on the surface of the depletion midden were removed and transferred to the addition midden.

During May 1991, the boundaries and areas of all control and experimental females that had survived the winter were re-mapped. This produced two maps of each female's territory: one for her territory prior to the removals, and one for the following spring, after the removal. To quantify shifts in each female's territory over this time period, the spring territory map was superimposed over the earlier, pre-removal territory map. Areas of the spring map which did not lie within the boundaries of the older map were calculated using Sigmascan® v.3.90 software on a SummaSketch®Plus digitizing table (Summagraphics® Model MM1201). The degree to which the territory had shifted was then expressed as a proportion (non-overlapping area/total area of spring territory). These proportions were submitted to arcsine transformation prior to statistical analyses.

Midden ownership in Spring 1991 was verified through live-trapping and behavioural observations (Chapter 2). During the ensuing summer, the reproductive success of each female was followed (Chapter 2), including the settlement patterns of their respective offspring.

RESULTS

PERMANENT REMOVAL EXPERIMENT 1989

Of the twelve Breeders left on the grid following the removals, five appeared to show some response to the removals. One individual relocated to a neighbouring midden, relinquishing ownership of its previous midden to an immigrant. Four Breeders maintained possession of their original middens but acquired ownership of an additional midden. Seven breeders showed no territory shifts in response to the removals.

In the Non-Breeder group, only one of the 12 females appeared to respond to the removals by giving up possession of her original midden and relocated to a neighbouring midden. The difference in the proportion of individuals responding to removals in the two groups (Breeders and Non-Breeders) was almost statistically significant (G_{adj}=3.49, df=1, P=0.062)

In the ensuing summer (1990) three of the four Breeders that had expanded their ownership of middens had offspring settle on the midden acquired during the removals. The fourth female failed to have any offspring emerge from her nest.

TEMPORARY REMOVAL EXPERIMENT 1990

A total of 86 different squirrels were observed intruding onto the vacated territories (Table 4.1). Not surprisingly, Dispersing Males and Dispersing Females were disproportionately represented in this sample, based on their relative proportion in the population at the time (G=26.93, df=4, P<0.001). Juveniles attempting to disperse make circling forays away from their mother's territory, in search of a location to settle (Chapter 5). Thus, they are more likely to become aware and/or investigate a vacant territory than the relatively sedentary adults.

There was no clear indication that any of the three categories of vacated territories (Breeder, Non-Breeder and Male) were subjected to more intrusions by squirrels (Males, Breeders, Non-Breeders, Dispersing Males, Dispersing Females) (*G*=2.76, *df*=8, *P*=0.948, Fig. 4.1, raw data in Appendix 3). Most of the settlement on the vacated territories involved a disproportionate number of dispersing juveniles (*G*=87.67, *df*=4, *P*<0.001, Table 4.1 and Fig. 4.2; data in Appendix 3), which was to be expected, given the tendency of these individuals to colonize territories that they determine are unoccupied (Chapter 5). One Breeder was observed to claim a vacant territory, but she also maintained control of her original territory in the process. On of the Males that claimed a vacant territory appeared to follow the same strategy. Regardless, there was no significant difference in the relative proportions of squirrel settling on the three categories of vacated territories (*G*=7.62, *df*=8, *P*=0.471).

Observations of chases on the vacated territories were relatively infrequent, with obvious differences in number of chases on the three categories of territories (N=5, and 9 for the Breeder, Non-Breeder and Male territories, respectively). Kruskal-Wallace tests (chi^2 approximation) were used to determine if there were differences between the three territory categories in the total number of rattles, screeches, barks and neighbourhood rattles tallied for each territory throughout the observation day. No significant differences were detected between the three groups for any of the fo vocalization types (all *P*s >0.13).

Since neither tree density nor mean DBH was significantly different between the three categories of removal territories (*F*=0.517, *df*=2,40, *P*=0.601, and *F*=0.27, *df*=2,38, *P*=0.769, respectively), I examined for correlations between the measurements of territory quality and the number of vocalizations recorded for eac vacant territory. There were no significant correlations between any of the four vocalizations and the number of trees/territory, or their mean DBH (*Pearson's r*, all *P*s >0.10). Also, there was no relationship between the number of intruders and either of the two indices of territory quality (*P*s>0.260).

A separate analysis was made to test specifically for the affinity of Non-Breeding females (including juveniles) for territories of high tree density and lower DBH. The number of females in this category that visited each of the 42 vacant territories was not significantly correlated with either tree numbers or DBH (*R*=0.21, *n*=42, *P*=0.182).

CHOICE EXPERIMENT 1990

Each female subjected to neighbour removals was located on the day following the removals, and observed for approximately 20 minutes. Four breeders and three non-breeders were observed moving cones from the hoard-supplemented midden back to their own midden. Other neighbouring squirrels were also observed moving cones from the supplemented hoards. Five of the target Breeders were observed rattling on or near the food-supplemented midden.

Table 4.2 shows the mean territory areas for Breeders and Non-Breeders, both prior to and after the experimental removals. A two-factor ANOVA (Reproductive Status and Experimental Status) indicated Breeders had significantly larger territories than non-breeders both prior to and after the removals (prior: *F*=6.48, *df*=1,34, *P*=0.016; after: *F*=4.36, *df*=1,24, *P*=0.048). Females selected to have their neighbours removed did not possess larger territories than control females, both prior to and after the removals (prior: *F*=0.16, *df*=1,34, *P*=0.695; after: *F*=0.26, *df*=1,24, *P*=0.959). The data set obtained in this experiment appears in Appendix 4.

Figure 4.3 shows some examples of the types of territory shifts seen in the females subjected to neighbour removals. Both Reproductive Status and Experimental Status influenced the proportion that females shifted their territories (two-way ANOVA: *Rep. Status* F=9.57, *df*=1,24, P=0.005; *Exp. Status* F=6.21, *df*=1,24, P=0.020). Breeders, more so than Non-Breeders, appeared to make significant changes to their territory boundaries in response to the neighbour removals (Fig. 4.4).

Within the experimental group, six of the seven Breeders that survived to Spring 1991 had shifted their territory boundaries such that they now owned both their original midden and a midden from one of the removal territories. Conversely, only one out of six surviving Non-Breeders in the experimental group made a similar shift (G_{adj}=11.325, *df*=1, P=0.001).

Of the seven females (6 Breeders + 1 NonBreeders) that shifted their territories to encompass a removal midden, six incorporated the midden with the supplemented hoard. Two out of eight control Breeders also made substantial overwinter shifts to their territory boundaries, incorporating middens which presumably had become vacant through natural processes. None of the control Non-Breeders made a similar territory shift.

The reproductive success in 1991 of those females (Breeders and Non-Breeders) that acquired removal middens was not significantly different from those females which had not shifted, in terms of proportion breeding, litter size, and subsequent survival of offspring (all Ps > 0.450, see Chapter 2 for methods). However, six females that had acquired a midden had at least one offspring reach age 80 days of age (≈weaning, see Chapter 2). In each case (6/6), the offspring had settled on the sequestered midden. This was a significantly higher proportion than that seen in the control group of the same year, where 15 females had an offspring reach age 80 days of age, but only 7 of the offspring had acquired a territory at the same time (G_{adj}=6.53, *df*=1, *P*=0.011). Further, in six of these seven 'control' cases the offspring had settled on a midden completely off its mother's territory.

GENERAL TREND IN THE POPULATION

During the years 1988 to 1990, inclusive, annual survival in the Fort Assiniboine adult squirrel population was high compared to that reported in other studies (Chapter 1). Thus, vacant territories may have been relatively scarce, and even if adults (particularly Breeders) were likely to relocate, they may have had difficulty doing so. During the three years, only nine of 86 monitored Breeders (including controls and females used in food experiments - see Chapter 4) were known to acquire a midden that was previously owned by a different squirrel. In seven of these nine instances, females allocated their most recently-acquired midden to an emergent offspring.

DISCUSSION

Results of the removal experiments may be summarized as follows: Female red squirrels that had previously given birth are more likely than non-breeding females to alter their territory boundaries in response to habitat vacancy. However, complete relocation of the territory does not appear to be a usual for either female category. Vacant territories that previously held a breeding female do not appear to be preferentially occupied by any category of squirrels in the population. Finally, and most interestingly, females with previous breeding experience will apparently shift their territory boundaries in order to acquire control over resources that may be of value to offspring *in the following year*. Conversely, non-breeding females show little affinity for vacated middens, suggesting that previous experience with offspring is needed to elicit the territory-shifting behaviour.

All three of the removal experiments should have provided resident females (and males, in the case of the Temporary Removal) with ample opportunity to relocate. In particular, squirrels with territories neighbouring the vacated territories should have been able to out-compete immigrants for preferred territory space (Stamps 1987). Obviously, relinquishing ownership of the original middens and territories was not a common strategy. Both the Permanent and Temporary Removal experiments were conducted at a time when midden hoards had not yet been replenished in preparation for the coming winter. Had this not been the case, one might have argued that territory owners would be hesitant to abandon their own hoard, lest the resources on the new territory and midden turned out to be of inferior quality. Probably the most important consideration in whether to relocate or not is the cost of surrendering the acquired local knowledge and experience on one's home territory, even for a short period of time. Familiarity with a territory increases an individual's capability to withstand attempted intrusions (Beletsky and Orians 1987), and likely it is of tantamount importance in detecting and escaping predators (see Appendix 5). A detailed knowledge of the resource structure and dispersion on a territory also may play a key role in achieving optimal foraging patterns (Becker 1992, Boonstra 1989). If differential territory quality does exist, then either the adult female squirrels (Breeders and Non-Breeders) are unable to recognize it, or the potential costs of complete relocation were too severe to warrant abandonment of the original territory and midden.

In the Temporary Removal Experiment, competition was not measurably stronger for the territories originally held by Breeders, or for the territories which had relatively high tree densities (and low DBH). This suggests that either the measurements of territory quality used here were unimportant in the evaluation process used by squirrels, or that squirrels do not assess territory quality when considering where to settle, at least using the criteria considered here (tree density). Whether or not individual animals actually *select* where to settle is unclear (see discussion in Bekoff *et al.* 1989). Weatherhead and Robertson (1977) found breeding success of female redwinged blackbirds to be correlated positively with several measured nest parameters, but these parameters appeared not to influence where some females decided to nest. Because of the harem breeding system, Weatherhead and Robertson suggested that these females were making their decisions based on mate quality as well as territory conditions. Other studies have suggested that in some species individuals are able to 'locate' sites that afford better reproductive success (e.g. Bekoff *et al.* 1989, and references therein). Food density may also be used in the assessment of territory quality (e.g. Trombulak 1990). However, as pointed out by Bekoff *et al.*, many factors such as habitat availability, social factors, and physical limitations may downplay the importance of territory quality assessment. As indicated by the Permanent Removal Experiment, individuals that already hold territories do not readily relocate, even when given ample opportunity. It is also quite likely that individuals *without* territories (i.e. dispersing juveniles) cannot afford to bypass a vacant territory even if it is of suboptimal quality, since possession of a territory is critical to survival (Chapter 5 and Appendix 5).

One territory attribute which was not considered in the Temporary Removal Experiment was the condition of the midden. In the Choice Experiment, six of seven females that acquired a vacant midden chose the one with the hoard supplement. Klenner (1991) suggested that the condition of the midden may be used as a cue for long-term habitat quality. Whether individuals actually assess territory quality could be explored further by conducting other removal studies in which some 'suboptimal' territories were equipped with a resource, such as a feeder station, a nest box, or an enhanced midden. One could then examine whether dispersing offspring would bypass other vacant territories in preference for these presumably 'high quality' territories.

Compared to complete relocation, the partial shifts of territory boundaries documented in both the Permanent Removal and Choice Experiments probably represent a less costly option. Females that performed these shifts were able to maintain possession of their original midden, and a large portion of their original territory, while garnering the resources of an additional midden. Middens often contain cones from hoarding in previous years (M.C. Smith 1968, Zimmerling 1990), and also provide refuge from most predators. Thus, having two established middens on one's territory probably has some direct benefit. However, because Breeders rather than Non-Breeders showed a greater tendency to appropriate vacant middens, other benefits related to reproductive success appear to be of more importance than simple food and refuge availability. The tendency for the hoard-supplemented middens to be acquired in the Choice Experiment may have been due to the females' perceiving the territory and its resources as being superior to the hoard-depleted middens (as suggested by Klenner 1991). However, a simpler explanation is that the larger hoard size simply provided the females with an opportunity to appropriate cones, and the familiarity they gained with the area during the 'stealing' period led to their subsequent takeover of the midden. Regardless of the precise mechanism(s), the breeding females obviously displayed relatively greater interest in the vacant territories than the non-breeders (and other squirrels in the vicinity of the vacant middens).

In the Fort Assiniboine population, juveniles are highly philopatric, and a large proportion of offspring settle on or adjacent to their respective mother's territory, suggesting the costs of philopatric settlement are not critical (Chapter 5). Further, movement off the mother's territory appears to render the offspring more susceptible to predation (Appendix 5; *cf.* Isbell *et al.* 1990). A trade-off seems to exist, in that offspring that manage to settle *away* from the mother's territory experience relatively greater survival. However, this may be related to the fact that offspring settling away from the mother's territory tend to secure larger, traditional middens, which may facilitate their overwinter survival (Appendix 5). Thus, mothers may be maximizing their potential reproductive success if they are able to provide an offspring with an established midden site within the boundaries of the maternal territory. The tendency for mother red squirrels to allocate parts or even all of their territory to offspring has been previously described (Price and Boutin in press, Zirul 1970, C.C. Smith 1968), although complete abdication of the maternal territory in the Fort Assiniboine population appears quite rare (Chapter 5).

Females that have not yet produced a litter (Non-Breeders) did not show a tendency to appropriate vacant middens, even if they did reproduce in the following year. The important issue here, of course, is whether these Non-Breeders 'knew' they would be producing offspring in the ensuing spring. The age at which female squirrels in the Fort Assiniboine population first begin breeding varies from one to three years (Chapter 2, Becker 1992). Becker (1992) argued that onset of puberty was dictated directly by spring body mass, as was reported for the European red squirrel, *Sciurus vulgaris* (Wauters and Dhondt, 1989). If so, nulliparous females may be unable to 'anticipate' the onset of their initial litter. Females that have already produced offspring, however, continue to do so in all ensuing years (Chapter 2, Chapter 3), so these females would be more likely to benefit from obtaining an additional midden, even seven months in advance of their next litter. Perhaps females also undergo some type of learning process during their first year of breeding, and this is what prompts the opportunistic shiftings of territory boundaries.

Spatial and temporal variation appears to have a strong influence on the response of female squirrels to habitat vacancy. As mentioned previously, earlier studies have documented territory shiftings or relocations of adult female red squirrels (Zirul 1970, C.C. Smith 1968). More recently, Boutin and Schweiger (1988) conducted removals in a Yukon population of red squirrels and found that females with offspring responded immediately to vacant territories by expanding their territories. Dispersing offspring subsequently settled in the expansion areas. Also in the Yukon, Price and Boutin (in press) found that 7/28 mother squirrels in one year relocated to vacant territories, thus providing their offspring with the natal middens. This tactic occured more frequently in late-breeding females, which the researchers felt was a reflection of the fact that early-born juveniles were more likely to acquire a territory without their mother's intervention. Adult females do occasionally relocate in the Fort Assiniboine population (see RESULTS). However, that behaviour rarely coincides with offspring acquisition of the natal midden (5/79 litters in three years, see Chapter 5), and in the population there appears to be no relationship between breeding date and acquisition of territories by offspring (Larsen unpubl. data). Experimental testing as done by Boutin *et al.* (in press) has not been conducted at Fort Assiniboine.

In central British Columbia, Klenner (1991) conducted spring removals of resident squirrels from experimental grids, and found that females in breeding condition were represented in the immigrant population. The reproductive status of these females prior to the relocation was not known, so it was impossible to assess the influence of the relocation on their individual reproductive success. His removals were also conducted in Douglas fir (*Pseudotsuga menziesii*) and white spruce (*Picea glauca*) habitat, which may have prompted immigration out of other less-optimal habitat (as measured by squirrel density). Obviously, timing, past reproductive experience and possibly habitat type may influence territory fidelity in adult female squirrels. Further experimental work and/or more extensive long-term documentation will be necessary to determine the relationship between the territory dynamics and reproductive success of females in this species.

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A. Categories of intruding squirrels

	Br	**NBr**	**M**	**dF**	**dM**	Total
Observed Frequency:	14	15	20	19	18	86
Observed Proportion:	0.16	0.17	0.23	0.22	0.21	1
Predicted Proportion:	0.20	0.29	0.32	0.09	0.10	1

B. Categories of settling squirrels

	Br	**NBr**	**M**	**dF**	**dM**	Total
Observed Frequency:	2	1	1	17	16	37
Observed Proportion:	0.05	0.03	0.03	0.46	0.43	1
Predicted Proportion:	0.20	0.29	0.32	0.09	0.10	1

TABLE 4.1. Summary of the total number of (A) intruding and (B) settling squirrels observed on the vacated territories (TEMPORARY REMOVAL EXPERIMENT). Intruders and settlers are grouped into five categories: **Br**eeding females, **N**on-**Br**eeding females, **M**ales, **d**ispersing **F**emales and **d**ispersing **M**ales. Also shown are the relative proportions of squirrels in each of these five categories, as well as the proportions predicted by their relative abundance in the population at the time of the experiment. As expected, dispersing juveniles were over-represented in both the intruder and settler data. See text for details on squirrel classification, and how predicted proportions were calculated.

	REPRODUCTIVE STATUS IN 1990		EXPERIMENTAL STATUS	
	Br	NBr	CONTROL	NEIGHBOUR REMOVAL
BEFORE	0.69	0.57	0.62	0.65
	REMOVAL	(20, 0.036)	(18, 0.031)	(22, 0.031) (16,
0.046)				
AFTER	0.69	0.57	0.61	0.65
	REMOVAL	(14, 0.045)	(14, 0.038)	(15, 0.036)(13,
0.055)				

TABLE 4.2. Comparison of the mean territory areas (h) of experimental and control females subjected to neighbour removals in Autumn 1990 (CHOICE 1990 EXPERIMENT). Respective sample sizes and standards error appear in parentheses under each mean figure. Females which bore offspring in 1990 (Breeders) had significantly larger territories than nulliparous females (Non-Breeders)both before and after the removals (Autumn 1990 and Spring 1991, respectively), but the difference between control and experimental females was not significant at either time.

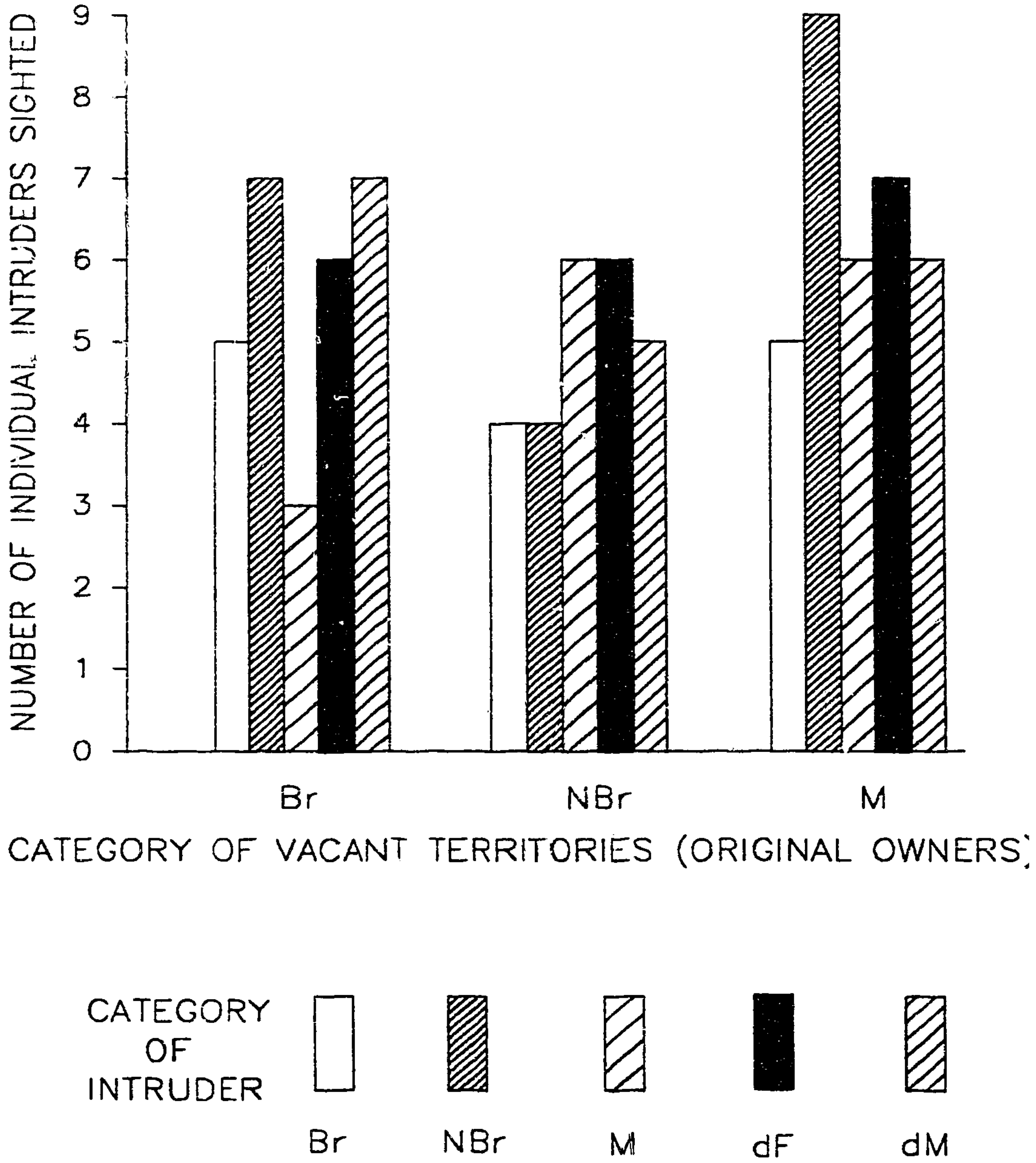

FIGURE 4.1. Numbers of individual squirrels observed intruding onto vacant territories (TEMPORARY REMOVAL EXPERIMENT). Territories are categorized by the status of their original owner: **B**reeding females, **N**on-**B**reeding females and **M**ales. Two additional categories were used in classifying the intruders: **d**ispersing **F**emales and **d**ispersing **M**ales (see text for details). There was no significant difference in the relative proportions of intruders observed on each of the three different category types.

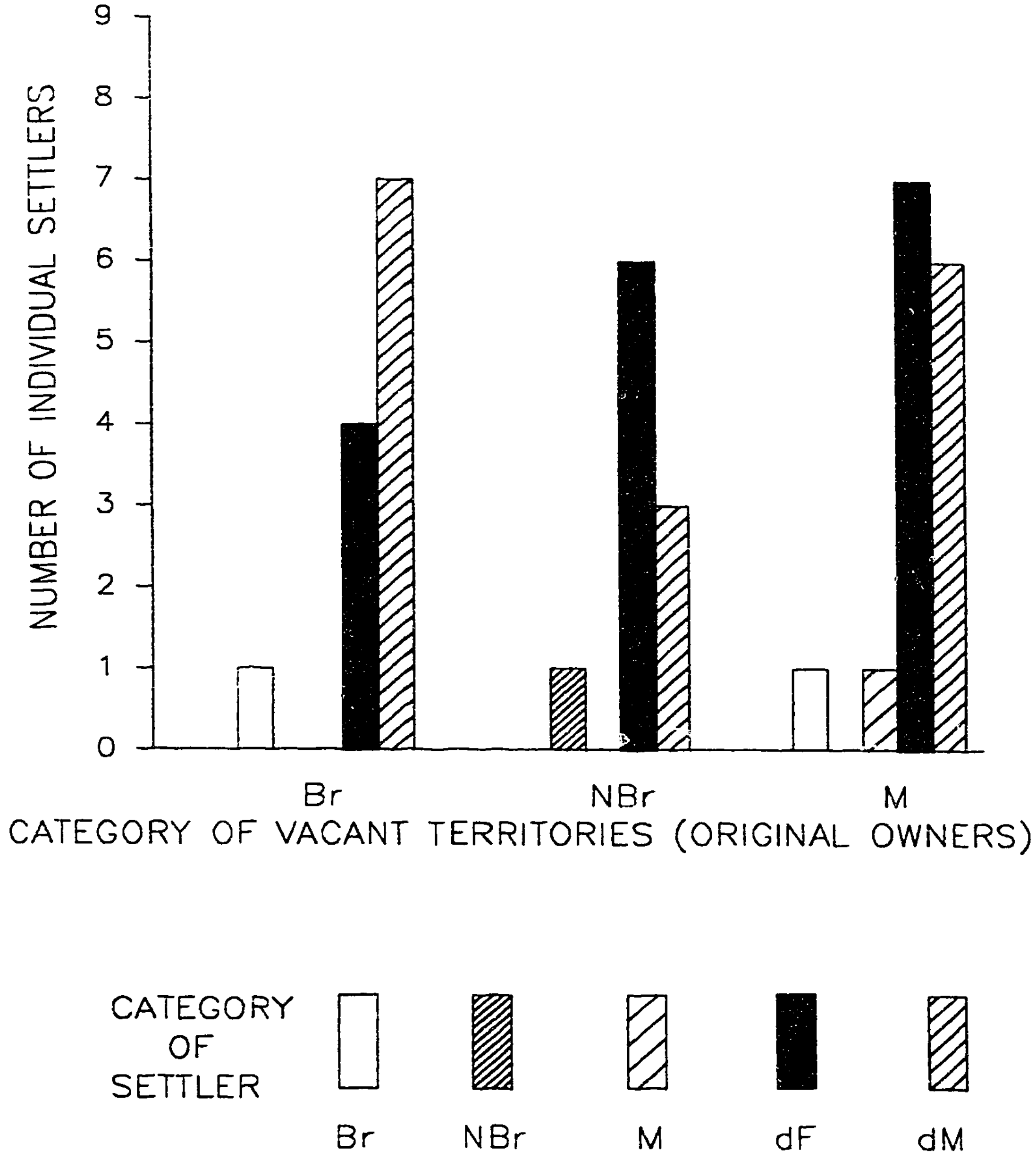

FIGURE 4.2. Numbers of individual squirrels observed settling on vacant territories (TEMPORARY REMOVAL EXPERIMENT). Territories are categorized by the status of their original owner: **B**reeding females, **N**on-**B**reeding females and **M**ales. Two additional categories were used in classifying the settlers: dispersing **F**emales and dispersing **M**ales (see text for details). There was no significant difference in the relative proportions of settlers observed on each of the three different category types.

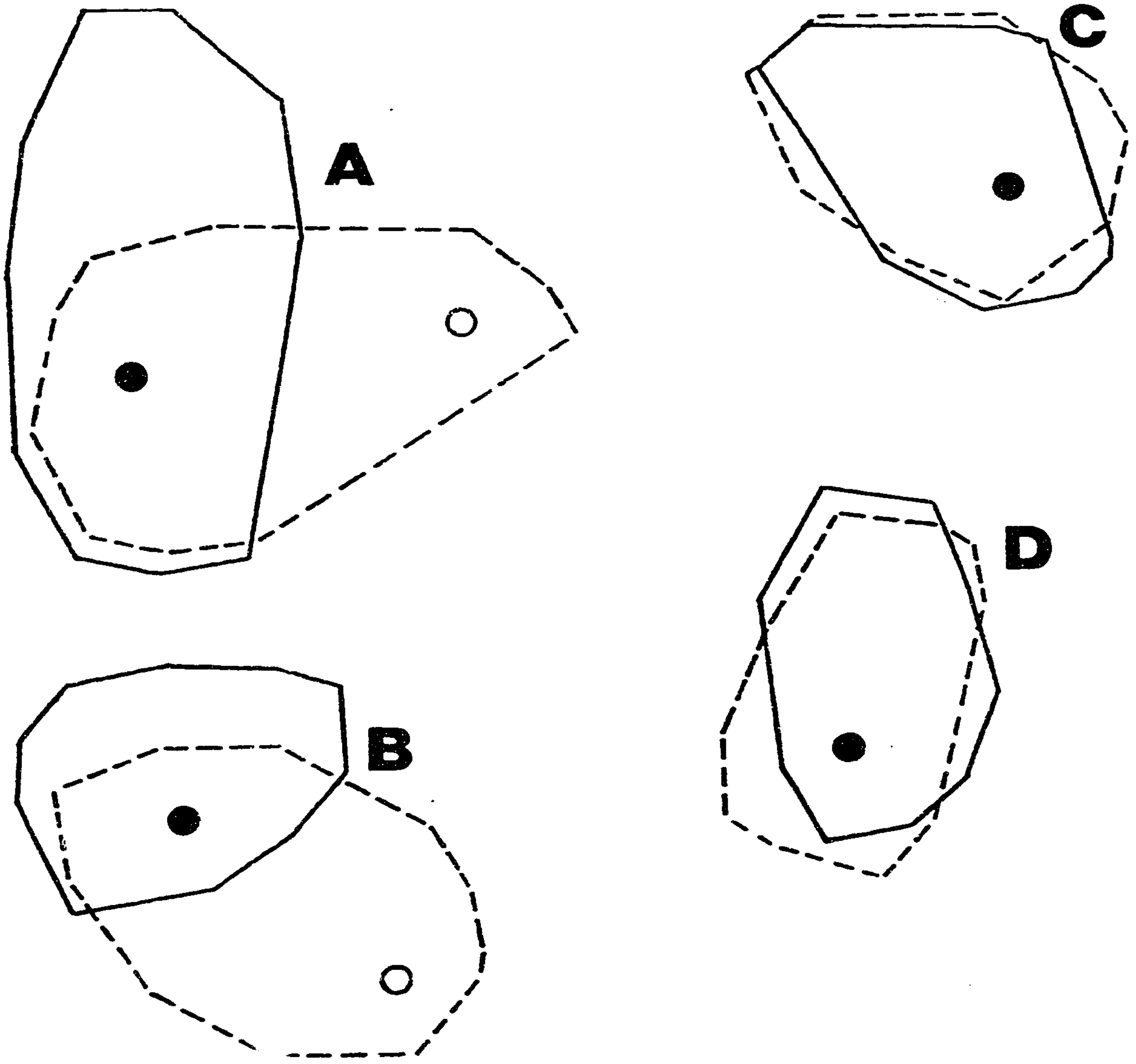

FIGURE 4.3. Examples of the territory shifts seen in females subjected to neighbour removals (CHOICE EXPERIMENT) and control females. Territory boundaries in Autumn 1990 (prior to removals) are portrayed by solid line; subsequent territory in Spring 1991 (after removal) is given by broken line. Each female's original midden is given by solid circle, and middens acquired through boundary shifts appear as open circles. Diagrams A and B depict two breeding females which made significant modifications to their territory boundaries in response to the removal of their neighbours. These females incorporated a vacated, neighbouring midden into their own territory. Breeding and non-breeding females in the control group, as well as non-breeding females in the experimental group, displayed relatively little change in territory boundaries over the course of Winter 1990/91 (diagrams C and D).

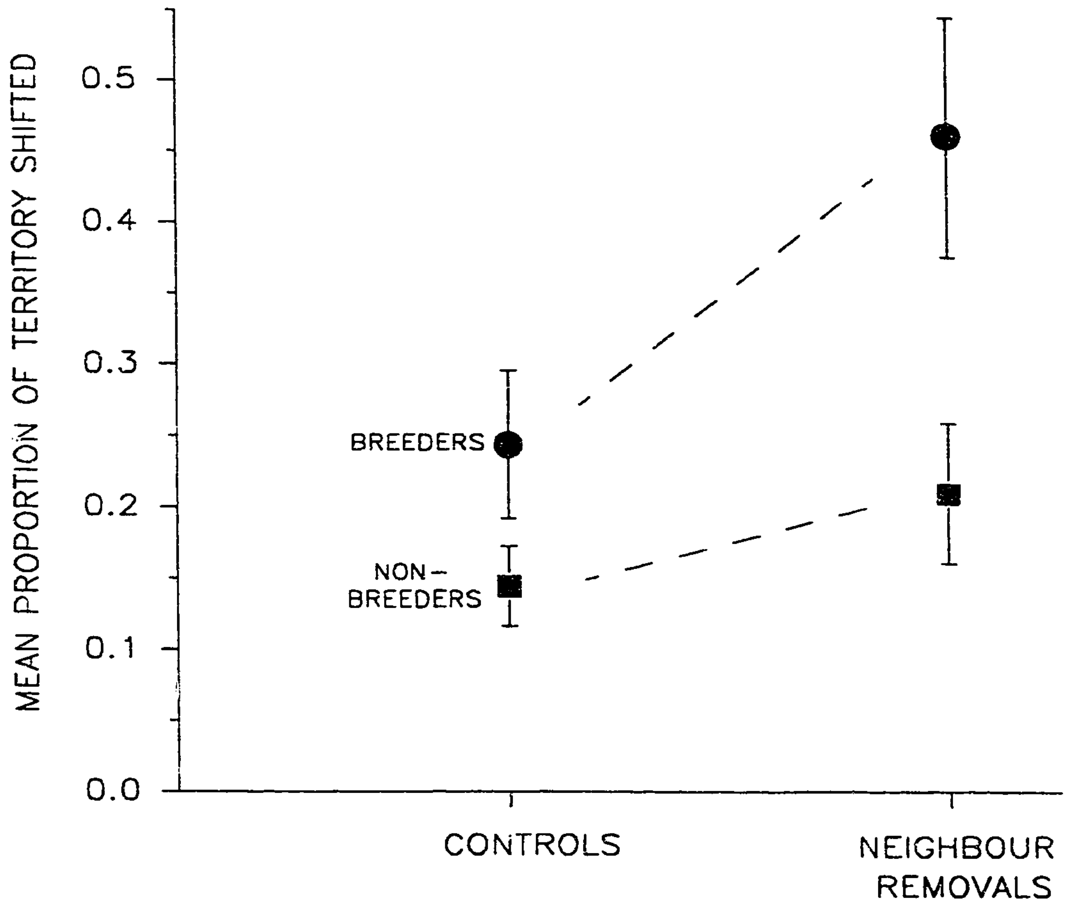

FIGURE 4.4. Mean proportions of territories shifted by control females and those subjected to neighbour removals (CHOICE EXPERIMENT). Females are also grouped by their reproductive status in the summer preceding the neighbour removals (BREEDERS and NON-BREEDERS). Territory shift was measured as the proportion of the individual's spring territory (following removals) which did not fall within the boundaries of its autumn territory (prior to removals - see Fig. 4.3.). Breeding females subjected to neighbour removals displayed higher proportions of territory shifts than any of the other three groups (see text). Error bars = ±1 SE. Samples sizes are 7 (BREEDERS, CONTROLS), 7 (BREEDERS, REMOVALS), 8 (NON-BREEDERS, CONTROLS), and 6 (BREEDERS, REMOVALS).

CHAPTER 5

NATAL PHILOPATRY IN RED SQUIRRELS

INTRODUCTION

The importance of natal dispersal to the ecology of animal populations was the focus of reviews by Lidicker (1975) and Gaines and McClenaghan, but a more recent review (Johnson and Gaines 1990) also pointed out the shortcomings of many dispersal studies. Our understanding of the proximate causes and evolution of dispersal has been severely hampered by the difficulty of monitoring individuals during the dispersal period. Most studies rely on the periodic relocation of previously-marked animals as a means of gathering information. Such indirect methods may lead to erroneous interpretations, make inter-study comparisons difficult (Gaines and McClenaghan (1980); Johnson and Gaines 1990), and provide little, if any information on the tactics offspring may use while dispersing. Advances in radio-telemetry have increased considerably the precision to which dispersal data can be collected (e.g. Holekamp 1986, Nelson and Mech 1987, Berger 1987, Wigget *et al.* 1989, Beaudette and Keppie 1992, etc.).

Despite the scarcity of direct measurements of dispersal, two general patterns have been shown convincingly. First, natal dispersal of mammals is known to be commonly philopatric; that is, individuals often establish residence at locations that do not preclude potential contact with the parents (Anderson 1989). Such behavior has been shown to be widespread in both gregarious and solitary taxon (Greenwood 1980, Armitage 1981, Waser and Jones 1983, discussed by Jones 1984). In fact, Anderson (1989) recently argued that rodents are philopatric by nature, and that emigration (settlement which precludes contact with the parents) is likely promoted through aggression from residents. Philopatry presumably arises because the costs associated with emigration outweigh potential benefits (although these costs have not been clearly demonstrated - see Beaudette and Keppie 1992). However, there are also three hypothesized costs to philopatry as outlined by Moore and Ali (1984) and Johnson and Gaines (1990): inbreeding depression, competition with kin for mates, and competition for environmental resources.

The second general pattern is that natal dispersal in mammals is male-biased. Greenwood (1980) hypothesized that this was due to most mammals being polygynous. Because females compete for resources while males compete for females, females gain more by remaining philopatric. Dobson (1982) generated predictions of which sex should be the predominant disperser under different mating systems, based on the three hypothetical costs of philopatry (inbreeding, mate competition, resource competition). He then tested the predictions of these hypotheses through a survey of the existing literature. In most polygynous and promiscuous species, males were identified as the predominant disperser, which was predicted if competition for mates made philopatry relatively more costly for males. Conversely, studies of monogamous species did not report sex-biased dispersal, as predicted by resource competition and competition for mates. There were some exceptions to these general patterns, however. For example, Dobson listed two instances, involving arboreal squirrels, where a clearly promiscuous species showed no sex-biased dispersal (Thompson 1977, 1978; Kemp and Keith 1970; Rusch and Reeder 1978; Smith 1968). However, these studies did not focus on natal dispersal

(Thompson 1978 being the exception), and information concerning dispersal was interpreted from indirect measures and very small samples.

Clearly, understanding dispersal in vertebrate populations will require study of those cases where exceptions to general trends occur (Pusey 1987). A recent example is Ribble's (1992) report of female-biased dispersal in a monogamous rodent. The purpose of this study was to document natal dispersal in a promiscuous mammal, the North American red squirrel (*Tamiasciurus hudsonicus*). I monitored individuals through the period of *attempted dispersal* (exploratory movements prior to settlement - see Holekamp 1984a), and determined if they were successful in acquiring a territory (i.e. dispersing). Knowledge of the precise origin of each offspring, and the movement patterns of adults, allowed me to judge where settlement occured in relation to the natal range. Specific objectives were to (1) determine the philopatric tendencies of offspring, (2) provide information on the means by which offspring disperse, and (3) compare dispersal between male and female offspring. The latter was designed to include tests of behavioral differences between male and female siblings.

METHODS

GENERAL METHODS

A 30 m interval grid was set up in approximately 1.75 km^2 of jack pine forest (*Pinus banksiana*) near Fort Assinboine, Alberta. Details on the study area and the natural history of the squirrel population are given in Chapter 1 and 2. Each Spring (25 April - 15 May) and Fall (23 August - 1 September) all middens in the study area were live-trapped at least once each day, weather permitting. See Chapter 2 for details of the efficiency of the live-trapping sessions. Squirrels trapped for the first time were marked with numbered metal eartags; females were equipped with small, colored tags threaded over the metal eartag, facilitating identification at a distance. Sex, weight, reproductive condition (Price et al. 1986) and behavior upon release were recorded for each trapped animal. Individuals trapped and released on their own territory often vocalize aggressively ('rattle' - Lair 1990), whereas trespassers remain silent, or are immediately chased off by the resident squirrel. From this information, along with recapture frequency and visual sightings, I was able to positively identify each territory owner.

We identified postpartum females by a drop in body mass (approximately 10%) and/or the presence of elongate nipples and matted fur. These females were equipped with radio-collars and subsequently located in their respective nests. Offspring were removed temporarily from the nest, and their sex was noted. Each litter was revisited approximately three weeks later, and the offspring were given metal and colored eartags (as above).

GENERAL MOVEMENT PATTERNS

When possible, offspring were fitted with radio-collars when they attained a body mass of ≥ 115 g (approximately 64 days old). Priority was given to those offspring living on or near the periphery of the study area. Collared offspring were located at least once every three days, using hand-held antennas and receivers, during the hours when the juveniles were most likely to be active (approximately 0800 - 1100, 1330-1700 h, Larsen and Boutin pers. observ.; *c.v.* Wauters *et al.* 1992). During extremely hot weather, or during periods of intensive rain, observations of the juvenile squirrels were not used to calculate movement indices, but did serve for determining whether the animal was alive or not, as did observations made outside the peak activity hours (above).

If a collared juvenile could not be located by extensive foot-tracking, the animal was located with tower antennas set up on the highest points near the study area and/or in the bed of a truck. Using this system, transmitters could be detected within a 2.25 km radius of the study site. The locations of offspring (collared and uncollared) were recorded whenever they were observed. When possible, body mass was measured following each observation, by setting traps on the natal territory and/or at the offspring's immediate location.

Movements of adults away from their home territory were recorded in order to assess whether the distances offspring dispersed were within the potential range of the mother. For adult females, data was collected through trapping records, locations determined through telemetry, and visual observations. For adult males, observations mainly consisted of trapping records, and a relatively small number of locations established through telemetry.

I calculated an index of movement by individual offspring prior to their settlement, using the locations of collared offspring taken every third day for fifteen days (= 5 locations). The distances from the natal midden to each location, and the distances between successive locations, were summed. This produced a Movement Index that incorporated the tendency of an individual to move away from the natal midden, as well as its tendency to move to different locations. Dates of collar attachment varied considerably, both across and within years, but all offspring were equipped with collars at virtually the same body mass and age. Offspring which obtained a territory prior to collection of the fifth successive location were excluded from the analysis. I used this index to provide a test of sex-biased movements, and also to determine if individuals displaying relatively less movement prior to settlement tended to acquire territories closer to the natal midden.

MAPPING AND CLASSIFICATION OF TERRITORIES

Data used to map the territory boundaries of mothers and dispersing offspring were obtained in several ways. When possible, focal observations were carried out on the squirrels while they were equipped with radio-collars. During these periods, territorial behavior and locational data were recorded (following Price et al. 1986). This information was supplemented with other incidental observations made of the squirrels. It was not always possible to collect data sufficient to delineate accurately each territory's boundaries, but the data did permit me to determine where the territory of an offspring lay in relation to that of the mother's. When sufficient data existed, territory boundaries were constructed by joining the outermost locations of territorial behaviors such as vocalizations (Boutin and Schweiger, 1988).

I classified all dispersing offspring according to the distance of their acquired territories from their mothers'. Class 1 offspring were those acquiring territories on or contiguous to their mother's territory. Class 2 offspring were those settling on territories not contiguous with the mother's territory. My reasoning behind this was as follows: territories belonging to Class 1 dispersers could be secured without leaving the familiar, protected confines of the mother's territory (at least during the early stages of the territory acquisition), while a Class 2 disperser was required to leave its mother's territory, and interact with relatively unfamiliar squirrels along all sides of its chosen territory.

Particular attention was paid to offspring that obtained the entire natal territory, along with its midden (see Price and Boutin in press and Boutin *et al.* in press). Unless the mother was outfitted with a radio-collar at the time, I used repeated trapping of the study area to determine whether these transfers of ownership were accomplished through death or abdication by the mother.

EXPERIMENTAL REMOVAL

During 23-25 August 1989, I conducted a separate experiment in which 53 resident adult squirrels were permanently removed from an experimental grid. The purpose of this experiment was to test the territory fidelity of female squirrels that had produced offspring (Chapter 4). Removal of immigrating squirrels from the experimental area continued for another five days. Following this, some of the vacated territories were claimed by untagged offspring (originating off the grid). This provided an opportunity to test the sex ratio of these emigrants against the sex ratio of the monitored 1989 cohort.

RESULTS

NUMBER OF JUVENILES MONITORED

One hundred thirty-four offspring emerged from nests during the study, and 107 reached 115 g body mass (approximately 64 days of age). Of these 107 individuals, 90 received radio-collars and provided detailed information on movements and settlement. Data were also obtained from some of the 17 uncollared individuals through trapping and visual observations. It is highly unlikely that the disappearance of emergent offspring prior to collaring was attributable to anything but death, for two reasons: (1) offspring are normally not weaned until 70-80 days of age and (2) offspring weighing < 115 g were rarely observed more than 75 m from their respective natal middens (8/127 offspring). For similar reasons it is unlikely that the 17 uncollared individuals moved out of the study area, especially given that collared animals were extremely philopatric (see below), and that the natal middens of uncollared offspring were located, by design, in the center of the study area.

'ATTEMPTED' DISPERSAL

General Movement Patterns - Offspring that moved off of their natal territories did not abandon their natal territories; instead, they made circling forays throughout neighboring areas (Fig. 5. 1). Radio-collared juveniles were usually observed within a 150 m radius of their natal midden (X=126.1 m, SE=3.72, 75th percentile=159.8 m, n=752), although one individual was located over 900 m away. Collared individuals found far from their natal midden (>500 m) were always located in spruce/tamarack bogs or aspen/birch parkland. These animals returned to their natal middens (unless killed while on the foray). Offspring that had not yet claimed a territory rarely stayed overnight away from their natal midden (n=6); when they did they were in tamarack bogs, where adults were not resident, and these offspring eventually returned to their natal territory. These and other less extensive forays continued until the animal was killed or obtained a territory.

The distance offspring were observed from their respective natal middens did not appear strongly related to age or body mass. Multiple regressions of distance on body mass and age were significant for the first two years of the study (1988: F=3.99, df=3,199, P=0.009; 1989: F=3.52, df=3,98, P=0.018) but not in 1990 (F=1.09, df=3,83, P=0.357). However, the percentage of variation in distance explained by the independent variables in any one year was very low (R^2s=0.09, 0.09 and 0.04, respectively). The maximum number of observations obtained from one individual animal was 13, and the mode in each year was 1.

Tests for sex-biased movements - I tested for differences between the sexes on several levels, and found no evidence of sex-biased movement patterns. First, I compared the maximum movements (meters) recorded for collared male and female offspring. I used only data collected from those individuals that were alive for 12-15 days prior to death or settlement, providing 4-5 locations for each individual offspring. There was no significant difference between the sexes (normal approximation to Mann-Whitney U, Z=-0.463, P=0.637). The mean maximum distance from the natal midden observed for 27 collared males was 274.7 m (SE=43.25), and for 28 females it was 298.8 m (SE=61.68). If these maximum movements were converted to territory increments, based on the average diameter of territory (approximately 45 m), there was still no difference between the sexes (Kolmogorov-Smirnov 2-sample test, D=0.159, 0.1<P<0.2, Fig. 5.2).

Sibling pressure (i.e. family size) may have a potential influence on the movements of individual offspring. To control for this, I conducted a second test for sex-biased movements by comparing the movements of pairs of male and female siblings, that had no other siblings alive during the time they were attempting to disperse. Siblings were located usually at approximately the same time each day, which controlled for potential temporal variations in movements. I took the mean distance recorded for the male sibling over the course of the observations, and compared it to the mean distance recorded for its sister over the same time period. The number of observations per sibling pair ranged from two to twenty (X=7.9, SD=4.81). A Wilcoxon paired-sample test (Zar 1984) revealed no significant difference between the distances recorded for male and female siblings (T=85, P=0.299, n=21 pairs of siblings).

I conducted a third test for sex-biased movements, similar to the previous one. However, in this test, I was concerned whether either sex moved further from the natal midden as time progressed (=increasing age). The measurement used here was the difference in the distances recorded for each male and female sibling on each observation day (i.e. distance of male sibling from natal midden minus distance of female sibling from natal midden). I used only data that was taken every third day, in order to standardize for age effects across the sibling pairs. Changes in the measurement through time were analyzed using an F-ratio statistic, based on Hotelling's T^2 test (Morrison 1976). This test is a form of multivariate analysis of variance (F ratio) applicable when one has repeated measures on a series of individuals (in this case, offspring pairs) and is interested in determining if the mean of the measurement remained constant over time (Fruend et al. 1986). This test also failed to reveal any differences between the two sexes (F=0.306, df=6,7, P=0.915, n=13).

Two additional tests failed to reveal sex-biased movements. The sex ratio of untagged juveniles (i.e. those originating off the study area) trapped on the study area in 1989 and 1990 did not differ significantly from the known ratio of males to females in each year's cohort on the study area (binomial test, 1989: 14 males, 12 females, known ratio 0.546, P=0.861; 1990: 11 males, 6 females, known ratio 0.556, P=0.393). Finally, there was no significant difference in the Movement Index obtained for 25 female and 21 male juveniles (normal approx. to Mann-Whitney U, Z=-1.213, P=0.225).

DISPERSAL

Territory settlement - Sixty-seven offspring obtained territories during the course of this study (31 males, 36 females, not significantly different from a 1:1 ratio, Z=0.669, P=0.503). Mean settlement distance was 86.1 m (range 0 - 323, 75th percentile=122.2). Just over half of the individuals (34) settled on or adjacent to the natal territory (=Class 1, Fig. 5.3). There was no significant difference in the settlement distances of the two sexes, in terms of actual distance (X_{male}=85.14, X_{female}=86.9, normal approx. to Mann-Whitney U, Z=-0.743, P=0.458) or in territory increments (Kolmogorov-Smirnov 2-sample test, D=0.13, P=0.917, Fig. 5.3; no difference within years, all P>0.45).

Interestingly, there was no difference in Movement Index values between offspring that eventually acquired Class 1 and Class 2 territories (Mann-Whitney U=172, $n1,n2$=16,18, P>0.20), suggesting that individual obtaining territories relatively close to home were not traveling any less beforehand. There also was no significant difference in the relative proportions of male and female offspring acquiring Class 1 and Class 2 territories, over the three years (*Ho: sex, territory category and year mutually independent* - G=3.08, df=7, n=67, P=0.878).

In only eight cases did a juvenile assumed complete ownership of its natal midden and territory; in five instances the mother was known to be alive during the transfer of ownership (in one of these cases, the offspring which first assumed control died, and was replaced by a sibling). Sex ratio of the offspring obtaining full ownership of their respective natal middens and territories was 5 males:3 females.

Test for Sex-biased Settlement in Removal Area - Only 10 offspring (6 males, 4 females) settled on the artificially vacated territories (prior to September 20, 1989). The sex ratio within this sample was not significantly different from that observed in the grid cohort (cohort ratio 0.546:0.454 male:female, binomial P=0.236).

MOVEMENTS OF ADULTS

Adult squirrels were usually trapped and observed within the borders of their respective territories. However, a large number of observations were made of adult squirrels more than 45 m from their respective middens. Figure 5.4 shows locations of adult squirrels relative to their home midden. These data do not represent a random sample of adult movements, particularly for females, because visual searches and trapping efforts were focussed around natal territories for most of the summers, increasing the likelihood that mothers would be observed close to home. Still, it is clear that adults of both sexes will move considerable distances off of their home territories, and these movements at the very least equal the dispersal distances exhibited by offspring (Fig. 5.3). Most observations of males off their home territories were made in early spring, when males spend considerable time away from their home territories searching for females in estrus ("spring shuffle" -Rusch and Reeder 1975).

DISCUSSION

Three important points emerge from the data. Firstly, offspring attempting to disperse did not abandon their natal territory permanently when searching for a location to settle; instead they conducted forays, and continued to return to the natal territory until they succeeded in acquiring a territory. Secondly, a variety of tests failed to detect sex-biased patterns in both movements prior to settlement, and actual dispersal distances. Thirdly, dispersal distances are extremely limited in thispopulation, with no offspring emigrating out of potential contact with their natal territory, their mother, and likely their father. Class 1 and Class 2 designations should not be construed as representing philopatric versus non-philopatric settlement. Even though Class 2 individuals settled on territories geographically separated from their natal territories, the potential for contact between them and their natal territory (and mother) remained high. Thus, all offspring which acquired territories in the Fort Assiniboine population were philopatric.

Lidicker and Stenseth (1992) outlined dispersal movement, or "quasi-dispersal", as taking three forms: (1) Nomadism, which occurs when a clearly-defined home range does not exist, (2) Shifting, the gradual relocation of a home range through changes in boundaries, and (3) Excursions, or short-term explorations out of the home range. Excursions have been reported in a variety of species (see review by Lidicker 1985, also Holekamp 1984b), but, as discussed by Lidicker and Stenseth, this and other movement categories are not clearly defined. Red squirrel offspring definitely do not display nomadism; the mother's territory is maintained as a home base while an attempt is made to acquire a territory. The forays away from the mother's territory could be classified as excursions, but in many cases settlement occured on an area either in or overlapping the mother's territory. Hence, this could be viewed as "shifting". However, offspring acquiring Class 1 territories do not exhibit less movement beforehand suggesting that these offspring are not inclined towards Class 1 settlement. This, coupled with the fact that age and weight were poorly related to the distance offspring traveled, indicates that acquisition of Class 1 territories did not follow a true "shifting" sequence, such as that seen in Belding's ground squirrels (Holekamp 1984b).

The absence of sex-biased movements and dispersal in the study population is predicted if competition for environmental resources is hypothesized to be the major factor influencing dispersal (Dobson 1982). One would expect to see sex-biased dispersal in a promiscuous mating system only if the acquisition of resources is relatively more critical to the reproductive success of one sex. Certainly, adult female red squirrels require territories and their resources for successful rearing of offspring, moreso than adult males. However, the acquisition of a territory prior to the first winter is crucial to the survival of both male and female offspring (Rusch and Reeder 1978, Zirul 1970, Smith 1968, Larsen and Boutin pers. obs.); failure to do so reduces any chance of survival, much less reproductive success. It is therefore quite reasonable to expect that resource competition should not result in sex-biased natal dispersal in this population.

The cost of inbreeding and mate competition for philopatric individuals, should they exist, must always be viewed in relation to the costs of emigrating (Anderson 1989). Waser *et al.* (1986), for example, presented models of dispersal which indicated that inbreeding depression would be less costly than mortality incurred during emigration. The potential for inbreeding may be minimized by kin discrimination (Hoogland 1992), the death of fathers prior to the maturation of females (Schwartz and Armitage 1980), and/or some other mechanisms. Unfortunately, I could not determine if inbreeding between close kin resulted from the strong philopatric tendencies of dispersing offspring (e.g. pikas, Smith 1987), but the data clearly indicates that emigration is not a viable tactic. Thus, I may conclude that if inbreeding does exist in the study population, it is obviously less costly than attempted long-distance dispersal. Also, the continuous habitat at Fort Assiniboine would ensure that some gene flow existed, despite philopatry.

An argument can be made that intrasexual mate competition should be important in determining dispersal patterns in this population, and that male-biased dispersal should be present. Mothers and daughters should experience no significant competition for mates, given the promiscuous mating system and the short, asynchronous estrus periods. However, the potential for mate competition between a male offspring and its father should increase the closer the offspring settles to its natal territory. If male offspring emigrate (or settle relatively farther away) this competition should be lessened. Obviously, this is not the case in the Fort

Assiniboine squirrel population, but without a knowledge of paternity I cannot determine how female mate choice and spatial and temporal overlap of sires and reproductively-mature sons might affect mate competition. If competition for mates exists between male squirrels, regardless of their relatedness, the continuous habitat at Fort Assiniboine suggests that a dispersing male offspring is quite unlikely to find an area where competition do not exist. Thus, emigration is less likely to increase his potential fitness.

The extreme high level of philopatry demonstrated in this population is due, in part, to the fact approximately half of the dispersing offspring acquired territories on or adjacent to their natal territories. Offspring likely become familiar with this area, both before and after they begin leaving the natal territory on their forays. This may make them more aware of a sudden territory vacancy, or allow them to gradually appropriate a territory through increasing familiarity with neighboring adults (*e.g.* Stamps 1987). One would assume that mothers assist their offspring in obtaining territories only if it does not limit their own future reproductive success (see Clutton-Brock 1991). Mothers could face resource competition from Class 1 offspring, but this may be relatively unimportant. Waser and Jones (1983), for example, found that philopatric tendencies were relatively frequent even in species with high adult survivorship.

Red squirrel offspring have been known to obtain part or all of the natal territory in more northern populations (Smith 1968, Zirul 1970, Price *et al.* 1986, Price and Boutin in press, Boutin *et al.* in press). Experimental manipulations at Fort Assiniboine indicate that this may be a deliberate action on the part of the mother (Chapter 4), as suggested by these previous studies. Smith (1968) and Zirul (1970) presented evidence that such nepotism was biased towards daughters, but their samples were small, and in the case of the latter, did not take into account the sex ratio of offspring at birth. Complete abandonment of the natal territory has been reported in several species (see review by Waser and Jones 1983). One notable example is Jones' (1987) study of banner-tailed kangaroo rats, where 32% of dispersing offspring remained on their natal mounds. In that study, neither sex was more likely to acquire the home mound, but such an event did confer survival advantages to the offspring (Jones 1986). I also found no evidence of sex-biased acquisition of the natal territory, but perhaps more importantly, only 7% of all dispersing offspring acquired a territory through direct maternal abandonment. Price and Boutin (in press) recorded a higher incidence of natal territory acquisition in dispersing red squirrels in the Yukon, but the fate of the mother was unclear. The rarity of maternal abandonment in the Fort Assiniboine population may have been due to the high adult survival during the study. Boutin *et al.* (in press) found that females were more likely to abandon their midden when neighbouring territories were vacated experimentally. Thus, maternal abandonment may be a more viable tactic in situations of lower density or higher adult mortality, when the mother is more likely to acquire a territory on her own.

One final point is worth noting. The longest movements off the natal territory by offspring occured in "sub-optimal habitat", or habitat unoccupied by resident adults. In some systems, such as pikas (Smith 1987), suboptimal habitat poses clear hazards for individuals attempting to disperse. At Fort Assiniboine, red squirrel offspring traveling or resting in bogs or muskeg are relatively free from potential harassment by resident adults. Hence, this habitat may be considered suboptimal only in that it does not permit overwinter survival. During dispersal it may actually facilitate long-distance forays. One may argue, but should not assume, that predation risks are higher in these areas. A decrease in adult survivorship and density may cause noticeable changes in offspring movements and settlement (*cf.* Waser 1985). Measuring the costs of attempted dispersal through both occupied and unoccupied habitat will be a difficult task, but it will be required if we are to understand fully this important component of dispersal.

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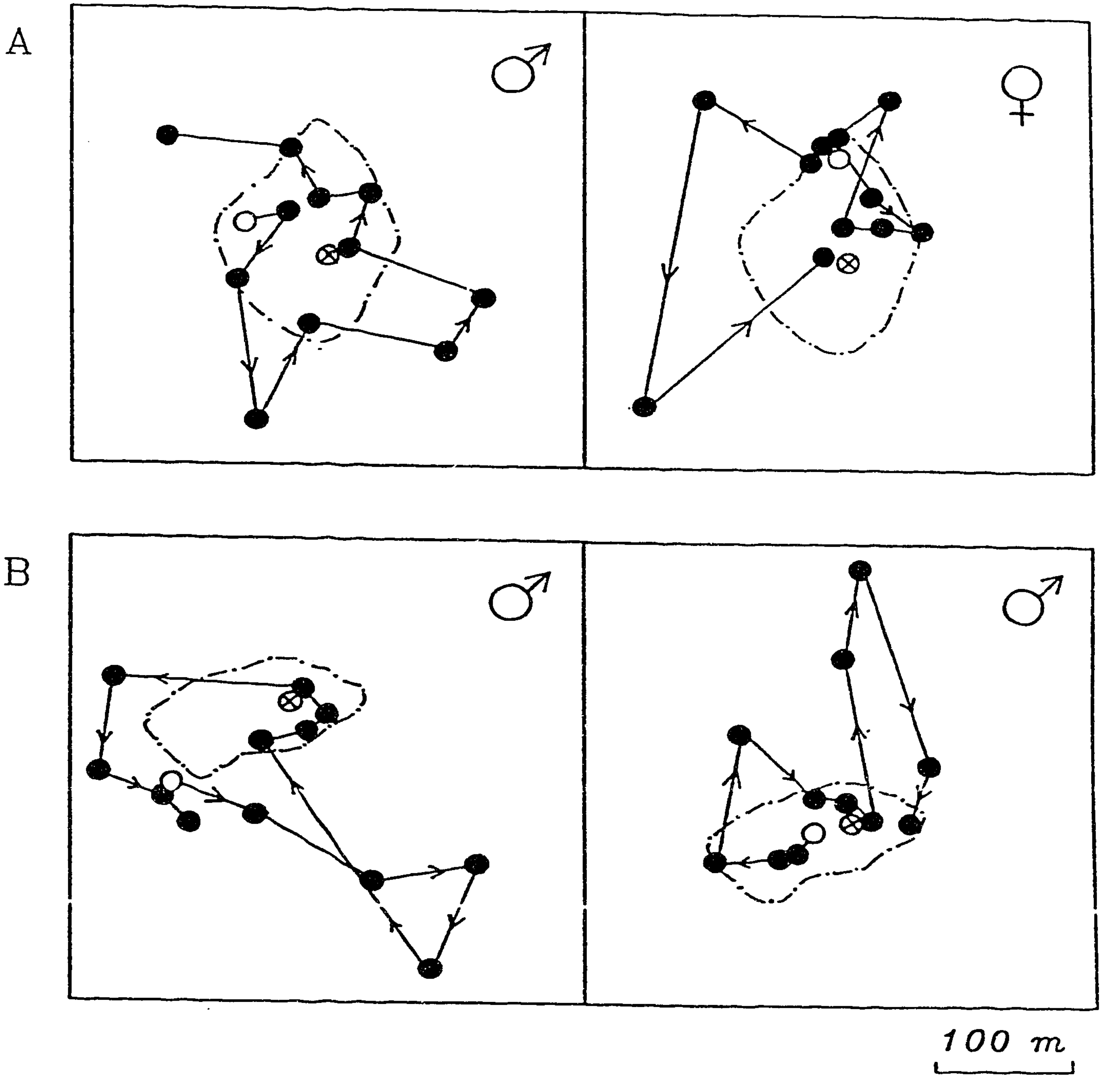

FIGURE 5.1. Movements of radio-collared red squirrel offspring. Figure 5.1A depicts the movements of a male and female sibling pair, weighing approximately 118 g each, that were tracked on July 23, 1989. Figure 5.1B represents the movements of another sibling pair, weighing 145 and 139 g respectively, that were followed on July 28, 1990. Starting at 08:00, each individual was located 12 times, at approximately 45 minute intervals. Open circles represent initial observations, with closed circles representing subsequent locations. Crossed circle indicates location of natal midden, and dotted line indicates boundaries of mother's territory.

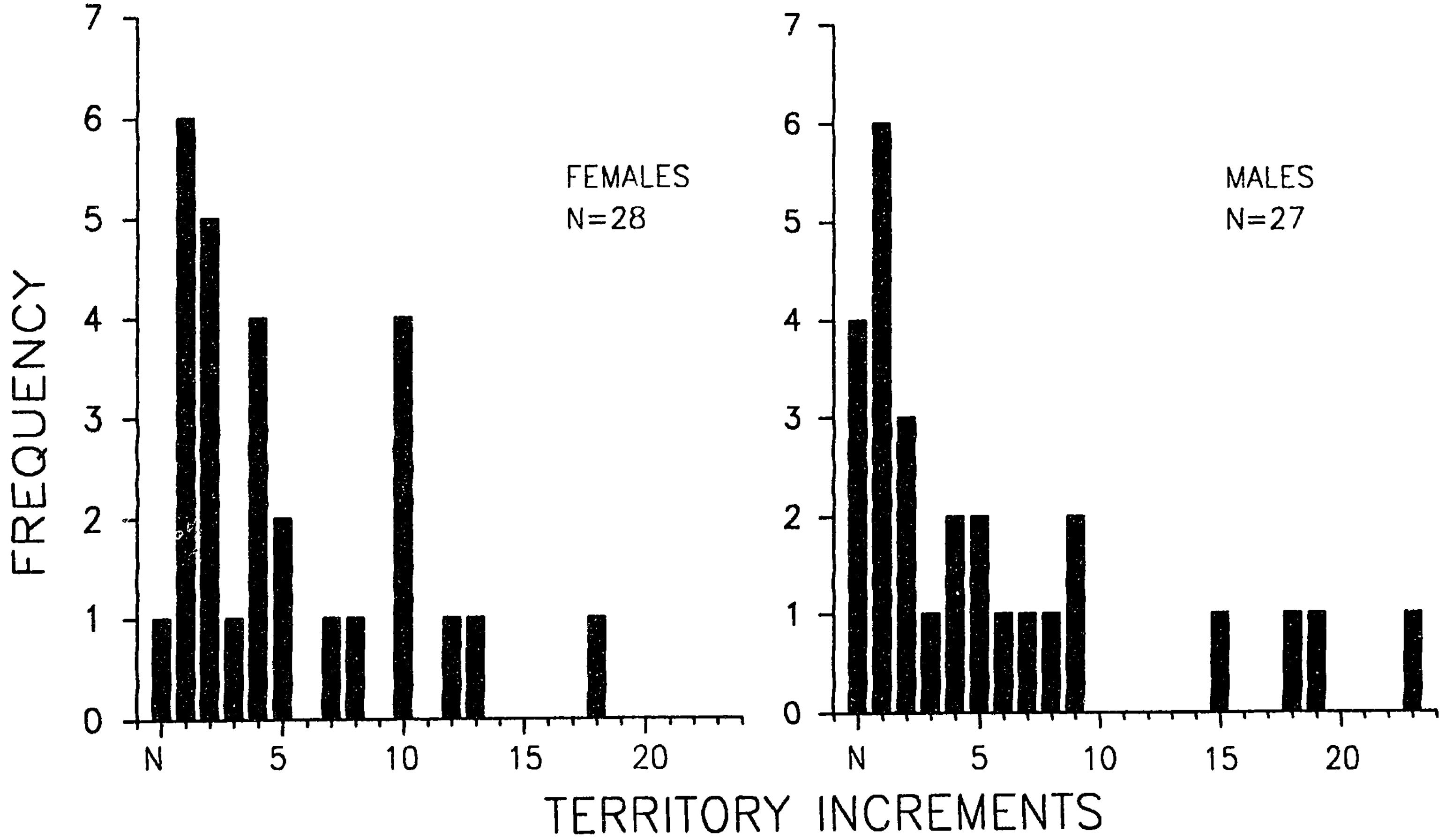

FIGURE 5.2. Maximum distances from natal midden recorded for radio-collared offspring, grouped by sex. Distance is given in territory increments. The first increment, N, includes all maximum distances that occured within the boundaries of the natal territory. Subsequent increments are in 45 m intervals, which represents the diameter of a circular territory of 0.65 h area (mean territory size).

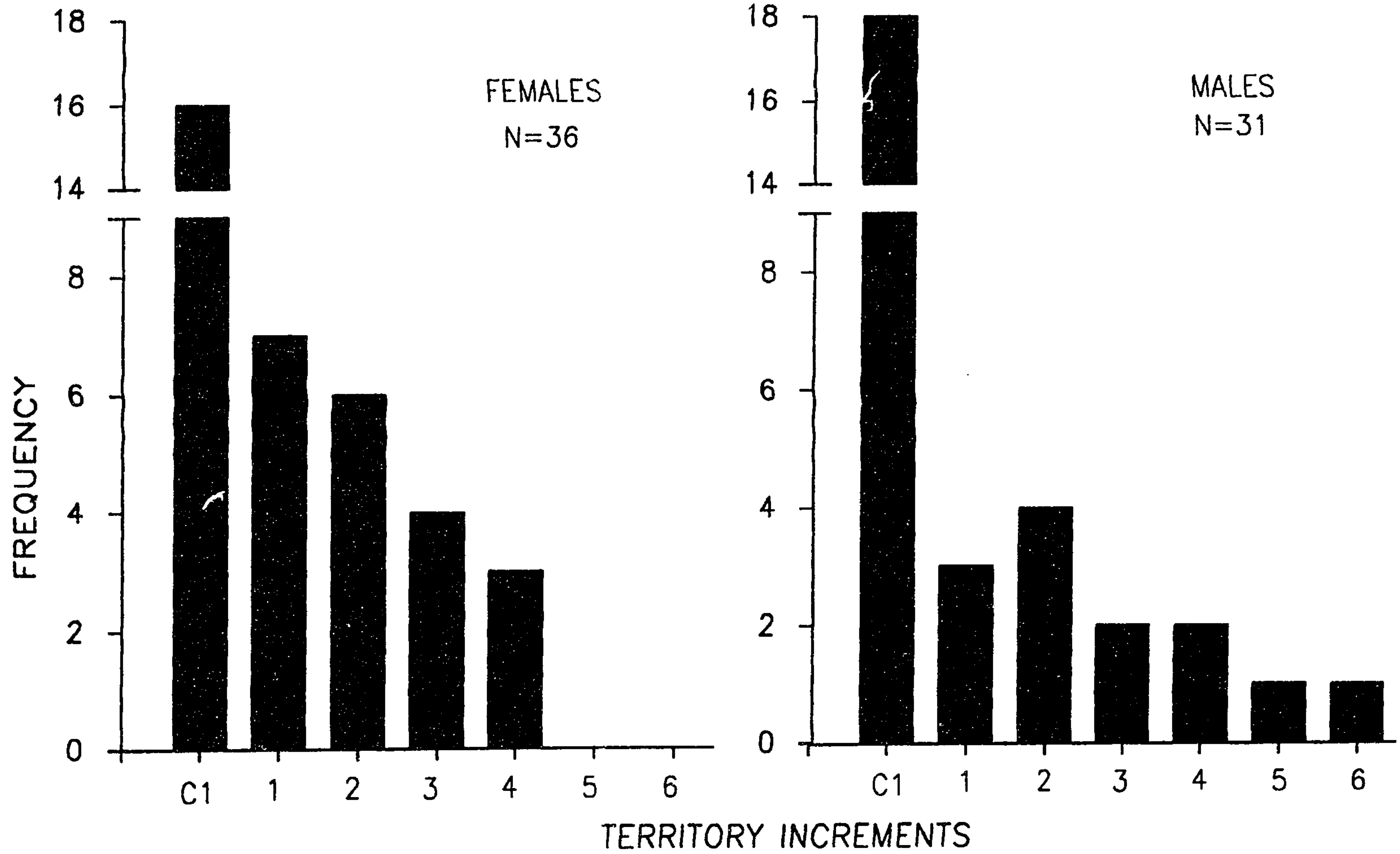

FIGURE 5.3. Locations of territories acquired by 67 dispersing offspring, as measured from their respective natal middens. The first interval, **C1**, represents Class 1 territories (see *Methods* for definition); otherwise, distance is given in territory increments (see Fig. 2 caption for details).

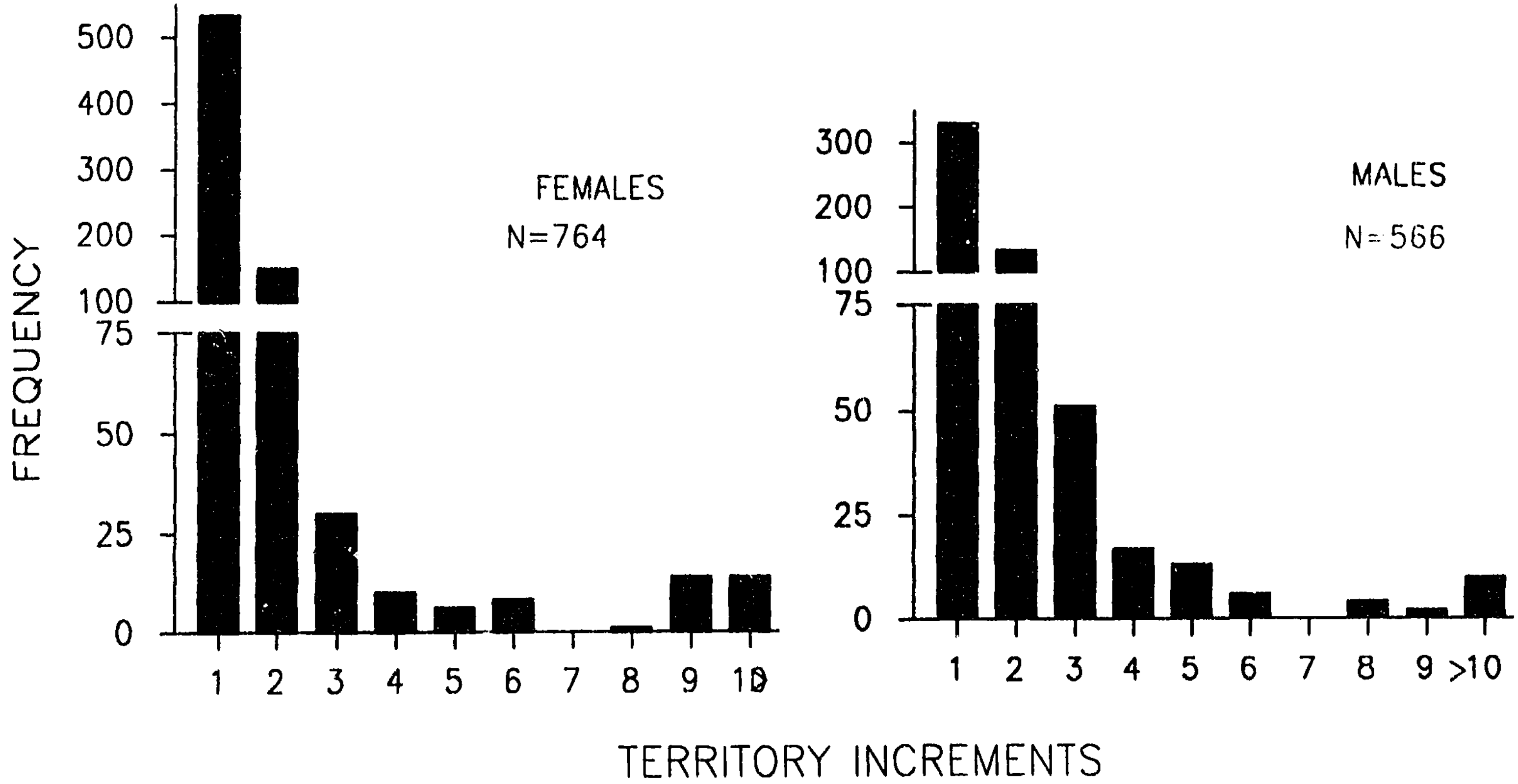

FIGURE 5.4. Locations recorded for adult, territory-holding squirrels, measured in territory increments (see Fig. 5.2 caption). Movements were recorded through visual observations, live-trapping records, and locations of radio-collared adults. Only movements >45 m are shown.

CHAPTER 6

GENERAL CONCLUSIONS

SUMMARY OF RESULTS

This study took place over three and a half years and provides only a brief glimpse of the ecological processes which may be influencing individuals and populations. Therefore, the results may not represent the processes going on in all red squirrel populations all the time. One still may conclude that in any given year, females in a population may not *necessarily* experience relatively high reproductive success simply because they bred earlier, were older or heavier, or had larger territories. However, as I have stated previously, it is difficult to decouple the relative effects of individual and territory quality. The results of Chapter 1 indicate that litter size is directly related to reproductive success: Females with larger litters tended to be more successful. The cone additions suggested that litter size may be limited, to some degree, by the amount of food available. However, these additions did not produce major increases in litter size, and food levels appeared to be much more important in affecting the timing and probability of estrous (Becker 1992).

There was some evidence that territory characteristics did influence reproductive success, in that higher tree density was correlated with increased juvenile survival after emergence (Chapter 1). If territory quality is important, then some females should try to acquire territories in areas with these characteristics, but the experiments outlined in Chapter 4 indicate that adult females do not relocate if given the opportunity. Instead, females that have bred react to nearby habitat vacancies by incorporating other middens into their territory. Offspring born in the subsequent year then have the opportunity to settle on the newly-acquired middens. Given that territory acquisition is a requirement for survival, females appear to be maximizing their chances for success by providing offspring with locations to settle. This may provide a partial explanation as to why settlement is so strongly philopatric in the population (Chapter 5). However, whether females or offspring actually benefit from philopatric settlement *per se* also is unclear (Chapter 5 and Appendix 5). Exactly where a female's offspring settle likely depends on several things, including the resources present on the female's territory and the probability of an offspring locating a vacant territory elsewhere.

I have mentioned several times in the preceding pages that adult survivorship was relatively high during this study, and that it may have had a strong influence on the patterns seen. Density-dependent factors may operate continuously, or they may be interrupted by stochastic processes. It has even been argued that such disturbances are necessary for long-term stability (Lewin 1986). The factors that influence reproductive success may very well be linked to density effects. For example, the empirical data in Chapter 2 suggests that previous breeding experience has no effect on reproductive success, but the removal experiments outlined in Chapter 4 suggest that females that have bred make adjustments to their territory in order to provide a territory to future offspring. On the surface, these findings appear to contradict one another. However, the high adult survivorship, which prevailed during the study may have prevented females from using tactics such as midden acquisition. Perhaps if females were monitored during periods of lower adult density, 'previous breeding experience' might prove to be a significant factor in determining individual reproductive success. Very low adult density may also mean that dispersing juveniles may not be restricted to settling in very close proximity to the natal midden, because vacant territories with good 'quality' resources are more readily available.

How unusual are the results of this study? Should one expect to be able to monitor a population at any given time, and detect the factors responsible for individual reproductive success? As mentioned above, litter size (and reproductive success) is influenced by some factor(s), and I hope this study will provide a basis for future, more directed experiments aimed at solving this problem. However, to reiterate a point made in Chapter 2, determining patterns and influences in reproductive success of small, relatively short-lived animals may prove more difficult than in longer-lived species, particularly those with extended periods of parental care (Clutton-Brock 1991). In the former, environmental influences such as food shortages and population density and predation (see below), may play a visible role in determining reproductive success within any one breeding period. Further, territory quality, age and previous breeding experience of females may play relatively more important roles in species that produce offspring more than two or three times in their lifetime (e.g. [illegible] *et al.* 1986, Clutton-Brock 1988).

FUTURE RESEARCH

The data used in completing this thesis was collected from Spring 1988 to Spring 1991, inclusive. Since then, I have been able to continue monitoring the reproductive success of females in the Fort Assiniboine population. With completion of the 1992 data set, it will now be possible to determine if certain factors have influenced the reproductive success of females over the course of their lifetime, which may encompass one, two, three or even four breeding episodes. It will not be too surprising if litter size and reproductive lifespan become the main causes of differential success. Certainly, females that bear only one litter of two offspring during their lifetime will be less likely to have surviving progeny than females that bear three litters of four offspring. If this is the case, three general questions still must be addressed:

(1) What factors influence litter size?

(2) What controls the age at which females first start breeding?

(3) what determines the longevity of females?

Solving the first two problems may prove difficult, but perhaps less so than answering the last question. Again, in populations of small animals such as squirrels, predation may prove to be a major influential, but unpredictable factor. Whether a female squirrel lives to breed another season may depend simply on whether a goshawk chooses to perch on a tree close to her territory.

Other intriguing observations have been made at Fort Assiniboine since completion of this study. The sudden appearance of litter sizes of five in 1992 was mentioned in Chapter 4. Also, the population has decreased significantly since 1991, yet during the winter of 1991/92, the numbers of offspring surviving their first winter equaled the sum total of the three previous years. Are these phenomena related, and if so, how? It has been said that Nature has nothing to gain by revealing itself (Hairston 1989). To understand fully the ecological processes at work in this and other populations will require long term study, coupled with carefully chosen experiments.

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APPENDIX 1

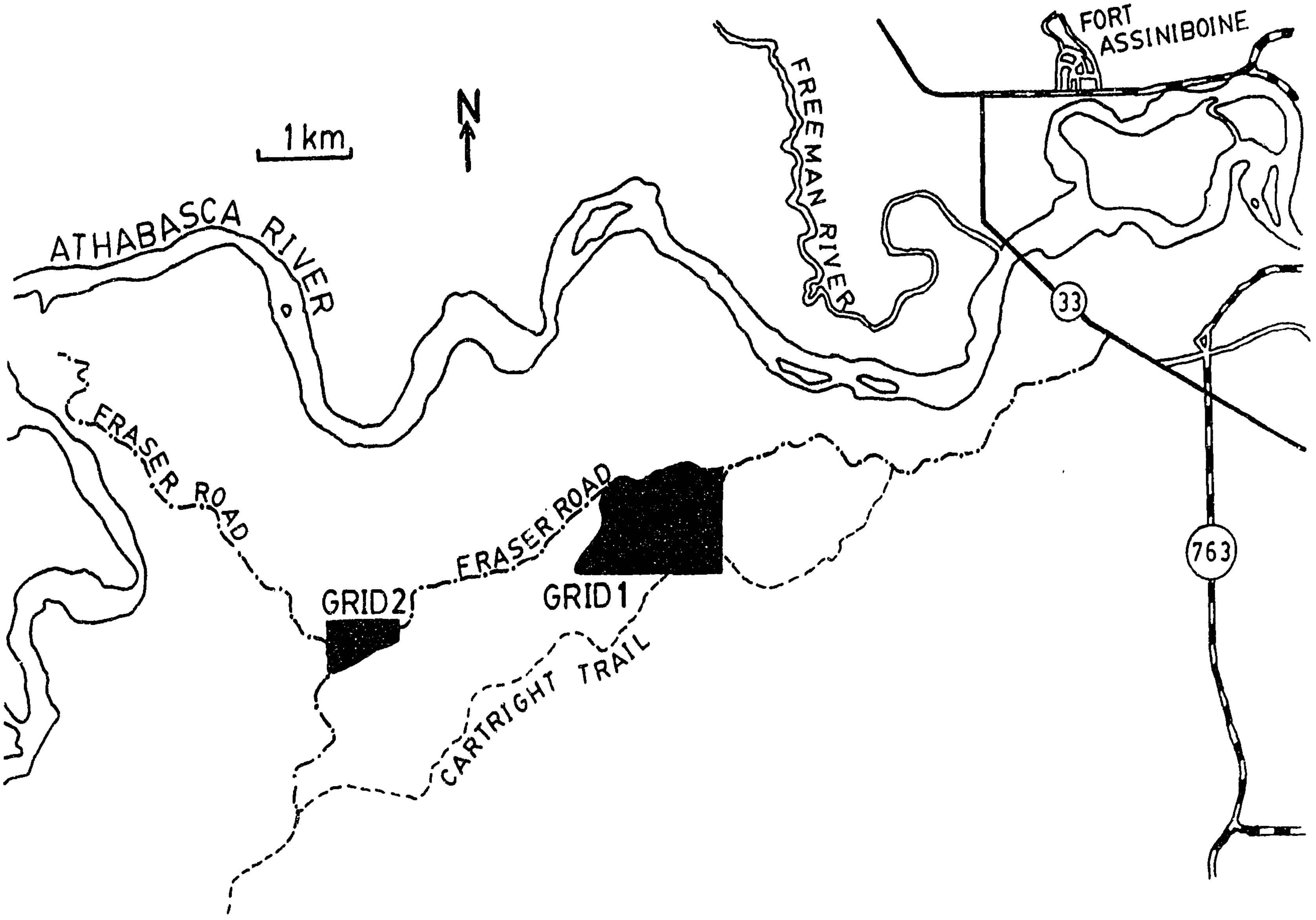
MAPS SHOWING PRECISE LOCATION OF FORT ASSINIBOINE STUDY AREA

MAP 1 - LOCATION OF STUDY GRIDS AT FORT ASSINBOINE

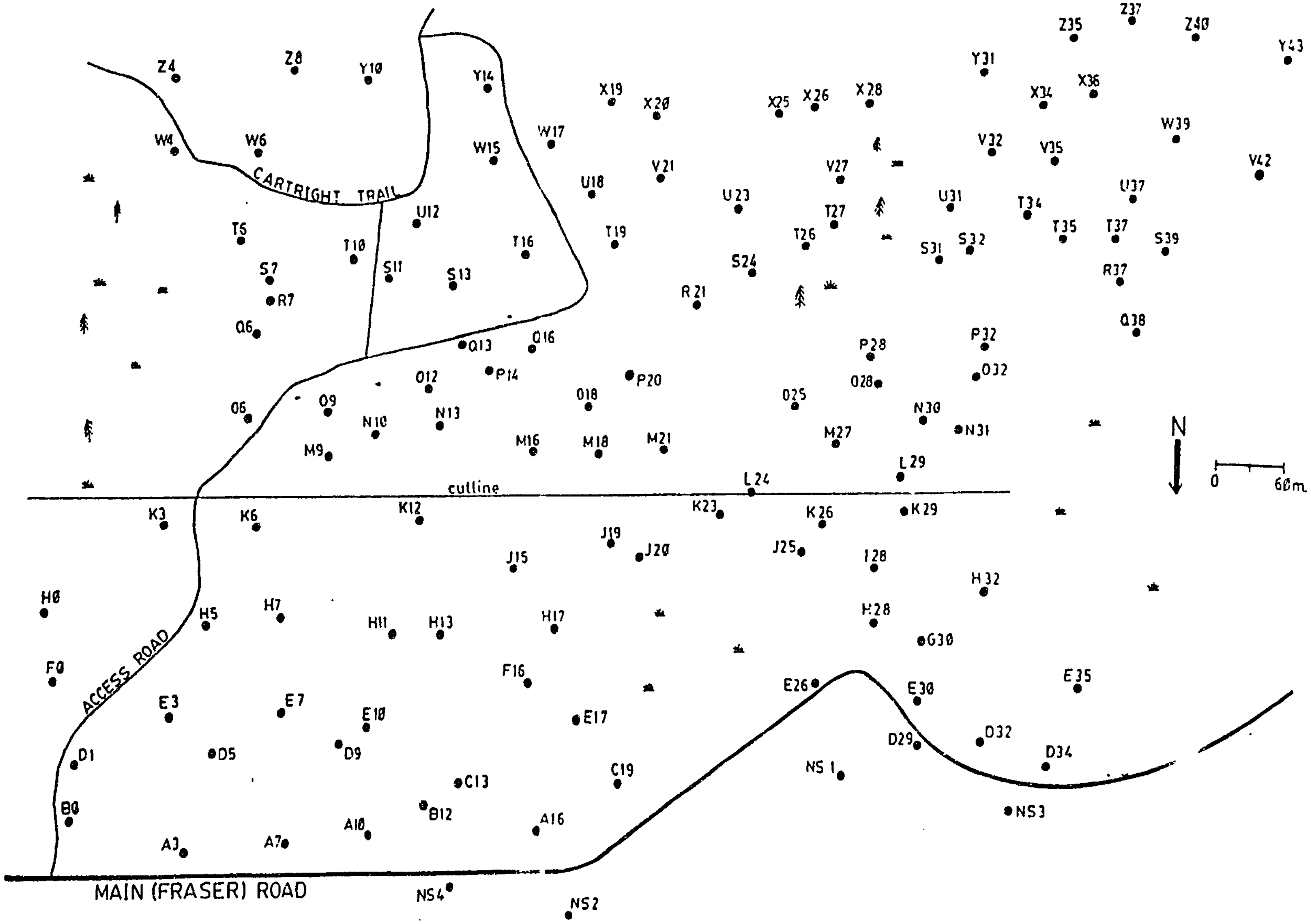
MAP 2 - GRID 1 SHOWING LOCATIONS OF SQUIRREL MIDDENS

MAP 3 - GRID 2 SHOWING LOCATIONS OF SQUIRREL MIDDENS

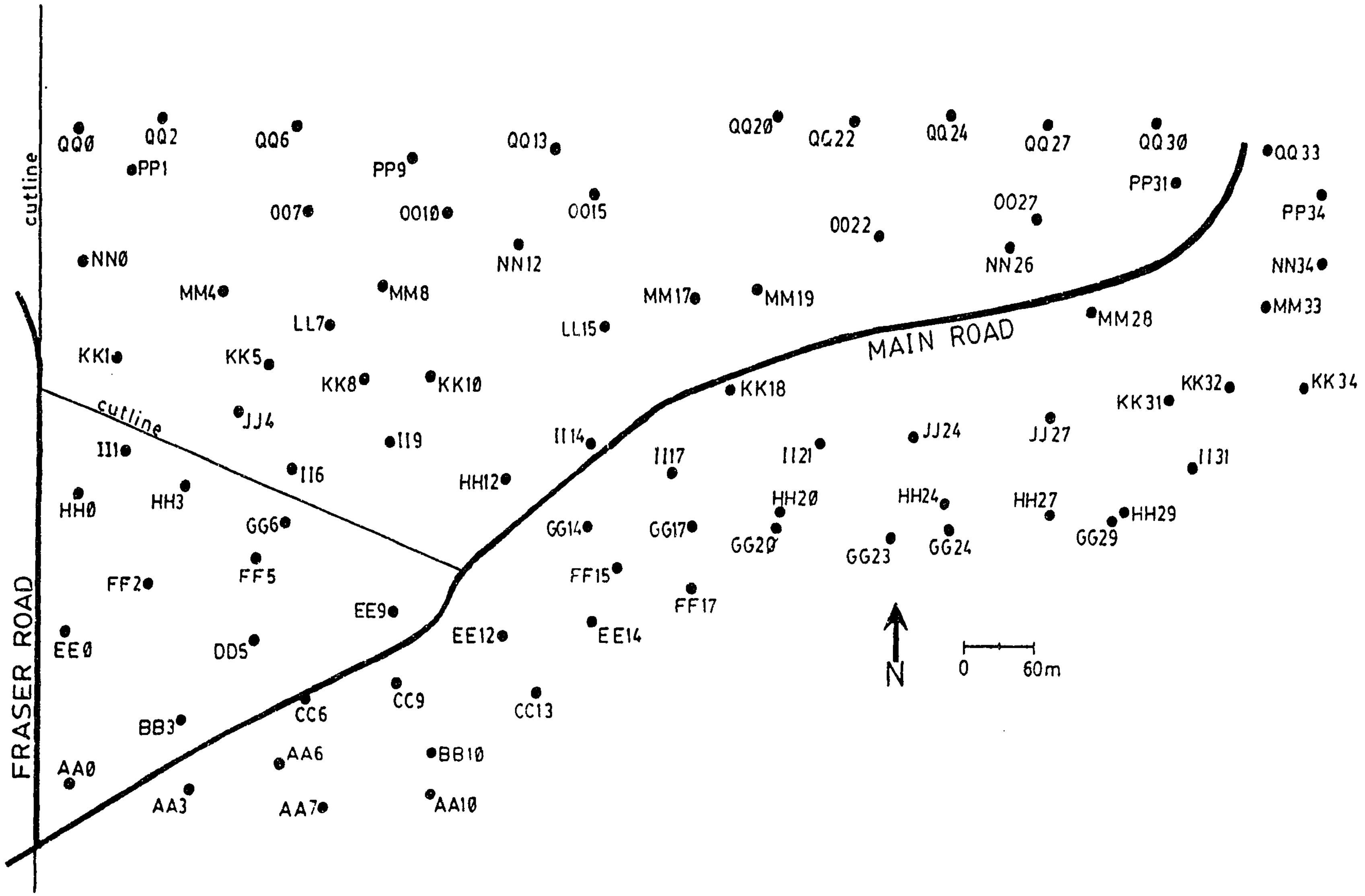
MAP 1 - LOCATION OF STUDY GRIDS AT FORT ASSINIBOINE



MAP 2 - GRID 1, SHOWING LOCATIONS OF SQUIRREL MIDDENS



MAP 3 - GRID 2, SHOWING LOCATIONS OF SQUIRREL MIDDENS



APPENDIX 2

DATA ON REPRODUCTIVE SUCCESS OF FEMALE RED SQUIRRELS

INCLUDING BODY MASS DATA, SETTLEMENT OF OFFSPRING AND TERRITORY QUALITY MEASURMENTS

KEY TO VARIABLES:
L# - litter identification number **YEAR** - year of litter
STATUS - experimental status of mother
MID - midden owned by mother **LS** - litter size
A - age of mother **AT** - breeding attempt of mother, i.e. first litter, second, etc.
POWT - postpartum weight **PRWT** - prepartum weight
SA* - did female survive to autumn? **SS*** - did female survive to spring?
PARTDATE - parturition date **#O** - number of offspring emerging from nest
#W - number of offspring weaned (reached age 80 days)
#A - number of offspring living to autumn **#S** - number of offspring living to spring
#C1 - number of offspring settling on Class 1 territories
#C2 - number of offspring settling on Class 2 territories
PROP - proportion of males in litter **AREA** - area of female's territory (h)
DBH - mean diameter-breast-height (cm) of pine trees sampled on female's territory
#PINE - number of pine trees sampled on female's territory

*binary data (0=no, 1=yes)

missing data indicated by period (.)

L#	YEAR	STATUS	MID	LS	A	AT	POWT
10	1988	CONTROL	NS3	1	.	.	.
25	1988	CONTROL	U12	1	.	.	.
2	1988	CONTROL	F0	2	.	.	.
13	1988	CONTROL	K12	2	.	.	260
20	1988	CONTROL	C19	2	.	.	206
26	1988	CONTROL	U18	2	.	.	.
1	1988	CONTROL	G30	3	.	.	.
4	1988	CONTROL	NS2	3	.	.	223
5	1988	CONTROL	H17	3	.	.	241
6	1988	CONTROL	D34	3	.	.	.
11	1988	CONTROL	N30	3	.	.	251
12	1988	CONTROL	O12	3	.	.	204
14	1988	CONTROL	O25	3	.	.	.
15	1988	CONTROL	S11	3	.	.	.
16	1988	CONTROL	H32	3	.	.	.
17	1988	CONTROL	O7	3	.	.	.
18	1988	CONTROL	T26	3	.	.	238
21	1988	CONTROL	T27	3	.	.	.
23	1988	CONTROL	?	3	.	.	.
24	1988	CONTROL	M18	3	.	.	.
3	1988	CONTROL	H28	4	.	.	257
7	1988	CONTROL	B12	4	.	.	.

L#	YEAR	STATUS	MID	LS	A	AT	POWT
8	1988	CONTROL	O18	4	.	.	233
9	1988	CONTROL	E35	4	.	.	.
19	1988	CONTROL	Q38	4	.	.	.
22	1988	CONTROL	Q6	4	.	.	.
27	1989	CONEADD	Z4	3	.	.	223
29	1989	CONEADD	F0	3	.	.	220
30	1989	CONEADD	X28	3	.	.	239
32	1989	CONEADD	HH27	3	.	.	233
45	1989	CONEADD	KK32	3	.	.	210
52	1989	CONEADD	PP1	3	.	.	238
53	1989	CONEADD	R7	3	.	.	232
66	1989	CONEADD	U37	3	.	.	224
86	1989	CONEADD	V21	3	.	.	220
44	1989	CONEADD	QQ13	4	.	.	221
57	1989	CONEADD	C13	4	.	.	248
58	1989	CONEADD	H17	4	.	.	241
61	1989	CONEADD	E35	4	.	.	218
84	1989	CONEADD	O25	4	.	.	233
40	1989	CONEDEL	Y10	2	.	.	.
89	1989	CONEDEL	KK1	2	.	.	218
33	1989	CONEDEL	W17	3	.	.	236
37	1989	CONEDEL	JJ24	3	.	.	.
41	1989	CONEDEL	Z37	3	.	.	230
43	1989	CONEDEL	MM19	3	.	.	195
50	1989	CONEDEL	G30	3	.	.	230
54	1989	CONEDEL	OO10	3	.	.	220
56	1989	CONEDEL	A7	3	.	.	223
62	1989	CONEDEL	C19	3	.	.	190
76	1989	CONEDEL	DD5	3	.	.	230
81	1989	CONEDEL	R36	3	.	.	.
49	1989	CONTROL	AA10	1	.	1	239
46	1989	CONTROL	EE9	2	.	1	228
59	1989	CONTROL	JJ4	2	.	1	237
75	1989	CONTROL	D29	2	.	1	213
82	1989	CONTROL	Y43	2	.	1	211
31	1989	CONTROL	JJ27	3	.	1	228
38	1989	CONTROL	HH29	3	.	1	214
39	1989	CONTROL	GG14	3	.	1	212
42	1989	CONTROL	NS2	3	.	.	225
47	1989	CONTROL	LL15	3	.	1	220
48	1989	CONTROL	NN34	3	.	1	227
60	1989	CONTROL	PP9	3	.	1	223
63	1989	CONTROL	GG6	3	.	1	198
64	1989	CONTROL	LL7	3	.	1	233
65	1989	CONTROL	T26	3	.	.	226
83	1989	CONTROL	Q38	3	.	.	247
85	1989	CONTROL	O18	3	.	.	252
87	1989	CONTROL	O12	3	.	.	207
88	1989	CONTROL	M30	3	1	1	195
90	1989	CONTROL	H32	3	.	.	220
91	1989	CONTROL	NS5	3	.	1	.
92	1989	CONTROL	ES1	3	.	1	.

L#	YEAR	STATUS	MID	LS	A	AT	POWT
93	1989	CONTROL	CRTRT19A	3	.	.	.
35	1989	CONTROL	NS1	4	.	1	208
36	1989	CONTROL	QQ20	4	.	1	223
55	1989	CONTROL	H28	4	.	.	239
96	1990	CONEADD	JJ24	2	.	.	222
97	1990	CONEADD	Y10	3	.	.	221
98	1990	CONEADD	GG14	3	.	.	243
105	1990	CONEADD	EE9	3	.	.	220
127	1990	CONEADD	AA10	3	.	.	230
128	1990	CONEADD	M16	3	.	.	217
129	1990	CONEADD	H2	3	.	.	225
143	1990	CONEADD	JJ4	3	.	.	224
156	1990	CONEADD	L24	3	.	.	220
159	1990	CONEADD	J11	3	.	.	.
126	1990	CONEADD	C13	4	.	.	.
135	1990	CONEADD	Q38	4	.	.	.
140	1990	CONEADD	T27	4	.	.	.
113	1990	CONTROL	R37	1	.	2	235
146	1990	CONTROL	AB3	1	.	.	.
108	1990	CONTROL	QQ13	2	.	2	230
109	1990	CONTROL	OO33	2	.	1	207
117	1990	CONTROL	D29	2	.	2	225
122	1990	CONTROL	NN30	2	.	1	222
124	1990	CONTROL	SH15	2	.	.	.
141	1990	CONTROL	J19	2	.	.	247
149	1990	CONTROL	WG8	2	.	.	.
152	1990	CONTROL	Z8	2	.	1	228
154	1990	CONTROL	II14	2	1	1	202
155	1990	CONTROL	V35	2	.	1	234
95	1990	CONTROL	H0	3	.	1	209
104	1990	CONTROL	NS2	3	.	.	221
110	1990	CONTROL	QQ6	3	.	2	225
111	1990	CONTROL	L18	3	.	.	.
112	1990	CONTROL	WG6	3	.	.	.
115	1990	CONTROL	L21	3	.	.	.
118	1990	CONTROL	WG23	3	.	.	.
120	1990	CONTROL	WG14	3	.	.	.
123	1990	CONTROL	F0	3	.	.	220
125	1990	CONTROL	JJ29	3	.	2	224
130	1990	CONTROL	SH1	3	.	.	.
131	1990	CONTROL	D5	3	.	2	231
132	1990	CONTROL	W6	3	.	1	215
133	1990	CONTROL	OO15	3	.	1	200
136	1990	CONTROL	X34	3	.	1	215
138	1990	CONTROL	D9	3	.	1	218
142	1990	CONTROL	CRTRT45	3	.	.	.
144	1990	CONTROL	CRTRT46	3	.	1	.
145	1990	CONTROL	U18	3	.	1	230
147	1990	CONTROL	R7	3	.	2	245
148	1990	CONTROL	WG24	3	.	.	.
150	1990	CONTROL	Z25	3	.	1	250
153	1990	CONTROL	HH27	3	.	1	200

L#	YEAR	STATUS	MID	LS	A	AT	POWT
157	1990	CONTROL	CC13	3	.	1	216
158	1990	CONTROL	NS5	3	.	2	.
137	1990	CONTROL	H5	4	.	1	236
203	1991	CHOICE	LL15	1	.	1	208
175	1991	CHOICE	CC13	2	.	2	.
192	1991	CHOICE	AA7	2	.	1	193
168	1991	CHOICE	QQ13	3	.	3	.
173	1991	CHOICE	II1	3	1	1	199
177	1991	CHOICE	WG25	3	2	1	.
164	1991	CHOICE	QQ6	4	.	3	235
166	1991	CHOICE	JJ29	4	.	3	243
172	1991	CHOICE	KK5	4	.	1	220
188	1991	CHOICE	GG23	4	.	1	224
199	1991	CHOICE	II14	4	2	2	202
170	1991	CONTROL	Z37	1	.	2	215
176	1991	CONTROL	WS 1	1	.	1	210
197	1991	CONTROL	Y31	1	.	1	204
186	1991	CONTROL	V32	2	3	1	231
187	1991	CONTROL	O18	2	2	1	210
190	1991	CONTROL	CC0	2	.	1	212
194	1991	CONTROL	T6	2	3	1	243
202	1991	CONTROL	T27	2	1	1	195
165	1991	CONTROL	OO15	3	.	2	232
169	1991	CONTROL	PP34	3	.	1	225
171	1991	CONTROL	J25	3	3	1	240
174	1991	CONTROL	H32	3	.	1	204
178	1991	CONTROL	D9	3	.	2	242
181	1991	CONTROL	S7	3	.	3	245
182	1991	CONTROL	H17	3	.	.	251
184	1991	CONTROL	E26	3	.	1	231
185	1991	CONTROL	V2	3	3	1	218
189	1991	CONTROL	NN26	3	.	1	200
191	1991	CONTROL	Q6	3	.	1	.
196	1991	CONTROL	O28	3	1	1	211
198	1991	CONTROL	R17	3	1	1	228
201	1991	CONTROL	K6	3	.	1	217
167	1991	CONTROL	F16	4	3	2	220
179	1991	CONTROL	D1	4	.	3	210
180	1991	CONTROL	X20	4	.	1	.
183	1991	CONTROL	O25	4	3	2	226
193	1991	CONTROL	M9	4	.	1	216
195	1991	CONTROL	Z8	4	.	2	216
200	1991	CONTROL	QQ27	4	2	1	205

L#	PRWT	SA	SS	PARTDATE	#O	#W	#A	#S
10	.	0	0	22APR1988	1	1	0	0
25	.	0	0	16APR1988	1	0	0	0
2	.	1	1	19APR1988	2	0	0	0
13	315	0	0	18MAY1988	1	1	1	0
20	240	1	1	13MAY1988	0	0	0	0

L#	PRWT	SA	SS	PARTDATE	#O	#W	#A	#S
26	.	0	0	04MAY1988	2	2	2	1
1	.	1	1	22APR1988	2	2	1	0
4	266	1	1	25APR1988	1	1	0	0
5	305	1	1	30APR1988	3	0	0	0
6	.	1	0	04MAY1988	3	0	0	0
11	275	0	0	31MAY1988	3	0	0	0
12	241	1	1	14APR1988	3	2	2	0
14	.	1	1	17MAY1988	2	1	1	0
15	.	0	0	20APR1988	3	1	1	0
16	.	1	1	06MAY1988	2	2	0	0
17	.	0	0	18MAY1988	3	0	0	0
18	273	1	1	27MAY1988	3	2	0	0
21	.	0	0	29MAY1988	2	2	2	0
23	.	1	1	29APR1988	1	1	1	0
24	.	0	0	01MAY1988	2	2	2	1
3	304	1	1	28APR1988	3	1	1	0
7	.	1	1	15APR1988	3	3	2	2
8	274	1	1	02MAY1988	4	3	2	2
9	.	1	1	24APR1988	2	0	0	0
19	.	1	1	17MAY1988	1	1	0	0
22	.	0	0	20MAY1988	4	3	2	0
27	226	1	0	25APR1989	2	2	2	0
29	240	1	1	30APR1989	3	0	0	0
30	232	1	1	04MAY1989	2	2	1	0
32	227	0	0	29APR1989	0	0	0	0
45	234	1	0	15MAY1989	2	0	0	0
52	253	1	1	17MAY1989	1	0	0	0
53	263	1	1	16MAY1989	2	0	0	0
66	240	1	1	26MAY1989	2	2	2	1
86	263	0	0	20MAY1989	1	1	1	1
44	200	1	1	11MAY1989	2	2	1	0
57	291	1	1	21MAY1989	3	3	3	0
58	305	1	1	18MAY1989	0	0	0	0
61	266	0	0	16MAY1989	4	3	1	0
84	285	0	0	16MAY1989	0	0	0	0
40	239	1	1	13MAY1989	0	0	0	0
89	243	0	0	27MAY1989	2	0	0	0
33	255	1	1	12MAY1989	3	3	2	1
37	257	1	1	13MAY1989	1	1	1	0
41	242	0	0	13MAY1989	0	0	0	0
43	225	1	0	15MAY1989	2	0	0	0
50	263	1	0	17MAY1989	2	1	0	0
54	258	1	1	13MAY1989	2	1	1	0
56	248	1	1	21MAY1989	3	1	1	0
62	[illegible]	1	0	18MAY1989	1	0	0	0
76	[illegible]	1	1	21MAY1989	2	1	1	0
81	268	1	1	28MAY1989	0	0	0	0
49	264	1	1	08MAY1989	0	0	0	0
46	252	1	1	13MAY1989	1	0	0	0
59	258	1	1	17MAY1989	2	2	2	1
75	241	1	1	17MAY1989	0	0	0	0
82	232	0	0	09MAY1989	0	0	0	0

L#	PRWT	SA	SS	PARTDATE	#O	#W	#A	#S
31	263	1	1	06MAY1989	3	3	2	2
38	244	0	0	02MAY1989	0	0	0	0
39	250	1	1	06MAY1989	3	1	0	0
42	258	1	1	09MAY1989	2	2	2	1
47	249	0	0	03MAY1989	2	1	1	0
48	257	0	0	15MAY1989	0	0	0	0
60	257	1	1	17MAY1989	2	2	2	0
63	232	1	0	20MAY1989	1	1	1	0
64	253	0	0	15MAY1989	0	0	0	0
65	258	1	1	16MAY1989	2	2	2	0
83	281	1	1	14MAY1989	1	1	1	0
85	282	1	1	23MAY1989	3	2	2	2
87	235	0	0	19MAY1989	2	0	0	0
88	215	0	0	23MAY1989	1	1	1	0
90	250	1	0	29MAY1989	2	1	1	0
91	.	1	1	21MAY1989	0	0	0	0
92	.	0	0	11MAY1989	2	2	2	2
93	.	0	0	01JUL1989	.	.	.	.
35	245	1	0	05MAY1989	2	1	1	0
36	253	0	0	30APR1989	4	4	3	1
55	274	0	0	17MAY1989	4	1	1	0
96	257	1	0	26APR1990	2	1	0	0
97	250	1	0	04MAY1990	3	2	0	0
98	250	0	0	24APR1990	2	0	0	0
105	252	0	0	27APR1990	2	2	2	0
127	270	0	0	07MAY1990	0	1	1	0
128	255	1	0	17MAY1990	2	1	1	1
129	243	1	1	26MAY1990	0	0	0	0
143	250	0	0	28MAY1990	0	0	0	0
156	284	1	1	05JUN1990	2	0	0	0
159	245	0	0	15JUN1990	3	0	0	0
126	247	1	1	10MAY1990	0	0	0	0
135	283	0	0	14MAY1990	1	1	0	0
140	258	1	0	17MAY1990	3	2	1	1
113	280	0	0	10MAY1990	0	0	0	0
146	.	0	0	10MAY1990	.	.	.	.
108	260	1	1	03MAY1990	2	2	1	0
109	225	0	0	05MAY1990	2	1	1	1
117	249	0	0	14MAY1990	0	0	0	0
122	247	0	0	11MAY1990	0	0	0	0
124	.	0	0	22MAY1990	.	.	.	.
141	274	1	1	28MAY1990	0	0	0	0
149	.	0	0	31MAY1990	.	.	.	.
152	247	1	1	24MAY1990	2	1	1	0
154	225	1	1	03JUN1990	2	1	1	0
155	260	1	1	23MAY1990	1	0	0	0
95	232	1	1	22APR1990	0	0	0	0
104	253	1	1	10MAY1990	0	0	0	0
110	265	1	1	07MAY1990	3	3	2	0
111	.	0	0	25APR1990	.	.	.	.
112	.	1	1	08MAY1990	.	.	.	.
115	.	1	1	11MAY1990	.	.	.	.

L#	PRWT	SA	SS	PARTDATE	#O	#W	#A	#S
118	.	0	0	15MAY1990	.	.	.	.
120	.	0	0	14MAY1990	.	.	.	.
123	251	0	0	14MAY1990	0	0	0	0
125	253	1	1	05MAY1990	3	2	2	0
130	.	0	0	21MAY1990	.	.	.	.
131	260	1	1	21MAY1990	3	0	0	0
132	235	1	0	13MAY1990	3	2	1	0
133	238	1	1	07MAY1990	2	1	1	1
136	242	1	1	15MAY1990	1	1	1	0
138	246	0	0	26MAY1990	0	0	0	0
142	.	0	0	07MAY1990	.	.	.	.
144	.	0	0	05MAY1990	.	.	.	.
145	266	0	0	30MAY1990	1	1	1	0
147	272	1	1	22MAY1990	2	2	2	0
148	.	0	0	05JUN1990	.	.	.	.
150	280	1	1	26MAY1990	0	0	0	0
153	230	1	1	13JUN1990	2	0	0	0
157	245	1	1	02JUN1990	1	1	1	1
158	.	1	0	21MAY1990	3	2	1	0
137	277	0	0	23MAY1990	4	1	1	0
203	235	1	1	19JUN1991	1	0	0	0
175	.	1	1	12MAY1991	0	0	0	0
192	215	0	0	31MAY1991	0	0	0	0
168	166	1	1	06MAY1991	3	1	0	0
173	220	1	1	12MAY1991	3	3	3	1
177	220	0	0	24MAY1991	0	0	0	0
164	275	1	0	04MAY1991	3	3	3	1
166	279	0	0	11MAY1991	2	1	0	0
172	265	1	1	15MAY1991	4	3	3	2
188	247	0	0	17MAY1991	4	4	2	1
199	238	0	0	25JUN1991	0	0	0	0
170	248	1	1	12MAY1991	0	0	0	0
176	230	1	0	16MAY1991	1	1	1	0
197	227	1	0	01JUN1991	1	1	1	0
186	254	1	0	05JUN1991	0	0	0	0
187	265	1	1	24MAY1991	0	0	0	0
190	235	0	0	23MAY1991	1	1	1	0
194	262	1	1	30MAY1991	2	1	0	0
202	250	1	1	10JUN1991	2	2	2	2
165	275	0	0	11MAY1991	3	0	0	0
169	265	1	0	16MAY1991	0	0	0	0
171	277	0	0	15MAY1991	3	2	1	1
174	236	0	0	23MAY1991	3	0	0	0
178	269	1	0	23MAY1991	3	0	0	0
181	275	0	0	25MAY1991	3	3	2	1
182	289	0	0	02JUN1991	0	0	0	0
184	266	0	0	24MAY1991	2	1	1	1
185	246	1	0	31MAY1991	3	3	3	1
189	215	0	0	05JUN1991	2	2	2	0
191	.	0	0	24MAY1991	0	0	0	0
196	240	0	0	11JUN1991	2	0	0	0
198	250	0	0	29MAY1991	3	2	2	0

L#	PRWT	SA	SS	PARTDATE	#O	#W	#A	#S
201	252	0	0	12JUN1991	0	0	0	0
167	257	1	0	11MAY1991	3	1	1	0
179	265	1	1	24MAY1991	4	1	0	0
180	.	0	0	17MAY1991	3	2	1	0
183	265	1	0	19MAY1991	3	2	1	0
193	240	1	1	19JUN1991	4	0	2	0
195	250	0	0	19JUN1991	0	0	0	0
200	238	1	0	15JUN1991	0	0	0	0

L#	#C1	#C2	PROP	AREA	DBH	#PINE
10	1	.	1.00	.	13.3226	23
25	.	.	1.00	.	17.6588	14
2	.	.	0.00	.	.	.
13	1	.	0.00	.	9.8364	47
20	.	.	0.50	.	13.2812	16
26	.	1	0.00	.	17.5692	13
1	.	1	0.66	.	13.3226	53
4	.	1	0.66	.	11.9071	42
5	.	.	0.33	.	9.8877	65
6	.	.	0.33	.	.	.
11	.	1	0.66	.	.	.
12	2	.	0.33	.	14.9565	23
14	1	.	0.33	.	17.2636	11
15	.	1	0.66	.	13.1084	19
16	1	.	1.00	.	10.5061	66
17	1	.	0.00	.	13.6875	32
18	1	.	0.33	.	10.4909	55
21	2	.	0.00	.	10.4909	64
23	.	.	0.33	.	.	.
24	.	2	0.33	.	11.6488	41
3	.	1	0.00	.	11.7311	45
7	1	2	0.75	.	11.9417	24
8	1	2	0.25	.	12.1613	31
9	.	.	0.25	.	15.2545	22
19	1	.	0.50	.	11.4000	28
22	.	2	0.25	.	12.3097	31
27	.	.	1.00	.	.	.
29	.	.	0.66	.	.	.
30	.	.	0.66	.	.	.
32	.	.	0.66	.	.	.
45	.	.	1.00	.	.	.
52	.	.	0.00	.	.	.
53	.	.	0.66	.	.	.
66	.	.	0.66	.	.	.
86	.	.	0.33	.	.	.
44	.	.	0.75	.	.	.
57	.	.	0.50	.	.	.
58	.	.	0.25	.	.	.
61	.	.	0.75	.	.	.

L#	#C1	#C2	PROP	AREA	DBH	#PINE
84	.	.	0.75	.	.	.
40	.	.	0.50	.	.	.
89	.	.	0.00	.	.	.
33	.	.	0.66	.	.	.
37	.	.	0.66	.	.	.
41	.	.	0.33	.	.	.
43	.	.	1.00	.	.	.
50	.	.	0.66	.	.	.
54	.	.	0.66	.	.	.
56	.	.	1.00	.	.	.
62	.	.	0.33	.	.	.
76	.	.	0.00	.	.	.
81	.	.	0.66	.	.	.
49	.	.	1.00	.	13.7333	12
46	.	.	0.50	0.4900	14.1500	48
59	1	1	0.50	0.3240	15.8414	29
75	.	.	1.00	0.9200	12.9233	30
82	.	.	0.00	0.5500	17.5688	16
31	.	3	0.33	0.3300	12.6963	27
38	.	.	1.00	.	.	.
39	1	.	0.00	0.4600	17.9333	18
42	2	.	0.33	.	11.9071	42
47	1	.	1.00	0.3200	12.9833	18
48	.	.	0.00	.	.	.
60	1	1	0.66	0.4900	.	.
63	1	.	0.66	0.2800	14.6075	40
64	.	.	0.33	.	.	.
65	1	.	0.00	0.7400	10.4909	64
83	.	.	0.00	.	11.4000	28
85	.	2	0.33	0.9065	12.1613	31
87	.	.	0.00	.	14.9565	23
88	.	1	0.66	2.3600	14.0208	48
90	1	.	0.66	0.8100	10.5061	66
91	.	.	0.33	.	.	.
92	1	1	0.00	.	14.8800	20
93	.	.	0.33	.	.	.
35	.	1	0.50	0.7300	15.2545	22
36	2	2	0.75	0.6600	7.4700	25
55	.	1	0.50	0.6370	11.7311	45
96	.	.	0.00	.	.	.
97	.	.	0.33	.	.	.
98	.	.	0.66	.	.	.
105	.	.	0.66	.	.	.
127	.	.	0.66	.	.	.
128	.	.	0.33	.	.	.
129	.	.	0.66	.	.	.
143	.	.	1.00	.	.	.
156	.	.	1.00	.	.	.
159	.	.	0.66	.	.	.
126	.	.	0.50	.	.	.
135	.	.	0.25	.	.	.
140	.	.	0.33	.	.	.

L#	#C1	#C2	PROP	AREA	DBH	#PINE
113	.	.	0.00	.	10.0178	90
146	.	.	1.00	.	.	.
108	1	.	0.50	0.7000	12.3687	32
109	1	.	1.00	.	17.7000	11
117	.	.	0.00	0.8900	12.9233	30
122	.	.	0.00	0.2700	17.7000	12
124	.	.	0.50	.	.	.
141	.	.	0.50	0.5800	14.5522	23
149	.	.	0.50	.	.	.
152	.	.	0.50	0.7500	17.8308	13
154	1	.	0.00	1.1500	14.0941	34
155	.	.	1.00	.	12.8341	38
95	.	.	0.33	.	.	0
104	.	.	0.33	.	11.9071	42
110	.	2	0.66	0.5200	10.9271	48
111	.	.	0.33	.	.	.
112	.	.	0.33	.	.	.
115	.	.	0.33	.	.	.
118	.	.	0.33	.	.	.
120	.	.	0.66	.	.	.
123	.	.	0.66	.	.	.
125	1	.	0.33	0.3100	9.7887	62
130	.	.	0.33	.	.	.
131	.	.	0.33	.	.	.
132	.	1	1.00	0.9600	9.9417	48
133	.	1	0.33	.	.	.
136	1	.	0.66	0.6900	17.1267	15
138	.	.	0.60	0.5200	.	.
142	.	.	1.00	.	.	.
144	.	.	1.00	.	.	.
145	1	.	0.33	0.6600	17.5692	13
147	1	.	0.66	0.4400	12.3097	31
148	.	.	1.00	.	.	.
150	.	.	0.67	.	15.0720	25
153	.	.	0.33	0.7300	9.3494	79
157	.	1	1.00	0.7600	12.2167	18
158	2	.	1.00	.	.	.
137	.	1	0.75	0.4500	17.5941	68
203	.	.	1.00	0.3060	12.9833	18
175	0	0	0.50	0.8330	12.2167	18
192	.	.	0.00	.	15.3600	20
168	1	0	1.00	0.7970	12.3687	32
173	.	.	1.00	0.5970	12.1316	38
177	.	.	0.33	0.8200	.	.
164	2	0	1.00	0.4500	10.9271	48
166	0	0	0.25	0.3500	9.7887	62
172	.	.	0.50	0.5490	.	.
188	.	.	0.25	0.7140	10.9237	59
199	0	0	0.50	1.0220	14.0941	34
170	0	0	0.00	0.7470	.	.
176	.	.	0.00	.	.	.
197	.	.	0.00	0.4300	.	.

L#	#C1	#C2	PROP	AREA	DBH	#PINE
186	.	.	1.00	0.3600	12.8341	41
187	.	.	1.00	0.9360	12.1613	31
190	.	.	0.50	0.4970	.	.
194	.	.	0.50	0.5510	12.8875	24
202	.	.	0.00	0.7700	10.4909	64
165	0	1	0.33	0.5840	.	.
169	.	.	1.00	.	.	.
171	.	.	0.33	0.4270	.	.
174	.	.	0.33	0.8250	10.5061	66
178	.	.	1.00	0.5400	16.5182	11
181	0	1	0.33	0.4520	.	.
182	.	.	0.00	0.5700	14.5522	23
184	.	.	0.33	0.6000	10.2910	100
185	.	.	0.33	0.7530	.	0
189	.	.	0.66	0.5120	13.5097	31
191	.	.	1.00	.	12.3097	31
196	.	.	0.67	0.5890	17.1125	8
198	.	.	0.66	0.7220	.	.
201	.	.	1.00	0.6420	.	0
167	.	.	0.50	0.5340	.	.
179	0	1	1.00	0.7770	.	.
180	.	.	0.25	.	.	.
183	.	.	0.75	0.7430	.	.
193	.	.	0.75	0.4630	17.9200	15
195	0	0	0.50	0.7150	17.8308	13
200	.	.	0.00	0.4740	14.4889	18

APPENDIX 3

DATA ON TERRITORIES USED IN TEMPORARY REMOVAL EXPERIMENT

KEY TO VARIABLES:

MID - midden subjected to temporary removal of owner
REPSTAT - reproductive status of midden owner
Br = breeding female, NBr = non-breeding female, M = male
DATE - date of temporary removal
#RAT - number of rattles recorded on vacated territory
#SCR - number of screeched recorded on vacated territory
#BARK - number of barks recorded on vacated territory
#NR - number of rattles recorded on territories neighbouring vacated territory

MID	REPSTAT	DATE	#RAT	#SCR	#BARK	#NR
H0	Br	15AUG1990	23	3	5	23
H15	Br	15AUG1990	0	0	1	4
J15	M	15AUG1990	1	0	0	1
M9	M	15AUG1990	0	0	1	25
K23	NBr	15AUG1990	1	1	0	3
O18	NBr	15AUG1990	5	0	1	7
A10	Br	16AUG1990	0	0	0	13
J19	Br	16AUG1990	1	0	0	36
F16	M	16AUG1990	15	8	1	27
T10	M	16AUG1990	8	1	3	7
O6	NBr	16AUG1990	0	0	0	7
R7	NBr	16AUG1990	9	5	0	27
HH27	Br	20AUG1990	1	0	1	88
JJ24	Br	20AUG1990	58	1	2	27
QQ24	M	20AUG1990	35	26	3	16
QQ27	M	20AUG1990	7	1	1	53
HH24	NBr	20AUG1990	52	17	4	31
KK15	NBr	20AUG1990	9	11	4	40
CC13	Br	21AUG1990	32	10	5	33
II14	Br	21AUG1990	7	7	0	45
AA0	M	21AUG1990	18	3	5	28
HH12	M	21AUG1990	8	6	4	44
AA7	NBr	21AUG1990	2	0	3	13
GG6	NBr	21AUG1990	30	17	9	16
QQ13	Br	25AUG1990	14	25	10	20
QQ6	Br	25AUG1990	3	0	0	10
KK1	M	25AUG1990	9	6	7	30
NN0	M	25AUG1990	14	6	18	31
ES1	NBr	25AUG1990	0	0	0	9
HH0	NBr	25AUG1990	0	0	0	4
W6	Br	28AUG1990	0	0	0	2
Z8	Br	28AUG1990	13	6	2	25
S11	M	28AUG1990	43	26	24	8
Y14	M	28AUG1990	14	7	15	20

MID	REPSTAT	DATE	#RAT	#SCR	#BARK	#NR
U18	NBr	28AUG1990	2	0	8	16
V2	NBr	28AUG1990	6	1	2	20
X34	Br	29AUG1990	2	2	4	13
Z25	Br	29AUG1990	15	6	1	68
O32	M	29AUG1990	0	4	4	24
P28	M	29AUG1990	10	9	5	32
V32	NBr	29AUG1990	42	15	6	17
X26	NBr	29AUG1990	51	15	33	92

APPENDIX 4

DATA ON FEMALES USED IN 'CHOICE' EXPERIMENT

KEY TO VARIABLES:

STATUS - experimental status of female
AUTMID - midden owned by female in Autumn 1990
REP1990 - reproductive status of female at end of 1990
1=had not produced litter 2=bore litter
AUTAREA - area of female's territory in Autumn 1990 (h)
ADDMID - neighbouring midden vacated and subject to cone additions
DELMID - neighbouring midden vacated and subject to cone deletions
SPRAREA - area of female's territory in spring 1991 (h); if
data missing, it indicates female died overwinter

STATUS	AUTMID	REP1990	AUTAREA	ADDMID	DELMID	SPRAREA
CHOICE	AA7	1	0.591	AA10	AA3	0.634
CHOICE	CC13	2	0.760	BB10	EE14	0.822
CHOICE	ES1	2	0.532	QQ30	ES2	0.822
CHOICE	GG23	1	0.612	GG24	GG20	0.713
CHOICE	HH0	1	0.545	FF2	HH3	0.593
CHOICE	HH27	2	0.732	II26	HH29	0.721
CHOICE	II14	2	1.148	HH12	KK10	1.020
CHOICE	JJ27	1	0.580	II26	JJ24	.
CHOICE	JJ29	2	0.387	KK31	KK32	0.356
CHOICE	JJ4	1	0.467	II6	KK5	0.600
CHOICE	KK15	1	0.735	MM19	MM17	0.670
CHOICE	NN12	1	0.354	MM8	OO10	0.309
CHOICE	OO15	2	0.635	QQ20	MM17	.
CHOICE	QQ13	2	0.703	PP9	NS7	0.792
CHOICE	QQ6	1	0.640	PP9	QQ26	.
CHOICE	QQ6	2	0.517	MM4	PP1	0.451
CONTROL	D29	2	0.770	.	.	.
CONTROL	D5	2	0.685	.	.	0.683
CONTROL	H2	2	0.515	.	.	0.544
CONTROL	J19	2	0.620	.	.	0.572
CONTROL	J25	1	0.454	.	.	0.427
CONTROL	JJ24	2	0.890	.	.	.
CONTROL	L24	2	0.704	.	.	0.744
CONTROL	M16	1	0.745	.	.	0.717
CONTROL	M9	1	0.398	.	.	0.464
CONTROL	O10	1	0.590	.	.	.
CONTROL	P28	1	0.628	.	.	0.588
CONTROL	R7	2	0.803	.	.	0.784
CONTROL	T19	1	0.610	.	.	.
CONTROL	V2	1	0.810	.	.	0.750
CONTROL	V21	2	0.650	.	.	.

STATUS	**AUTMID**	**REP1990**	**AUTAREA**	**ADDMID**	**DELMID**	**SPRAREA**
CONTROL	V32	1	0.320	.	#	

APPENDIX 5

DISPERSAL MOVEMENT OUT OF FAMILIAR TERRITORY INCURS COSTS

Natal dispersal is common in animal populations, and constitutes an important component of population demography and genetics (Barton 1992, Johnson and Gaines 1990, Shields 1987, Lidicker 1975). Most theoretical models developed to explain the evolution of dispersal require a measure of the costs of dispersal (Johnson and Gaines 1990). It is generally assumed that dispersers face increased risks while moving through unfamiliar habitat (Lidicker 1975, Gaines and McClenaghan 1980). However, studies cited as demonstrating these costs are anecdotal (Errington 1946, Carl 1971), have been conducted under laboratory conditions (Ambrose 1972, Metzgar 1967), have measured survival of animals that had already undergone part of the relocation process (Garrett and Franklin 1988), or have measured survival of individuals that have succeeded in settling (Krohne and Burgin 1987, Jones 1986, Johnson and Gainers 1990).

I studied natal dispersal within a red squirrel (*Tamiasciurus hudsonicus*) population occupying jack pine (*Pinus banksiana*) forest in central Alberta, Canada (54.20°N, 114.45°W), from Spring 1988 to Spring 1991. Red squirrels exhibit a promiscuous mating system, and all individuals maintain separate, non-overlapping territories. Conifer cones are larderhoarded prior to winter, creating a midden (Gurnell 1984) composed of underground tunnels and accumulations of cone bracts. During periods of winter cold, squirrels remain near or in the middens feeding on the stored cones (Obbard 1988, Kemp and Keith 1970). In summer, mothers raise their offspring within their respective territories. Upon emergence, offspring do not have to risk direct confrontations with other conspecifics until they begin leaving the mother's territory. At that time they make forays off of the territory (up to 900 m) throughout neighbouring areas, apparently searching for habitat vacancies (Chapter 5). Complete abandonment of the natal territory by offspring prior to settlement has not been observed. Philopatry is pronounced in the population, with all offspring settling at distances that do not preclude contact with the mother (Chapter 5). During this study approximately 50% of the offspring acquiring territories settled on or adjacent to the mother's territory, often through acquisition of part of the maternal territory (Chapter 5). Settlement distances did not differ significantly between the years of the study (Chapter 5), nor did the overwinter survival of offspring that acquired territories (*Kruskal-Wallis* chi^2=1.67, *df*=2, *P*=0.432).

Offspring were outfitted with radio-collars as they began moving off of the mothers' territories (Chapter 2) and were monitored at least every third day thereafter. Through behavioural observations, it was possible to differentiate between offspring that had succeeded in acquiring a territory and those that had not settled (Chapter 2). I also used behavioural observations and locations of radio-collared mothers and dispersing offspring to map the boundaries of territories (Chapter 2). In this study, goshawks (*Accipiter gentilis*) were the major predator, based on predator sightings, visual observations of predation, and evidence of kills (see also study by Meng 1959). I identified where offspring were killed by locating their radio-collars and carcass remains. These locations were considered to represent the approximate site of the kills, based on (1) the fact that remains of most radio-collared, sedentary (territory-holding) juveniles and adults killed during the dispersal period were found on the respective territories (31/33) and (2) three observations of predatory attacks.

All observations made of live, radio-collared offspring that were *not* holding territories at the time of sighting were classified as being either on or off the natal territories (Fig. A-1A). These data were then used to generate expected frequencies of where offspring kills should occur, relative to the boundaries of the natal middens. Contained in this data set were multiple observations of the same individuals (X=10.2 observations/individual, maximum 16/individual).

Once offspring had acquired a territory, their survival was monitored through radio-telemetry, visual observations and live-trapping. Offspring surviving to 1 May of the following spring were considered to have successfully overwintered (Chapter 2). Territories acquired by dispersing offspring were categorized by whether or not they encompassed a traditional midden which had been used by an adult squirrel in the preceeding summer. Dispersal distance was measured from the natal midden to the midden of the newly-established territory or, if the new territory did not contain a discernable midden, to the arithmetic mean of boundary coordinates. Territory mapping was accomplished by conducting focal observations on the resident squirrels (Chapters 2 and 5).

Twenty radio-collared offspring were killed before they acquired a territory. Seven of these animals were killed within the boundaries of their mother's territory, which was significantly less than that predicted by the proportion of time juveniles were found on their natal territories (Fig. A.1B). Offspring that acquired territories and survived through the winter had significantly greater dispersal distances and larger territories than those that obtained territories but died overwinter (distance: *normal approximation to Mann-Whitney U*, Z=1.95, P=0.05; area: t=2.89, df=17, P=0.011;

Table A.1). Also, dispersers that survived the winter tended to have territories containing a traditional midden site (G=7.53, df=1, P=0.006, Table A.1).

These results indicate that offspring attempting to disperse were more vulnerable to predation while off of their mother's territories. This may have occured because they were not familiar with escape routes and/or because they were preoccupied with avoiding resident territory holders (Metzgar 1967). My data also indicate that dispersal distance was indirectly related to higher mortality. Offspring settling relatively close to the natal midden may be able to take advantage of familiar conspecifics (e.g. mothers, immediate neighbours) (Stamps 1987), but they appear unable to appropriate as large a territory as if they had located a completely vacant territory elsewhere. Further, acquiring part of the mother's territory may mean that offspring do not obtain a previously existing midden, which may provide optimum winter refuge (Kemp and Keith 1970, Smith 1968). In this system, dispersers apparently must risk movement through unfamiliar areas, if they are to experience the benefit of acquiring an optimum territory.

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disperser survived winter?	*mean dispersal distance (N)*	*mean territory area (SE,N)*	*% with traditional midden*
No	75.8 (49)	0.45 (0.032,12)	41% (20/49)
Yes	113.9 (18)	0.62 (0.039,5)	78% (14/18)

TABLE A.1. Comparison of territories acquired by dispersers. Offspring which acquired territories, but failed to survive the winter, had significantly smaller dispersal distances and territory sizes than offspring which obtained territories *and* survived the winter. Also, territories of offspring which did not survive the winter were more likely not to encompass a traditional midden. Distance and area are expressed in meters and hectares, respectively.

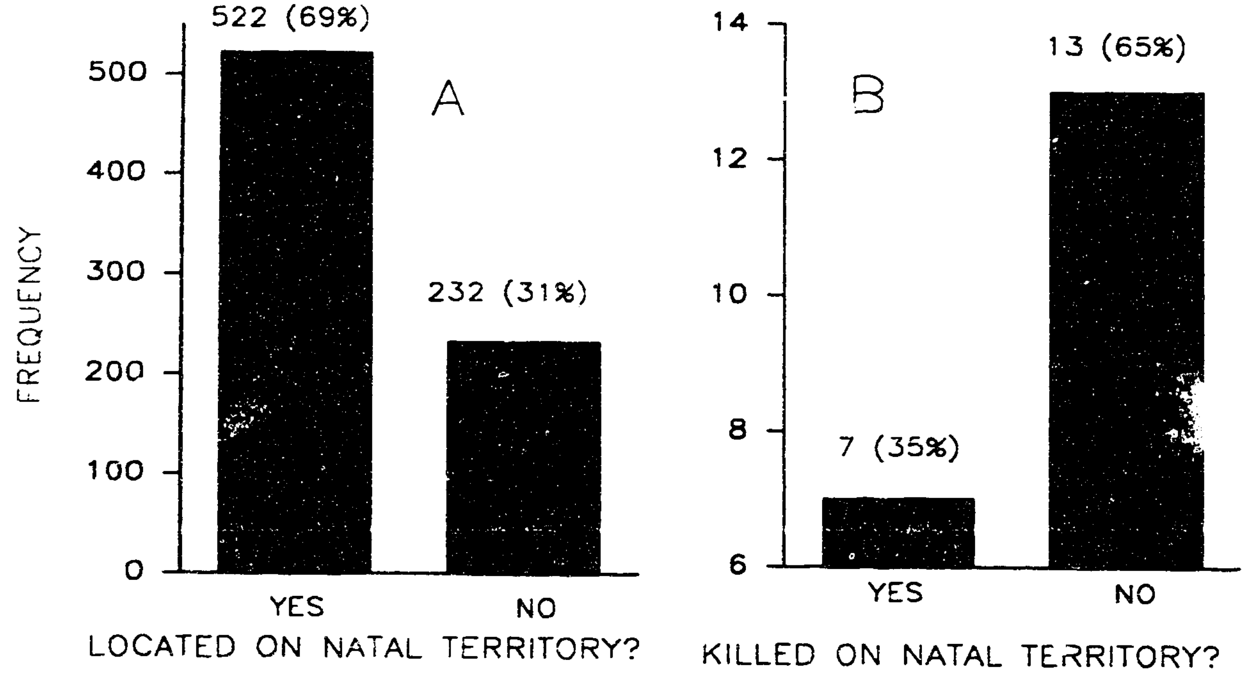

FIGURE A.1. **A.** Total number of observations made on live, radio-collared offspring which were not holding territories at time of sighting. **B.** Kill sites of red squirrel offspring attempting to disperse. Both sets of observations were classified by whether they were on or off of the offsprings' respective natal terrerritories.
Based on the frequencies generated from the data in **A**, the proportion of individuals killed off of the natal territories (**B**) was significantly greater than that expected.