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INTRASEXUAL COMPETITION AND REPRODUCTIVE SUCCESS IN FEMALE BUSHY-TAILED WOODRATS

by

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of the requirements for the degree of
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ABSTRACT

Bushy-tailed woodrats (*Neotoma cinerea*) are nocturnal rodents that are usually confined to discrete rock outcrops. Several females may bred on one outcrop, and are expected to compete for limited resources. I monitored individual reproductive output of female woodrats on 22 outcrops in the Kananaskis Valley in Alberta during the breeding seasons from 1987 to 1989 to investigate the influence of competition among females on reproductive success.

My aims were two-fold. First, I tested the hypothesis that competition among females on outcrops reduces reproductive success in yearling females. I reduced densities of breeding females by approximately 50% on 11 outcrops at the initiation of the three breeding seasons, and compared reproductive success of yearlings breeding on experimental and unmanipulated ($N=11$) outcrops. Relative to yearlings on control outcrops, those on removal outcrops raised more offspring to weaning, their female offspring exhibited faster post-weaning growth, and they and their daughters tended to exhibit higher annual survival. Among females that were known to have bred in one year only, those on removal outcrops produced more offspring to weaning and more daughters to breeding (in their lifetime) than did those on control outcrops. I conclude that yearling bushy-tailed woodrats experience significant socially-mediated fitness costs.

My second goal was to investigate the influence of mother-offspring relationships on space use, behaviour, and reproductive success. Adult mothers and yearling daughters that bred simultaneously on their natal outcrop were closely associated in space throughout the breeding season. Behavioural interactions between mothers and daughters were amicable, while those between adult females and non-kin were strongly agonistic. This behavioural asymmetry was maintained when all females were reproductively active. Matrilineal females (those that shared an outcrop with their mother) experienced enhanced survival over their first winter, and raised more offspring to weaning than did non-matrilineal females. I suggest that adult mothers provide their daughters with access to critical resources (e.g., den sites), and provide a protective environment against aggressive conspecifics.

Woodrat sociality appears to be characterized by 1) competitive interactions among non-kin, and 2) cohesive, beneficial relationships among mothers and daughters.

ACKNOWLEDGEMENTS

Woodratting in the Kananaskis Valley was a wonderful challenge. Murray Snicks Manson, Mike Norrie, Donna Tysdale, and John Wilmshurst were everything that I'd ever hoped field assistants would be, and much more. They helped immensely to make the Kananaskis experience a great one that I will not easily forget. The staff at the Kananaskis Centre for Environmental Research, especially Grace LeBel and Pete Wallis, were always ready and willing to help. The compassionate cooks helped to keep the fires stoked on those cold and rainy days, and every other day, for that matter. The personnel at the Safety Office, University of Calgary, and Jack Cornett and Ed Cooper, AECL, Chalk River, were extremely helpful in making the use of radioisotopes in the field possible. Road access to otherwise inaccessible study sites was kindly provided by the staff at Alberta Recreation and Parks, and the Alberta Forest Service.

The unshakable support, encouragement, and patience afforded by Jack Millar, my supervisor, was far beyond expectation, and greatly appreciated. The judicious combination of criticism and support provided by Dave Ankney and Paul Handford, my advisory committee members, was most constructive. Thanks to Paul and David Ribble for critically reading most or all of this thesis. Ian Craig went out of his way to help me out of a couple of tight spots, and Mary Martin, the graduate secretary, was always of great help. My Collip experience was enriched by graduate students far too numerous to mention, many of whom I hope to have as close friends for a long time to come.

Thanks to the family members and other long-time friends that were always there from the beginning to the very end. Ryan James was a continual source of joy, and unknowingly helped to maintain my perspective in the last two years. Finally, to my most enduring and very special friend, Faye Smith, I could never thank you enough, and I look forward to an opportunity to return the kind of support and sacrifices that you have so willingly given to me.

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CHAPTER 1

GENERAL INTRODUCTION

The fundamental asymmetry in the allocation of parental investment between the sexes in most animals (Williams 1966; Trivers 1972) gives rise to the fact that reproductive success is generally limited among males by the number of females that they are able to gain access to, but, among females, by the ability to gain access to resources necessary for successful reproduction and the rearing of offspring. Because maternal investment is particularly high in mammals (i.e., it includes costs of gestation and lactation), the opportunities for enhancing reproductive success through intrasexual competition are expected to be considerably lower in females than in males. That variance in lifetime reproductive success (LRS) is generally higher in males than in females is now well established empirically (Clutton-Brock 1988a), although this does not imply, as some authors have suggested (see Hrdy and Williams 1983), that variance in LRS among females is negligible. Like male-male competition for mates, competition among females for critical resources causes unequal access to those resources, and concomitant variance in reproductive success among conspecifics. Indeed, in a recent volume of studies that measured LRS in insects, birds, and mammals (Clutton-Brock 1988b), most studies documented considerable variation in LRS among conspecific females. Further, 4 of 5 studies of non-human mammals reported that some of the variation in female LRS was explained by competitive abilities associated with age, size, and dominance (Altmann et al. 1988; Clutton-Brock et al. 1988; Le Boeuf and Reiter 1988; Packer et al. 1988).

Although few other studies have measured LRS in mammals (but see Boyce and Boyce 1988; Ostfeld et al. 1988; Sheridan and Tamarin 1988; Wauters and Dhondt 1989; Ribble 1992), a vast amount of recent work has recognized the existence and importance of variation in reproductive success in females, and has focused on female-female competition and its effect on some measure of reproductive success. Competitive interactions among associated females in the wild appears to be virtually ubiquitous in mammalian species (Hrdy 1981; Wasser 1983; Wasser and Barash 1983; Clutton-Brock and Albon 1985; Rubenstein and Wrangham 1986; Clutton-Brock 1988a). Females typically compete by 1) excluding others from access to critical resources (e.g., food, nest sites, shelter), and 2) by reducing, delaying, or inhibiting the reproductive output of conspecifics via direct behavioural interference. Generally, socially subordinate and/or young individuals bear the highest cost of competition through reduced reproductive success (Wasser and Barash 1983; Clutton-Brock and Albon 1985).

A female should not remain in a social environment that is the source of her reduced reproductive success unless 1) there are no alternatives available (i.e., LRS would be greater as a solitary female), or 2) she is receiving benefits associated with grouping that outweigh the reproductive costs (i.e., LRS is higher in the presence of conspecifics than in their absence). The most common advantages accruing to members of social groups in mammals are enhanced utilization of food resources, and protection from predators and interfering conspecifics (Wrangham and Rubenstein 1986), and are most likely to be shared with close relatives (Hamilton 1964; Vehrencamp 1979; Wrangham and Rubenstein 1986).

To understand the relative costs and benefits of being associated with other females is to gain insight into the adaptive significance of the prevailing social organization, and of the behavioural and reproductive strategies that individuals may be expected to pursue (Smith and Sibly 1985). Costs and benefits of group living in large, diurnal mammals have been well investigated (primates: Dunbar 1988; carnivores: Packer 1986; Rood 1986, 1990; Gittleman 1989; Moehlman 1989; ungulates: Gosling 1986; Rubenstein 1986; Clutton-Brock et al. 1982, 1988; ground-dwelling squirrels: Sherman 1980; Hoogland 1981a, 1981b; Armitage 1986), although relatively little is known of the net effects of female-female interactions on reproductive success in small, nocturnal mammals in the wild. It is the purpose of this thesis to explore the reproductive and behavioural consequences of female social organization in bushy-tailed woodrats (*Neotoma cinerea*), a nocturnal, cricetid rodent.

The genus *Neotoma* currently consists of 20 species (Hall 1981; Honacki et al. 1982) distributed from Nicaragua to the Yukon Territory in Canada. *Neotoma cinerea* is the most northerly-distributed species (the only one found in Canada), and is found throughout western North America from northern New Mexico to the Yukon (Burt and Grossenheider 1976). It is the largest species in the genus, and it exhibits a large degree of sexual size dimorphism (Finley 1958). The distribution of *N. cinerea* within its range is highly localized. Bushy-tailed woodrats are largely restricted to the use of discrete, patchily-distributed rock outcrops, caves, and talus slopes, at mid to high elevations (1500-3000 m) in the mountains. Within outcrops, they utilize a limited number of permanent den (i.e., shelter and food storage) and nest (i.e., offspring rearing) sites (Finley 1958; Escherich 1981; Hickling 1987). Woodrats are non-hibernating, generalist herbivores, capable of deriving considerable amounts of energy from high fibre diets (Justice and Smith 1992). Many species, including *N. cinerea,* cache large amounts of food (typically shrub foliage) in den sites, presumably required for surviving inclement conditions over the winter months (Finley 1958; Hickling 1987; Hickling et al. 1991).

Reproduction is seasonal; litters are born from February to August in the south, and from April to August in the north. Mean litter size varies from 2 to 4, and females in the wild have 1 to 3 litters in a season (Finley 1958; Escherich 1981; Hickling 1987). Bushy-tailed woodrats do not breed in their year of birth, and virtually all individuals are reproductively active during their first breeding season (i.e., as yearlings). A more complete description of the biology of *N. cinerea* is found in Finley (1958).

Although limited information on the social organization of *N. cinerea* is available, it is clear that several breeding females often share an outcrop (Escherich 1981; Hickling 1987), densities of breeding females on a given outcrop are remarkably stable among years (Hickling 1987), and some females on an outcrop may exhibit considerable overlap in space (Escherich 1981). In addition, because females tend to be philopatric (i.e., most females breed on the outcrop that they were born on) and may live for 2 or more breeding seasons (Escherich 1981; Hickling 1987), it has been suggested that female social organization in bushy-tailed woodrats is based on matrilineal (mother-daughter) associations (Escherich 1981; Kelly 1989), although this has not been clearly established.

Information on the genetic contribution of males to breeding females is currently lacking. However, larger home ranges in males than in females, the tendency for sex ratios of adults within outcrops to be female biased, a large degree of sexual size dimorphism, and a high environmental potential for polygyny afforded by discrete rock outcrops, suggests that the modal mating system is polygynous (Ralls 1977; Emlen and Oring 1977; Mares and Lacher 1986; Hickling 1987), or perhaps promiscuous.

Because females are dependent on a limited number of established den sites for rearing offspring, some form of competition among females for access to this resource is expected. That all females on an outcrop are reproductively active within a given breeding season (i.e., do not exhibit delayed sexual maturation) is expected to further intensify competition among females (Armitage 1981). Hickling (1987) provides the only quantitative evidence of competition among associated females on an outcrop. He documented a weak inverse relationship between per capita reproductive output and the number of females on an outcrop, and suggested that yearling females exhibit reduced reproductive output relative to older females, although he was unable to quantify individual reproductive output. How intrasexual competition in females may vary with relatedness is unknown. Some authors have speculated on the potential benefits of cooperative relationships among close kin, including sharing of den sites and food caches, inheritance of the maternal home range and resources, and cooperative predator defence (Escherich 1981; Kelly 1989; Newton 1990).

This thesis is divided into 4 chapters. Chapter 2 describes my study area and general methods used throughout the study. In Chapter 3, I describe and discuss the results of a female removal experiment that tested the hypothesis that female social organization in bushy-tailed woodrats is competitive and entails net reproductive costs to some females. In Chapter 4, I investigate the possibility that social relationships among bushy-tailed woodrats may vary with relatedness; specifically, I address the question of whether mother/offspring relationships are more cohesive than adult female/non-kin relationships. In addition, I test the hypothesis that woodrats that share an outcrop with their mother experience enhanced reproductive output and survival, relative to those that reside on an outcrop without their mother.

CHAPTER 2

GENERAL METHODS

2.1 STUDY AREA

This study was conducted in the Front Ranges of the Rocky Mountains, approximately 80 km west of Calgary, Alberta, Canada, from mid-April to mid-September 1987-1989, inclusive, and mid-May to early July in 1990. The sites that I monitored were situated along a part of the lower Kananaskis River Valley, bounded in the south by Rocky Creek (50°51' N, 115°10' W) and in the north by Sibbald Creek (51°03' N, 114°57' W; Figure 1). Sites were first located visually from roads or aerial photographs, and were selected for their proximity to the Kananaskis Centre for Environmental Research (KCER), from which all research activities were coordinated, and their relative ease of access from Highway 40 South and Highway 68 (Sibbald Creek Trail). With one exception (a concrete bridge spanning Highway 40 S), all sites could be generally described as discrete patches of exposed rock on steep slopes, varying in length from 50 to 430 m. Henceforth, I will refer to these sites, including the bridge, as "rock outcrops", or simply "outcrops". Twenty outcrops were intensively monitored in 1987, and 22 in 1988-90. Precise locations of outcrops used in this study are given in Table 1. Although I monitored most of the obvious outcrops in the area, it is possible that some were not detected, and therefore not monitored. In many cases, however, an outcrop and its nearest adjacent outcrop (separated by 100 to 2000m) were monitored.

All outcrops were in the subalpine vegetation zone (Ogilvie 1969) at elevations ranging from 1515 to 1740 m a.s.l. (Table 1). Outcrops were typically surrounded by continuous forests of 1) mature mixed spruce-fir (*Picea glauca, P. engelmannii, Abies lasiocarpa, Pseudotsuga menziesii*), or 2) ≈ 30-year old post-fire lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) (Rowe 1972). Understory vegetation, and vegetation on steep, unstable slopes was typified by mixed shrubs (*Arctostaphylos uva-ursi, Betula glandulosa, Juniperus communis, Potentilla spp., Ribes spp., Shepherdia canadensis*) and various herbaceous plants.

The small mammal fauna in the Kananaskis Valley is diverse. Millar et al. (1985) identified 25 species of small mammals in the valley, and several were observed regularly near my study sites. These included golden-mantled ground squirrel (*Spermophilus lateralis*), least chipmunk (*Eutamias minimus*), pika (*Ochotona princeps*), red squirrel (*Tamiasciurus hudsonicus*), and snowshoe hare (*Lepus americanus*). Potential predators of woodrats sighted in the vicinity of the study sites included pine marten (*Martes americana*), great gray owl (*Strix nebulosa*), and great horned owl (*Bubo virginianus*).

Temperatures in the Kananaskis Valley are highly seasonal (Figure 2). Mean monthly temperatures (°C) are below 0 from November to March, (based on 1951-80 average; Environment Canada 1983). January is typically the coldest month, with a mean temperature of - 10. Mean monthly temperatures are usually above freezing from April to October, attaining a maximum of 14 in July. Mean annual precipitation is 657 mm, of which 292, on average, fall as snow. Precipitation is generally less variable over the year than temperature (Figure 2). There were no striking differences in patterns of temperature or precipitation among the years of my study, and conditions were generally warmer and drier than average from September 1986 to June 1990 (Figure 2).

2.2 LIVE-TRAPPING

Woodrats were captured in model 201 Tomahawk® live traps (41 x 13 x 13 cm, with 2.5 x 1.3 cm mesh). All outcrops were trapped for 2 nights (a "trap session"), approximately every 2-3 weeks, between April 15 and September 10 in 1987-89, and May 16 and July 4 in 1990. There were 6-8 trap sessions per year on each outcrop in 1987-89, and 2 sessions on each outcrop in 1990.

A grid system of trap placement was not feasible on the highly irregular outcrops, and most traps were placed non-randomly near areas showing obvious signs of woodrat activity (i.e., den sites, food caches, areas near urine and/or faecal deposits). In addition, traps were placed at regular intervals between areas of activity. Most traps sites were established in dry, sheltered areas. Those traps that were exposed to wind and rain were covered with wood shingles and rocks. All trap sites were permanently numbered. A session began when traps were set in the evening during the last 2-3 hours of daylight. Traps were baited with peanut butter and a slice of apple, and were checked the following morning between 0700 and 1100 hr. If it was the first morning of a session, traps were closed for the day, reset that evening, and checked again the next morning. Traps were left in place between sessions (with the entrance locked open) on most outcrops. I ensured that I had an adequate number of traps on each outcrop by adding traps until approximately 1/3 to 1/2 were vacant in a given trap session.

Each captured woodrat was transferred to a cotton pillow case for handling. First-time captures were marked with a numbered metal ear tag (National Band and Tag®, model 1005-1) in the right ear. Tag and trap site number were recorded for all captures. Every woodrat that was caught for the first time within a session was weighed to the nearest 5g with a Pesola® spring scale. Spring scales were regularly calibrated with known weights. Morphological measurements were not routinely recorded. However, skull length and width was recorded from 25 males and 25 females in the spring of 1990 to investigate the relationship between a measure of skeletal size and body weight. Weight was strongly associated with skull area (length x width) in males (r=0.91, p=0.0001), indicating that body weight was a good measure of skull size. The relationship was not as strong in females (r=0.58, p=0.002); considerable variation in body weight was unexplained by skull area. Some of that variation may have been due to the fact that body weight was recorded for many females after the initiation of reproductive activity. However, only 1 female was pregnant when weighed. Eighteen others were lactating, and the remaining 6 were non-reproductive. Hence, it is likely that some variation in body weight in females reflected weight independent of size and reproductive activity (i.e., condition). Hickling et al. (1991) found that 25% of the variation in total body fat was explained by body weight in female bushy-tailed woodrats.

In addition to body weight, sex and reproductive state were also recorded for all first captures within a session. For females, stage of pregnancy and condition of teats were recorded. Stage of pregnancy was estimated by gentle palpation of the abdomen, and was recorded as not pregnant, early pregnant (embryos ≈ 0.5-1 cm in diameter), mid-pregnant (embryos ≈ 1-2 cm), or late pregnant (embryos ≥ 2 cm; body parts discernible). Teats were scored as not active (small and indistinct), enlarged (some lactational fat, but no milk expressed when palpated), lactating (milk easily expressed), or post-lactational (small, with signs of dried milk). Males were scored as abdominal (testes not evident in scrotum), or scrotal (testes clearly descended, or descended easily in response to palpation).

A juvenile (i.e., an individual in its year of birth) could be readily identified as such, based on pelage colour (grey) and, generally, small size. However, maternity of juveniles could not be determined confidently, based on information gathered from routine live-trapping. I determined maternal relationships of all juveniles born on the outcrops using radioisotopes, following Tamarin et al. (1983). All females in late pregnancy or early lactation were anaesthetized with ether, and injected intraperitoneally with 15 microCuries of one or two of ^{54}Mn, ^{59}Fe, ^{65}Zn, ^{75}Se, or ^{85}Sr. No two females on an outcrop were injected with the same isotope (or combination of 2 isotopes) within a year, and each female was injected with the same isotope(s) among years. Isotopes are transferred from mother to offspring in utero and/or through lactation (Tamarin et al. 1983), and each isotope possesses unique spectral characteristics (Adams and Dams 1970). I tested for the presence of isotopes in all juveniles during their initial capture with a 7.6 cm NaI detector housed in an aerated plastic chamber and connected to a Ludlum® model 2200 single channel analyzer. Thus the detection of an isotope in any juvenile allowed me to unambiguously assign a mother to that juvenile. Isotope dosages were designed to permit detection in juveniles for approximately 3-4 months after birth. I assumed that a juvenile was an immigrant (i.e., not born on the outcrop that I captured it on) if I failed to detect an isotope in that juvenile. This assumption could potentially lead to misclassification of juveniles as immigrants if some females that were resident on the study outcrops eluded capture and tagging by radioisotopes. However, trappability in bushy-tailed woodrats is high ($>$ 80%; Hickling 1987). Further, I detected isotopes in all juveniles that were captured close to weaning age, suggesting that classification of juveniles in which isotopes were not detected as immigrants was reasonable.

The success of the isotope technique also depended, in part, on woodrats not nursing communally. If female woodrats did nurse communally, I would expect to have detected combinations of isotopes other than those I administered. Although there were many cases of closely associated females breeding synchronously during the study, I found no unexpected combinations of isotopes, and assumed that communal nursing was absent or minimal on my study sites. The use of radioisotopes thus allowed me to 1) unambiguously quantify reproductive output of each breeding female on an outcrop, 2) determine relatedness among philopatric breeding females (except in 1987), and 3) differentiate between immigrant and philopatric young.

Non-juvenile woodrats were classified as yearling (alive in the year after birth), or adult (alive in the 2nd or 3rd year after birth). Hickling (1987) monitored woodrats during the breeding seasons of 1985 and 1986 on all the outcrops that I monitored in 1987. Hickling kindly made his records available to me, and I was able to classify the age of all tagged woodrats as of April 1987. I initially considered all non-juveniles that were first captured as untagged individuals (usually in the spring) to be of unknown age. However, because I found that inter-outcrop movement was rare in reproductively-mature individuals (see section 3.3.6), I assumed that untagged non-juveniles were yearlings. That mean body weight of these individuals in the spring (females: 269g±7 [SE], [N=30]; males: 314g±5 [95]) appeared to be more similar to that of known yearlings (females: 266g±5 [31]; males: 318g±9 [28]) than of known adults (females: 299g±7 [23]; males: 412g±10 [22]) suggests that the assumption was not unreasonable.

Any non-juvenile that was captured on the same outcrop in at least 3 trap sessions in a year (in 1987-89) was considered to be a resident. In 1990, only 2 trap sessions were conducted, and I assumed that all non-juveniles captured in both sessions were residents. Most individuals that were classified as non-residents were captured once or twice in the early spring, and never again. Most residents were captured in every trapping session in a given year.

2.3 STATISTICAL ANALYSES

All statistical analyses were performed using SAS® statistical software package (SAS Institute Inc., 1990). I used analysis of variance (ANOVA; PROC GLM), analysis of covariance (ANCOVA; PROC GLM), or multiway contingency table (log-linear) analysis (PROC CATMOD) for many of my analyses. I used Type III sum of squares in all ANOVA and ANCOVA models. For all multiway analyses, I progressively removed non-significant interaction terms (i.e., highest order first) from the models, beginning with a fully saturated model (i.e., incorporating all interaction and main effects). If none of the interaction terms (or combination of terms within an order level) were statistically significant, I used the model with all main effects only. Effects tested in multiway models are denoted in capital letters, and interaction terms are denoted with a "*" (e.g., REMOVAL*YEAR). Statistical significance was generally accepted at the 0.05 level. However, I recognize the continuous nature of the probability of making a Type I error, and report probabilities associated with most tests. If a *p*-value is not indicated, it was > 0.10 in the analysis in question. All tests are 2-tailed, unless noted otherwise. Means are usually presented ± 1 standard error, with sample size, *N*, in square brackets. Means presented ± 1 standard deviation (SD) are indicated as such. All dates are presented as Julian dates, unless otherwise indicated.

Table 1. Location, length, and elevation of all rock outcrops monitored in 1987-1990.

Control Outcrops					Removal[a] Outcrops				
#	Name	Location	Length	Elevation	#	Name	Location	Length	Elevation
1	Elbow	460562	170	1670	1	Beaver	435570	130	1515
2	Pika	432575	260	1515	2	Sibbald	431570	150	1515
3	Shady[b]	428566	180	1515	3	Mossy	422563	60	1515
4	Raven	412565	290	1670	4	Kel's	416565	350	1670
5	Mud-1	407566	70	1670	5	Mud-2	407563	120	1590
6	Aspen	312482	350	1575	6	Dusty	402558	230	1670
7	Marmot	293465	310	1700	7	Barrier	361536	330	1515
8	Ranger	328443	430	1740	8	Gulch	359511	310	1670
9	Fire	328439	150	1670	9	Slippery[b]	325453	160	1515
10	Hidden	290358	280	1740	10	Bridge	311391	30	1515
11	Power	287354	200	1575	11	Shale	327379	120	1575
12	Wedge	291352	210	1740	12	Rocks	285357	50	1545

[a] See Chapter 3 for description of removal experiment.

#: corresponds to number on map of study area (Figure 1); ordered from north to south.

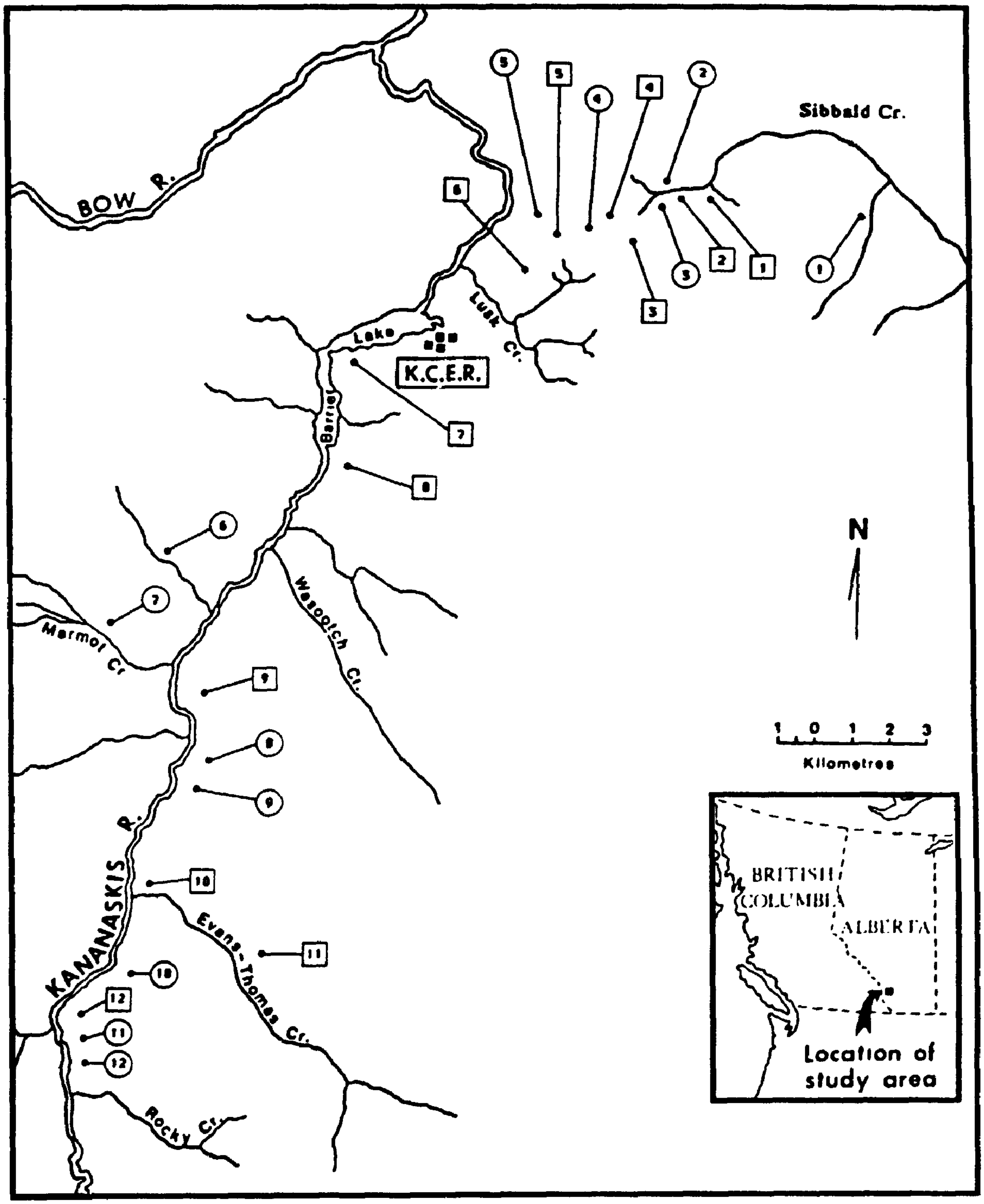
Location: corresponds to Universal Transverse Mercator Grid reference number, from 1:50,000 scale topographical maps (82J/14, 820/3, 820/2). Accurate to within 100 m.

Length: length in metres of outcrop base, along which traps were placed. Estimated from 1:20,000 scale aerial photographs (series 82-176C; Alberta Ministry of Energy and Natural Resources) enlarged 4-10 times. Mean of 3 measurements with "map wheel" for each outcrop, to nearest 10 m.

Elevation: elevation, in metres, above sea level. Determined from 1:50,000 scale topographical maps.

[b]: Shady was a removal outcrop in 1989-90; Slippery was a control outcrop in 1987.

Figure 1. Map of study area, indicating location of all rock outcrops that were intensively live-trapped from April to September 1987-89, and May to July 1990. Control outcrops are indicated by numbers within circles, and removal outcrops (see Chapter 3 for explanation of removal experiment) by numbers within squares. KCER is the Kananaskis Centre for Environmental Research. Map adapted from Hickling (1987).


BOW R.
Sibbald Cr.
Lusk Cr.
Lake
K.C.E.R.
Barrier
Marmot Cr.
Wasootch Cr.
KANANASKIS R.
Evans-Thomas Cr.
Rocky Cr.
N
1 0 1 2 3
Kilometres
BRITISH COLUMBIA
ALBERTA
Location of study area
5
5
4
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2
6
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8
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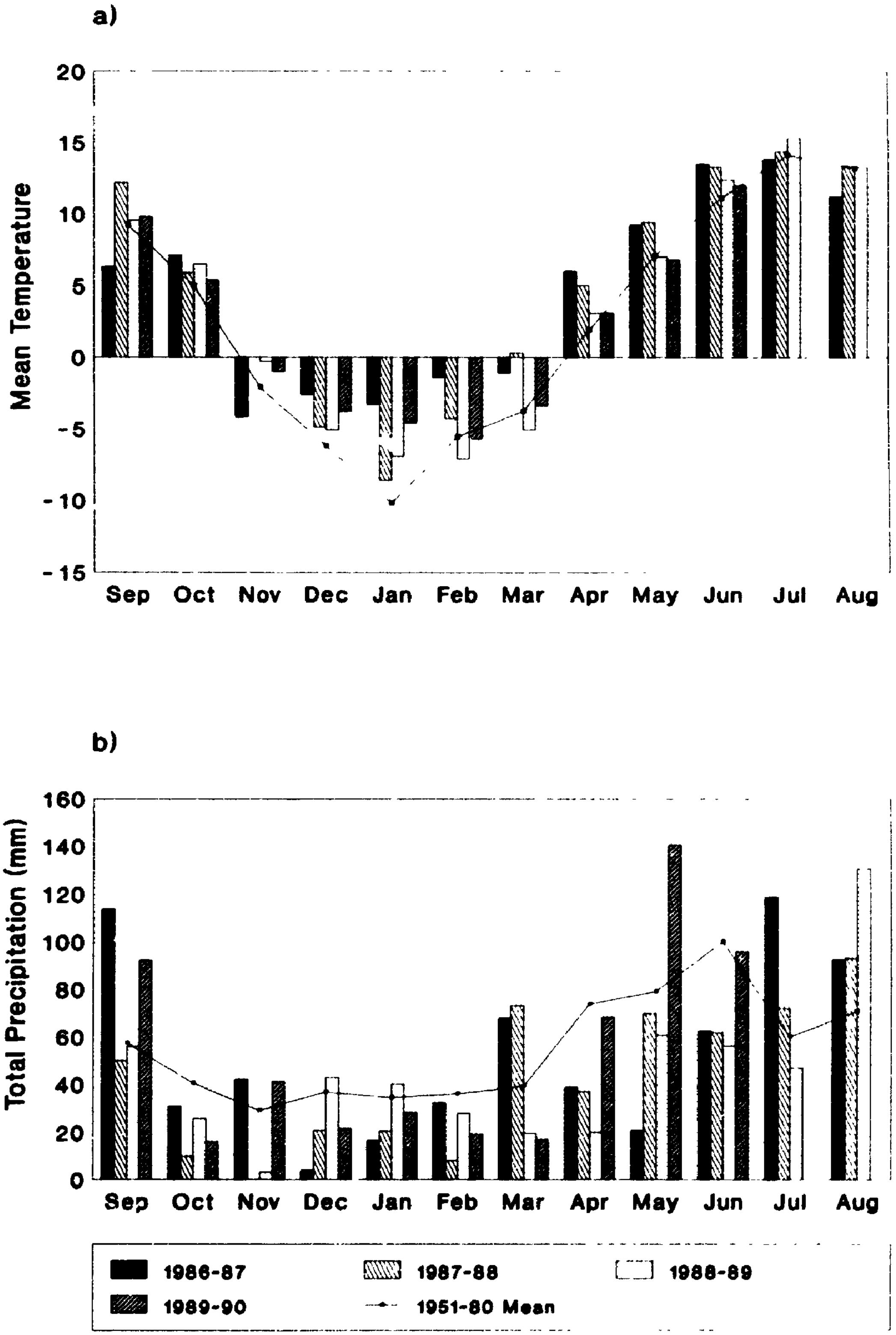
12

Figure 2. Climatic conditions recorded at the Kananaskis Lodge weather station in the Kananaskis Valley from September 1986 to July 1990, and 1951-80 (30 year mean). a) Mean monthly temperatures (°C). b) Total monthly precipitation (mm). Most precipitation from November to March, inclusive, is snow, but is given in rain equivalents (10 cm of snow ≈ 10 mm of rain).


a)
20
15
10
5
0
-5
-10
-15
Mean Temperature
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
b)
160
140
120
100
80
60
40
20
0
Total Precipitation (mm)
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
1986-87
1987-88
1988-89
1989-90
1951-80 Mean

CHAPTER 3

EFFECTS OF CONSPECIFICS ON REPRODUCTIVE SUCCESS: A REMOVAL EXPERIMENT

3.1 INTRODUCTION

Females often compete for resources necessary for successful reproduction and rearing of offspring. Many female mammals live and compete within groups of varying degrees of complexity and cohesiveness (Wilson 1975; Eisenberg 1981). To understand the adaptive significance of a prevailing social organization, and the behavioural and reproductive strategies available to individuals within it, it is necessary to quantify the effects of intra-group competition on individual reproductive success (Pulliam and Caraco 1984; Smith and Sibly 1985).

Extensive work on diurnal, social mammals has shown that young, socially subordinate individuals typically bear the highest costs of intrasexual competition, manifested as reduced reproductive success (Wasser and Barash 1983; Clutton-Brock and Albon 1985; Clutton-Brock 1988a). In many cases, advantages of group membership (e.g., protection from predation and/or conspecifics, enhanced utilization of resources) may reduce or eliminate costs of intra-group competition: the social organization provides subordinates with their best available option (Pulliam and Caraco 1984; Wrangham and Rubenstein 1986). For example, Cheney and Seyfarth (1987) provide evidence that large groups in some primates are favoured due to their ability to exclude small groups from clumped food resources, even though enhanced intra-group competition associated with large groups may reduce reproductive success in some individuals. In others, survival benefits of large groups associated with enhanced predator defence may outweigh reproductive costs to subordinates (Dunbar 1988). Many females in large groups of dwarf mongoose (*Helogale parvula*) experience complete reproductive suppression, perhaps for several years, but enhanced survival and inclusive fitness benefits (through cooperative breeding), relative to females in small groups, favour membership in large groups (Rodd 1990; Creel and Creel 1991).

Alternatively, females may form groups in response to a limited availability and/or clumped spatial distribution of critical resources, and advantages may not necessarily accrue to group members (Alexander 1974; Emlen and Oring 1977; Pulliam and Caraco 1984). For example, female yellow-bellied marmots (*Marmota flaviventris*) form small groups at limited, patchily distributed rock outcrops that serve as den sites and hibernacula, and sociality appears largely competitive (Armitage 1986). Many females experience reproductive suppression, and reproductive success is inversely related to group size: reproductive success is maximized in solitary females (Armitage 1988).

The effects of social organization, or social dynamics among conspecifics, on female reproductive success in small, nocturnal mammals are poorly understood. Although much work had been devoted to the investigation of aspects of social behaviour in small mammals (Krebs 1985; Cockburn 1988; Anderson 1989; Wolff 1989; Tamarin et al. 1990), it has invariably been concerned with demographic responses and population regulation, rather than responses at the individual level. Much of the work, however, has incorporated the paradigm that females compete for critical resources, and has focused on the role of females in population regulation. Experimental removal studies have clearly indicated that adult females limit the immigration, sexual maturation, and/or survival of young females in many species (*Apodemus sylvaticus*: Montgomery 1981; *Clethrionomys gapperri*: Bondrup-Nielson 1986; *C. glareolus*: Bujulska 1973; Gipps et al. 1985; *C. rufocanus*: Saitoh 1981; *C. rutilus*: Gilbert et al. 1986; *Lepus americanus*: Boutin 1984; *Microtus pennsylvanicus*: Rodd and Boonstra 1988; *M. townsendii*: Boonstra 1977; 1978; Krebs et al. 1978; Redfield et al. 1978; *Mus musculus*: DeLong 1978; Vandenbergh 1987; *Peromyscus maniculatus*: Galindo and Krebs 1987; Lusk and Millar 1989). However, the adaptive significance of female-female competition in small mammals remains unclear, as none of these studies have quantified reproductive success among individual conspecifics, and few have been able to convincingly differentiate between immigrants and young produced by resident females. To document accelerated sexual maturation or enhanced survival in juveniles after some or all breeding females have been experimentally removed, or in response to "naturally" occurring low densities (Bujalska 1985; Vandenbergh 1987), certainly illustrates the effects of female-female competition, but does little to address the question of how the social environment affects the fitness of individual breeding females (Haigh 1987). In addition, the possibility that social relationships among conspecific females may be cooperative in small mammals has rarely been investigated (but see Madison et al. 1984; Boyce and Boyce 1988; Solomon 1991, for notable exceptions).

Bushy-tailed woodrats (*Neotoma cinerea*) are an ideal species in which to investigate the effects of intrasexual competition on reproductive success in females. A limited number of breeding females co-exist on discrete habitat patches (rock outcrops), thus forming definable groups within which an individual may be expected to interact (Finley 1958; Escherich 1981; Hickling 1987). Density is not a confounding variable, as numbers of females within outcrops are relatively stable among years

(Hickling 1987). Immigration during the breeding season is limited, and it is possible to unambiguously quantify the reproductive output of each female on an outcrop (see Chapter 2).

The reliance of woodrats on highly clumped rock outcrops, and of females on a limited number of den sites within outcrops (Finley 1958) suggests that female sociality may be largely competitive (Alexander 1974; Emlen and Oring 1977). However, the alternative that the social organization is beneficial to some or all females on an outcrop (e.g., through increased defensibility of resources, protection from predation) may exist. Close kin may share outcrops in many cases (Escherich 1981; Hickling 1987), increasing the potential for cooperative interactions (Hamilton 1964). Here, I attempt to differentiate between these alternatives; I test the hypothesis that female social organization in bushy-tailed woodrats is competitive and entails fitness costs to breeding females. The test consists of two parts; one descriptive, and the other experimental. First, assuming that young females are more likely to experience costs of competition than are older females (Reiter et al. 1981; Clutton-Brock and Albon 1985; Clutton-Brock 1988a), I compare several measures of reproductive success between yearling ($\approx$ 1 year old), and adult ($\geq$ 2 years old) females from unmanipulated outcrops over 3 years. Lower reproductive success in yearlings, relative to that in adults, would be consistent with a competitive sociality among females. However, equally consistent with this result would be the interpretation that 1) yearlings exhibit lower reproductive success due to physiological and/or experience-related limitations associated with age, or 2), although yearlings experience some costs of lowered reproductive success in the presence of adults, the social organization still affords some benefits, and represents the best alternative available to yearlings; reproductive success would be lower in the absence of adults.

To distinguish between these alternatives, I reduced densities of breeding females on a number of outcrops over 3 successive breeding seasons. If female sociality is competitive, and causes variation in reproductive success among females, then yearlings breeding on outcrops with experimentally reduced densities should exhibit enhanced reproductive success, relative to those on unmanipulated outcrops. Alternatively, if the presence of other females on an outcrop is beneficial to yearlings, then reproductive success should be depressed in yearlings breeding on experimental outcrops, relative to those on unmanipulated outcrops. Lastly, if female sociality is, in effect, neutral, or if reproductive success in yearlings is physiologically constrained, reproductive success should not differ between females breeding on unmanipulated outcrops, and those breeding on experimental outcrops.

Note that this experimental design had the ability to detect only *net* effects of sociality on any component of reproductive success. If, for example, the presence of several females on an outcrop provided benefits to nestlings through cooperative defence against predators, as well as costs related to infanticide from neighbouring females, then the removal experiment would detect the net effect of reduced costs and benefits. In other words, if the costs of infanticide were greater than the benefits of protection from predators, the experiment would be unable to infer any benefits of sociality. However, it is the net effect of such possible countervailing factors that is of the most interest, in that it is the net effect that selection acts upon (i.e., to favour one form of sociality over another).

The variables that I considered to be components of reproductive success included: date of initiation of reproductive activity, litter size at weaning, number of litters produced, total number of weaned offspring produced, juvenile and yearling growth, and juvenile and yearling summer, winter, and annual survival. Given that females typically compete by excluding others from access to critical resources (e.g., food, shelter), and/or by direct interference (e.g., infanticide, physical harassment; King 1973; Clutton-Brock and Albon 1985), some or all of these measures of reproductive success may be expected to be negatively affected by intrasexual competition.

I also considered the possibility that females may facultatively adjust their litter sex ratios in response to intrasexual competition. The direction of an adaptive sex ratio shift is difficult to predict *a priori*, as current theory predicts that competitively superior individuals should produce either male-biased (Trivers/Willard hypothesis; Trivers and Willard 1973) or female-biased (Local resource competition hypothesis; Clark 1978; Silk 1983) litters, depending on the relative costs and benefits of producing sons and daughters. Generally, if maternal condition affects offspring condition, then mothers in good condition are expected to invest in the sex that benefits most from an improvement in condition. The Trivers/Willard hypothesis predicts that, in dimorphic, polygynous species, males are more likely to benefit from an increase in condition, due to higher variance in reproductive success in males than in females. Bushy-tailed woodrats are assumed to be polygynous (Escherich 1981; Hickling 1987; Kelly 1989), and they are sexually dimorphic. Male bushy-tailed woodrats are more energetically expensive to raise to weaning than are females. Males a slightly, but consistently heavier than females at birth (Hickling 1987; Moses, unpublished data), and pre-weaning growth rates are clearly faster in males than in females (Egoscue 1962; Martin 1973; Hickling 1987). Hence, one might expect that females in good condition would be best able to afford the energetic costs of raising male offspring. The local resource competition (LRC) hypothesis (Clark 1978; Silk 1983) incorporates the costs of potential competition with a philopatric offspring, and predicts that when daughters are philopatric (as in *N. cinerea*), socially dominant (good condition) mothers should preferentially invest in (e.g., adjust their sex ratios to favour) females.

If adult bushy-tailed woodrats are competitively superior to yearlings, then sex ratios of litters born to adults would be expected to be either male-biased (Trivers/Willard) or female-biased (LRC) on unmanipulated outcrops. If the presence of adults depresses competitive abilities in yearlings in ways that affect the costs of producing sons or daughters, then litters born to yearlings on experimental outcrops should be biased in the same way as those born to adults on unmanipulated outcrops.

Finally, I tested a general prediction arising from the hypothesis that females compete aggressively for access to limited resources. Given that some level of immigration of female woodrats is known to occur (Hickling 1987), if females are successfully excluding conspecifics from access to resources on outcrops, then more immigrant females would be expected to settle on experimental outcrops than on unmanipulated outcrops. Confirmation of this prediction alone would not indicate whether sociality among females within outcrops is inherently competitive or cooperative; rather it would lend support to the general hyoothesis that competitive behaviour in female woodrats adversely affects reproductive success of some conspecifics by excluding them from critical resources.

3.2 METHODS

3.2.0 REMOVAL EXPERIMENT

I assessed the size of groups of resident woodrats on 20 outcrops during the first 2 trap sessions in 1987 (April 19-May 30). I ranked the outcrops with respect to the number of females captured on each one, and designated every other outcrop as an experimental female removal outcrop. Henceforth, I refer to experimental outcrops as "removal outcrops", and those that were not manipulated as "control outcrops". Removal and control outcrops were interspersed more or less evenly throughout the study area (Figure 1).

I permanently removed females from removal outcrops as the females became reproductively active, until approximately 1/2 (45-67%) of the resident females were removed. When possible, females were removed from locations throughout the length of an outcrop. Females were removed in advanced stages of pregnancy, or in early stages of lactation. In order to maintain reduced densities of breeding females, I removed all untagged, non-juvenile females (i.e., immigrants), regardless of reproductive state, if they were captured in more than 1 trap session on a given removal outcrop.

There was an accidental trap death of a lactating female on an outcrop that had been designated as a control outcrop in 1987. Because the outcrop initially had only 2 resident females on it, I considered it as a removal outcrop; there were 9 control outcrops, and 11 removal outcrops in 1987 (Table 2). All outcrops that were designated as removals in 1987 were maintained as such in 1988 and 1989. In 1988, 2 removal outcrops (Bridge, Rocks) were not manipulated, as there was only 1 female on each outcrop in the spring of 1988. A third outcrop (Shale) had no resident females on it in 1988, and was not considered for purposes of analysis. In addition, I removed females from a 1987 control outcrop (Slippery), and added 2 new control outcrops (Elbow, Raven) that I had censused twice (2 trap sessions) in the summer of 1987. In 1989, 2 removal outcrops (Dusty, Mud-2) were deleted, as there were no breeding females on them, and 6 others (Beaver, Bridge, Kel's, Shale, Sibbald, Slippery) were not manipulated due to low densities. I used 1 1988 control outcrop (Shady) as a removal in 1989, and added a new control outcrop (Aspen) that had been censused in 1988. The net result in 1988 and 1989: 11 removal, and 11 control outcrops (Table 2). No outcrops were manipulated in 1990. Two trap sessions were conducted on all outcrops in 1990 to census the size of resident groups. The number and age distribution of females and males that were resident on all outcrops in 1987-1990 is listed in Table 2.

A total of 59 resident females (29 adults, 30 yearlings) were removed in 1987-89. The earliest removal of a resident in any year occurred on May 6, and the latest on June 15. In addition, 17 immigrants were taken from removal outcrops over the 3 years between June 20 and September 10. All of the females that were not pregnant when removed were released outside the study area, at least 5 km away from the nearest outcrop. Thirty-two of the experimental females were removed when pregnant, and 7 of these were also released outside the study area on the day of capture. The remaining 25 pregnant females were held in captivity at the KCER (4 in 1987, 14 in 1988, 7 in 1989) to determine 1) days to parturition from the stages of pregnancy estimated in the field, 2) litter size at birth, and 3) potential negative effects of isotopes on juvenile survival (see sections 3.1.1, 3.1.2).

Captive females were held in plastic cages (40 x 70 x 20 cm), provided with artificial nesting material and bedding, and maintained on ad libitum laboratory rat chow, fresh herbaceous plants, and water, under ambient temperature and light regimes. All females were checked daily to determine date of parturition and litter size at parturition. Juveniles were kept with their mothers for about 25 days ($\approx$ 5 days post-weaning), at which time they were released outside the study area with their mother. None of the released woodrats were subsequently caught on an outcrop in the study area.

3.2.1 INITIATION AND TIMING OF REPRODUCTION

I considered the estimated date of parturition of a female's first successful litter of the year to be a measure of initiation of reproduction. Methodology used to estimate parturition dates is fully described in Appendix 1. A litter was considered successful if it had at least one offspring at weaning associated with it. I used maximum body weight that a female attained prior to the onset of reproductive activity in the spring ("pre-breeding weight") as a covariate in an ANCOVA to test for weight, mother age (yearling, adult), and year effects on date of first parturition in females on control outcrops. Date of first parturition did not vary with pre-breeding weight ($F_{(1,62)}=0.14$, $p=0.71$), and I removed the covariate from the analysis, and tested for mother age and year effects with a 2-way ANOVA. To test for removal effects on date of first parturition, I used 2-way (REMOVAL, YEAR) ANOVA within each age class for 1) all breeding resident females, and 2) all breeding females, including those females that were permanently removed from experimental outcrops (referred to as "captive removals"). Exact dates of parturition were known for females that gave birth in captivity. For those females that were removed during early lactation (for which a parturition date was unknown), I estimated a maximum date of parturition by assuming they had given birth the day prior to removal.

Because a small percentage of litters were born very early or late in some years, I defined the length of a breeding season as the number of days over which 80% of all litters were born, and the date of termination as the date that the 90th percentile was born.

3.2.2 MEASURES OF REPRODUCTIVE OUTPUT

I considered reproductive output to be the number of offspring produced to weaning age (i.e., date of first capture) by a female in a breeding season. Only 5 of 186 resident female/years failed to show any reproductive activity within a breeding season, and they were excluded from analyses of reproductive output. Components of reproductive output include litter size at weaning, number of failed reproductive attempts (0 offspring weaned), number of successful (≥ 1 offspring weaned) litters produced, and sex ratio of weaned offspring. By labelling all breeding females with radioisotopes, I was able to unambiguously determine the maternity of all juveniles born to resident females. My measure of post-weaning litter size was simply the number of juveniles caught during the breeding season that were thus assigned to a known pregnancy of a labelled female.

Twenty-five females that were removed from the field when pregnant gave birth to a litter in captivity within 5.5 days (±4.6 [SD]) of removal. Size of these litters at birth varied little about their mean of 3.2 (2 litters of 2, 16 of 3, and 7 of 4). Assuming that exposure to lab conditions for an average of 5-6 days did not affect pre-birth mortality, it follows that variation in size of successful litters caught in the field largely reflected variation in survival from birth to weaning, rather than differential pre-birth survival. Hickling (1987) presented similar results from a sample of 15 captive and kill-trapped females from the Kananaskis Valley (10 litters of 3, 4 of 4, and 1 of 5).

Many (73 of 262 [28%]) reproductive attempts of labelled females that were captured in advanced pregnancy or during lactation had no juveniles associated with them, and were considered failed breeding attempts. Pre-weaning loss of complete litters could be caused by 1) a mother's inability to provide sufficient nourishment and/or insulation for thermoregulation, and 2) inter- or intraspecific nest predation. Before I could consider failed reproductive attempts as "real" biological phenomena, I had to first consider the possibility that they may have been artifacts of my livetrapping protocol.

To test whether the use of radioisotopes on breeding females may have contributed to pre-weaning loss of litters, I injected 11 captive females (4 in 1987, 7 in 1988) with radioisotopes when the females were in late pregnancy, and monitored the growth and survival of their young in captivity until weaning. The protocol used in the handling of subjects and administration of isotopes was the same as that used in the field. Of the 33 individuals born in the 11 litters, 32 were born alive, and all of these survived until weaning. Hence, it is unlikely that the use of radioisotopes contributed directly to the frequency of failed litters in the field.

I livetrapped on each rock outcrop for 2 nights, approximately every 3 weeks, throughout the breeding season. It is possible that a captured lactating female could have been separated from her dependent offspring for up to 12 hours on 2 consecutive nights. To test the effects of this "worst case" separation on neonate mortality due to starvation and/or hypothermia, I separated 1 or 2 offspring of each of 7 litters (7 females, 6 males) born to captive females in 1989 from their mothers for 2 consecutive nights, approximately 12 hours a night, during the first week of lactation. The neonates were left in the artificial nest of the holding cage, protected from wind, but under ambient temperature and light conditions. The young were cold and moved slowly when returned to their mother in the morning, but all 13 survived the separations, and were weaned at the same time as their littermates that had not been separated from their mother prior to weaning. Although I cannot exclude the possibility that lab conditions may have buffered the potential negative effects of separation, this experiment suggests that trapping-induced starvation and/or hypothermia were not likely causes of reproductive failure. But neonates that were separated from mothers caught in traps may also have been susceptible to nest predation. Gestation in bushy-tailed woodrats is $\approx$ 4 weeks (Egoscue 1962), and weaning $\approx$ 3 weeks (Hickling 1987). Because I trapped on each outcrop, on average, every 3 weeks, a breeding female was usually caught either 1) in early pregnancy and then later in early lactation, or 2) in mid- to late pregnancy, and then in late or post lactation. If dependent neonates that were separated from their mother by my trapping regime were more susceptible to predation (or any other source of mortality) than those neonates that weren't separated, then litters that were associated with mothers caught in early lactation should have failed more often than those associated with mothers caught in advanced stages of pregnancy. A 2-way (MOTHER CONDITION, YEAR) log-linear analysis indicated that the frequency of failed litters did not differ significantly between the two groups of females on control outcrops (pregnant: 26% fail [N=108], lactating: 35% fail [N=43]; $X^2=1.29$, df=1, $p=0.26$), on removal outcrops (pregnant: 24% [N=62], lactating: 35% [N=29]; $X^2=1.15$, df=1, $p=0.28$), or for all outcrops pooled ($X^2=2.48$, df=1, $p=0.12$, $N=242$). These differences suggest the presence of a weak trap effect at best, and I conclude this digression by stating that the incidence of failed litters in the field was probably not unduly influenced by my protocol, and could be fairly considered as "naturally" occurring phenomena. Similarly, there was no indication that size of successful litters was affected by the reproductive stage of the mother at capture. Mean size of successful litters did not differ (*t*-test; $p \geq 0.48$) between mothers captured when pregnant and those caught lactating within any mother age/removal class.

To test for removal, mother age, and year effects on reproductive output, I used litter size and total number of weaned offspring produced per female as response variables in ANOVA models, and the frequencies of failed litters, as well as the number of successful litters produced (1 or 2) as response variables in log-linear models. I tested for covariation between 1) date of birth and litter size, 2) date of 1st parturition and number of successful litters, as well as total weaned offspring per season, and 3) pre-breeding weight and each component of reproductive output.

If competition for limited resources causes variation in reproductive output among females, then reproductive output should vary negatively with density of female residing on an outcrop. If the removal experiment was successful in reducing the level of competition, the relationship between reproductive output and female density should be less obvious or absent on removal outcrops. I calculated density as the number of resident females per 100 m of outcrop (see Chapter 2), and examined the correlation between number of offspring weaned (per season) per female and female density. I assumed that the relationship between the 2 variables was independent within outcrops among years.

To ensure independence of data points between year and age classes, I used reproductive data from one breeding season per individual whenever sample sizes were sufficient. For example, in models testing for differences in reproductive output between yearlings and adults in more than one year, only individuals that did not live to breed as adults were included as yearlings. Further, for those females that bred in more than one year as an adult, only their first breeding season as an adult was considered. Pseudoreplication was not a problem in models testing for removal effects among yearling mothers; data from all yearlings were used in these cases. I used all litters produced by an individual in a given breeding season in the analysis of litter size. The decided lack of correlation between size of first and second litters within individuals (r_s=-0.03, p=0.79, N=74), suggests that these data may be considered as independent.

A reproductive response by breeding females to changing ecological conditions could take the form of facultative sex ratio adjustment (Silk 1983; Trivers and Willard 1973; Clutton-Brock and Iason 1986). I tested for evidence of sex ratio adjustment with respect to 1) lowered densities of breeding females, and 2) pre-breeding body weight. I used log-linear models to quantify differences in sex ratios (i.e., the proportion of juvenile males) produced by resident females on removal and control outcrops. However, overall sex ratios may not reflect the presence of facultative sex ratio adjustment of individual litters; equal numbers of male- and female-biased litters produce a 50:50 sex ratio. I used X^2 analysis to compare the observed distribution of litter sex ratios between removal and control outcrops to the distribution expected (i.e., binomial) if the sexes were occurring randomly within litters.

Spearman rank correlation was used to evaluate the association between maximum pre-breeding weight attained in the spring prior to the onset of reproductive activity and the sex ratio of the first successful litter of that season, within removal and age classes. Lastly, I compared the observed relative frequencies of male-biased and female-biased litters to the expected binomial distribution for light (below median weight) and heavy (above median weight) females, within mother age classes. For these analyses, I included data from those females that had a litter in captivity, and for which I knew pre-breeding weight prior to removal from the field. Because no interaction effect between pre-breeding weight and the removal experiment could be expected in 1987, I used data from 1988 and 1989 only for females on removal outcrops. Data from all 3 years were included for females on control outcrops.

3.2.3 GROWTH

Juvenile Growth

Age of juveniles was estimated as described in Appendix 1. Linear models of weight on age in juveniles explained as much variation in weight (all females: r^2=0.82; all males: r^2=0.84) as did the best fit non-linear models (see Appendix 1). Further, there was no obvious heteroscedasticity in residual variation in the linear models, and log-transforming the variables did not improve r^2. Hence, I was able to use linear models of weight on age to describe and analyse growth in juveniles from weaning to early autumn in their year of birth. I used 2-way ANCOVA models with age as a covariate and body weight as a response variable to test for 1) mother age and year effects on growth of juveniles on control outcrops, and 2) removal and year effects on growth of juveniles born to yearling mothers. Analysis of growth of juveniles born to adult mothers on removal outcrops was precluded by small sample sizes. Because post-weaning growth of juvenile bushy-tailed woodrats clearly differs between the sexes (Egoscue 1962; Martin 1973; Hickling 1987), all growth analyses were conducted separately for each sex.

I insured independence of data points within individuals by randomly selecting one datum point (i.e., weight and age) only for each juvenile captured at least once during its year of birth. In order to increase sample sizes, I used all juveniles within litters for these analyses.

Hickling (1987) reported that late-born (weaned after July 1) juvenile bushy-tailed woodrats grew more slowly than those weaned before July 1. To test for covariation between growth and date of birth, I regressed variation in juvenile weight unexplained by age (i.e., residuals from weight on age regressions) on birthdate, for each sex within and among mother age, removal, and year classes. No consistent patterns were evident, and regressions were significant only among juvenile males on removal outcrops, in 2 of 3 years. Further, the relationship was positive in one year and negative in the other (Moses, unpubl. data). Hence, it was unnecessary to control for date of birth statistically in the analysis of post-weaning growth.

I used the same approach to test for covariation between juvenile growth and body weight of mothers. I examined the relationship between residual variation from juvenile weight on age regressions, and weight (both pre- and post-breeding) of each juvenile's mother, within mother age class, and with age classes pooled. To insure independence of data points, one juvenile of each sex (if possible) was randomly selected from all juveniles born to each mother in a breeding season.

Yearling Growth

I considered the proportional change in body weight over an individual's 1) first winter season, and 2) first breeding season as measures of growth in yearling females. Change of weight for the "winter" interval was measured from the last trapping session (August 16 or later) in an individual's year of birth to the date of first capture in the following spring. Only those animals that were caught in non-reproductive condition on their natal outcrop in the autumn and following spring were included. The second interval spanned the breeding season from the date of first capture in the spring (i.e., the end of the winter interval) to the date of last capture in the autumn following the breeding season. Only those yearlings that were caught in non-reproductive condition in the spring and autumn were included for this interval. Because few yearling males overwintered on their natal outcrop, and a growth response over the breeding season by immigrant yearling males to the reduction of density of breeding females was unlikely, I analyzed yearling growth in females only.

Measures of growth were calculated as the proportion of weight gained during an interval, relative to weight at the start of the interval. To facilitate an arcsine transformation of these data (Sokal and Rohlf 1981), I assigned a 0% weight gain to those few yearlings that experienced a net loss of weight during an interval (2/45 for winter period; 1/71 for breeding period; 2%, 5%, and 7% loss, respectively). To test for potential removal effects on growth in yearling females, I subjected the (arcsine-transformed) measures of growth from each interval to a 2-way (REMOVAL, YEAR) ANOVA.

3.2.4 SURVIVAL

I considered that an animal survived until it was no longer captured on any outcrop. I was unable to distinguish between death and permanent emigration from an outcrop for those individuals that disappeared during the study. Because immigrants constituted less than 30% of all breeding females (i.e., most females bred on their natal outcrop; see section 3.1.5), loss of females from outcrops probably indicated death in many cases. Males, however, did not often breed on their natal outcrop; 80% of breeding males were immigrants. Hence, my measure of survival among males is best viewed as a measure of residency on a given outcrop. Due to the markedly different patterns of philopatry between the sexes, I analyzed survival within each sex.

Juvenile Survival

I used log-linear analysis to test for removal and mother age effects on the proportion of young of the year surviving from 1) weaning to the last trapping session on a given outcrop in each year (August 16 or later) ("weaning to autumn"), 2) autumn to the initiation of the following breeding season in the spring ("autumn to breeding", or "winter", interval), and 3) over the entire weaning to breeding interval. Only those juveniles that survived long enough in the spring to become breeding residents on their natal outcrop were considered to have survived the overwinter interval.

In addition to considering mother age and removal effects on juvenile survival, I tested for the influence of date of birth, and pre-breeding, spring weights of mothers on juvenile survival over the weaning to autumn interval, and of juvenile autumn weight on survival over the winter interval. To test for a birth date effect, I compared mean date of birth between juveniles that survived the interval, and those that didn't. Because mean date of birth (of all litters) differed among years within removal class, I adjusted dates to the 1988 mean (for each removal class) to facilitate pooling among years. To investigate the possibility that mother weight may affect juvenile survival, I compared the proportion of juveniles surviving the weaning to autumn interval between those born to light (below median weight) and heavy (above median weight) mothers within mother age/removal class.

To test for a juvenile weight effect on overwinter survival, I compared mean weights at last capture in the year of birth between juveniles that survived the winter interval, and those that survived until autumn, but did not survive overwinter. I did not control for date of last capture, because it did not differ ($p > 0.70$) between the two groups of juveniles for any combination of mother age/removal class, for either sex.

Yearling and Adult Survival

Because few resident woodrats disappeared from outcrops during the breeding season (females: 17 of 186 [9.1%]; males: 20 of 181 [11.0%]), I did not analyze yearling survival for the breeding period. Removal and year effects on the survival of yearlings from their first breeding season to the initiation of the following breeding season (including those that disappeared during the first breeding season) were tested with log-linear analysis. I did not statistically analyse survival of adults due to small sample sizes.

I used 2-way (REMOVAL, SURVIVAL) ANOVA to test for weight effects on overwinter survival of yearling females. I compared maximum post-breeding weights between yearlings that survived the winter interval, and those that disappeared from their breeding outcrops between autumn and spring. Similarly, I tested the possibility that overwinter survival in yearlings may be related to reproductive output in the breeding season preceding the winter interval; I compared 1) litter sizes, and 2) total offspring weaned, between survival classes with 2-way AVOVA. Small sample sizes required pooling among years within removal class for these analyses.

3.2.5 LIFETIME REPRODUCTIVE SUCCESS

I considered an individual's lifetime production of 1) weaned offspring ("LRS1"), and 2) female offspring that became breeding residents on their natal outcrop ("LRS2"), as measures of lifetime reproductive success (LRS) in female woodrats. All females that were first captured as juveniles, became breeding residents for at least one breeding season, and subsequently disappeared from their breeding outcrop during the study period, were included in this analysis. In addition, I included females that were breeding residents for at least 2 years and were 1) born before 1987, or 2) alive at the initiation of the breeding season in 1990. Because I did not monitor reproductive output before 1987, or in 1990, my estimates of LRS for these individuals were minimums. Females that were taken from their breeding outcrops for the removal experiment (i.e., in their 2nd or 3rd breeding seasons) were not included in this analysis.

In order to investigate potential influences on LRS in female woodrats, I correlated my measures of LRS (within removal class) with 1) an individual's mean (year-adjusted) date of first parturition, 2) maximum pre-breeding and post-breeding weight that a female attained in her lifetime, and 3) the number of years that a female was reproductively active. I compared frequency distributions and mean measures of LRS, and considered the different influences of correlates, between removal classes.

3.2.6 DISPERSAL AND IMMIGRATION

I defined dispersal as permanent emigration from an outcrop where an individual was either born or had been a breeding resident, to any other outcrop. Dispersal distances were measured as the shortest distances between outcrops, using 1:50,000 topographical maps, to the nearest 100 m, and should be considered as crude estimates of mimimum dispersal distances. I considered all juveniles for which I was unable to detect the presence of any isotope at first capture to be immigrants (i.e., to have been born on another outcrop). Non-juvenile woodrats that first appeared on an outcrop as unmarked individuals (as of the autumn of 1987) were also considered to be immigrants, as were those that were known to have dispersed from their natal or breeding outcrop. I used X^2 contingency analysis to compare the proportions of breeding residents that were known to be immigrants (within each sex) between control and removal outcrops. For this analysis, I used the number of immigrant and philopatric individuals known to have bred on any given outcrop during the breeding seasons of 1988, 1989, or 1990, including those females that were removed for experimental purposes. Those woodrats that were tagged as yearlings or adults in 1987 (i.e., immigrant/philopatric status unknown) were not included in this analysis.

3.3 RESULTS

3.3.0 GENERAL DEMOGRAPHY

The number of female and male woodrats breeding on control outcrops was generally stable over the 4 breeding seasons from 1987-1990 (Figure 3), although numbers did fluctuate considerably among years on some outcrops (e.g., Marmot, Pika; Table 2). In contrast, the number of females breeding on removal outcrops changed drastically from post-removal 1987 and 1989 to the initiation of the breeding season in 1988 and 1990, respectively (1987-1988; control: 3% decrease; removal: 115% increase; 1989-1990; control: 26% incease; removal 89% increase; Figure 3), due to enhanced reproduction, survival, and immigration of yearlings on removal outcrops, relative to control outcrops (see sections 3.2.2-3.2.5). Reproductive output and survival of yearlings was relatively low in 1988 (see 3.2.2, 3.2.4), and there was little change (11% incease) in numbers of breeding females on removal outcrops from post-removal in 1988 to the start of the breeding season in 1989. The number of breeding males on removal outcrops exhibited little change between years, except from 1989-1990, when there was a 33% decrease (Figure 3).

Sex ratio of breeding woodrats were female-biased on approximately half of all outcrops (control: 51% [*N*=43 outcrop-years]; removal [before removal]: 52% [*N*=42 outcrop years]. There were equal numbers of females and males breeding on one third of all outcrops (control: 33%; removal: 33%), and the remainder of the outcrops supported male-biased breeding groups (control: 16%; removal: 14%; Table 2).

3.3.1 INITIATION AND TIMING OF REPRODUCTION

Mean dates of first parturition varied among years and between yearlings and adults on control outcrops (Table 3a). Reproduction was initiated earliest in 1987 (yearlings: May 27, adults: May 16), and latest in 1989 (yearlings: June 12, adults: June 9) in both age classes (Table 3b), and generally appeared to be inversely related to winter and spring temperatures (Figure 2). Adults generally initiated breeding earlier than yearlings, although the effect was obvious only in 1987 and 1988 (Table 3b).

The interval over which all litters were born varied from 100 days (April 19-July 28) in 1987, 81 days (May 3-July 23) in 1988, to 68 days (May 14-July 21) in 1989. However, a small percentage of litters were born relatively early and late each year, and the length of the breeding season (defined as the interval over which the 10th-90th percentiles were born was considerably shorter. Although a statistical appraisal of the length of breeding season was not possible, it was apparent that, for adults, the length of the breeding season was remarkably similar over the 3 years (46, 49, and 48 days, respectively), because termination dates (Julian dates 167, 178, and 191) varied positively with dates of initiation. However, for yearling females, termination date varied little among years (184, 185, and 189), and the length of the breeding season (58, 45, and 37 days) varied inversely with dates of initiation.

Because dates of first parturition differed between yearlings and adults on control outcrops, I investigated potential removal effects within age class. Dates of first parturition for both yearling and adult females on removal outcrops varied among years they did for females on control outcrops (Tables 4,5). If the removal of some breeding females from the experimental outcrops stimulated an early onset of reproduction in the remaining females, then mean date of first parturition would be expected to be earlier on removal outcrops, relative to control outcrops. This did not occur. Yearling females on removal outcrops initiated reproduction, on average, at the same time as those on control outcrops, even when the parturition dates of females permanently removed from outcrops early in the breeding season ("captives") were included in the analysis (Table 4). Adults on removal outcrops tended ($p=0.06$) to initiate later than those on control outcrops, when the parturition dates of captives were excluded from the analysis (Table 5). The differences were due to having removed adults that initiated early in the season; no differences were apparent ($p=0.23$) when parturition dates of captives were included in the analysis (Table 5).

The length of breeding seasons varied little between yearlings on removal outcrops and those on control outcrops. The season was 4 days longer on removal outcrops than on control outcrops in 1987, 7 days shorter in 1988, and 9 days longer in 1989. Breeding seasons were, however, consistently longer for adults on removal outcrops than for those on control outcrops (12 days longer in 1987, 37 days in 1988, and 16 days in 1989). Sample sizes for removal outcrops were small; after adjusting birth dates for year differences and pooling among years, the breeding season for removal adults ($N=19$) was 23 days longer (73 vs. 50) than for control adults ($N=59$). However, the effect was strongly influenced by the late birth of 3 litters on removal outcrops; only 7 days separated the dates by which 75% of all litters had been born.

Mean date of first parturition did not vary significantly with pre-breeding spring weight of females on control outcrops in a 2-way (MOTHER AGE, YEAR) ANCOVA (see section 3.1.1). Further, there was no evidence of a relationship between the 2 variables within any mother age/removal class (control adults: $r=0.05$, $p=0.79$, $N=33$; control yearlings: $r=-0.17$, $p=0.35$, $N=34$; removal adults: $r=$-

0.06, $p=0.87$, $N=11$; removal yearlings: $r=-0.21$, $p=0.27$, $N=29$).

3.3.2 MEASURES OF REPRODUCTIVE OUTPUT

Litter Size

Litter size at weaning varied from 0 to 4, and exhibited considerable variation among mother age and removal classes. The 2nd-order interaction term (MOTHER AGE*REMOVAL*YEAR) was not significant ($F_{(2,166)}=0.13$, $p=0.88$) in a 3-way ANOVA on litter size, but a significant MOTHER AGE*REMOVAL term ($F_{(1,176)}=5.32$, $p=0.02$) in the final model indicated that an analysis by removal class and/or age class would be appropriate. Litter size varied between age classes on control outcrops only, where adults raised more offspring per litter than did yearlings (Table 6). The overall distributions of litter sizes did not differ between age classes ($X^2=6.82$, $df=4$, $p=0.15$), but adults had more litters of 3 than did yearlings ($X^2=5.22$, $df=1$, $p=0.03$; Figure 4a).

Almost one third (29% of 164) of reproductive attempts by females on control outcrops failed completely. A 2-way (MOTHER AGE, YEAR) log-linear analysis indicated that the proportion of litters that failed on control outcrops varied among years (YEAR: $X^2=7.19$, $df=2$, $p=0.03$; MOTHER AGE*YEAR: $X^2=0.38$, $df=2$, $p=0.83$); the highest proportion of failed litters clearly occurred in 1988 (Table 8). A tendency for a greater proportion of litters to fail among yearlings (33%) than among adults (25%; MOTHER AGE: $X^2=2.83$ $df=1$, $p=0.09$; Table 9), resulted in more yearlings (29% of 63) experiencing complete reproductive failure in a breeding season than adults (14% of 50; $X^2=3.44$, $p=0.06$; Figure 5a).

Some of the variation in litter size between yearlings and adults on control outcrops could be explained by differences in pre-breeding weights. Adults were heavier than yearlings (adults: 309.8g±5.7 [42]; yearlings: 261.0g±4.7 [47]; $t=6.61$, $p=0.0001$) and litter size (averaged within individuals if >1 litter per season) was positively correlated with pre-breeding weight ($r=0.24$, $p=0.02$, $N=91$) when age classes were pooled. Within age class, litter size varied with weight in yearlings only (yearlings: $r=0.28$, $p=0.05$, $N=49$; adults: $r=0.10$, $p=0.51$, $N=42$), although ANCOVA indicated that litter size tended to vary with weight (WEIGHT: $F_{(1,88)}=3.29$, $p=0.07$), but not between age classes when differences in weight were controlled for (MOTHER AGE*WEIGHT: $F_{(1,90)}=0.80$, $p=0.37$, MOTHER AGE: $F_{(1,88)}=0.04$, $p=0.84$). Pre-breeding weight varied with mean litter size class (LS) as follows: 1) LS=0: yearlings: 251.9g±8.60 [13]; adults: 300.0g±17.98 [6]; 2) $0>LS\leq2$: yearlings: 262.2g±5.71 [27]; adults: 309.6g±6.31 [25]; 3) LS>2: yearlings: 279.4g±13.70 [9]; adults: 315.5g±14.13 [11].

Little of the variation in sizes of successful litters on control outcrops could be explained by date of birth. Litter size did not vary significantly with (year-adjusted) date of birth in litters of all mothers ($r=0.05$, $p=0.57$, $N=113$), or in litters within mother age classes (adults: $r=0.22$, $p=0.10$, $N=58$; yearlings: $r=-0.10$, $p=0.46$, $N=55$).

On removal outcrops, yearlings raised as many young per litter as did adults (Table 6), and litter size varied between removal classes in yearlings only (Table 7a). Yearlings on removal outcrops consistently had larger litters than yearlings on control outcrops (Table 7b). Although the overall distribution of litter sizes did not differ between removal classes ($X^2=7.76$, $df=4$, $p=0.10$; Figure 4b), yearlings on removal outcrops had more litters of 3 (26% vs. 12% of all litters, $X^2=4.64$, $df=1$, $p=0.03$), and tended to have fewer litters of 1 (12% vs. 25%, $X^2=2.73$, $df=1$, $p=0.09$), than yearlings on control outcrops.

Small sample sizes of adults on removal outcrops, particularly within years, restricted an analysis of removal effects on reproductive failures to yearlings. The proportion of litters that failed did not differ between yearlings on control and removal outcrops (2-way [REMOVAL, YEAR] log-linear analysis; REMOVAL: $X^2=0.47$, $df=1$, $p=0.49$; Table 8). There was a weak tendency for all yearlings to experience greater losses in 1988 (YEAR: $X^2=4.76$, $df=1$, $p=0.09$). Although yearlings on removal outcrops appeared to incur lower losses in 1988 than yearlings on control outcrops (Table 8), the differences were not significant in the log-linear analysis (REMOVAL*YEAR: $X^2=1.47$, $df=2$, $p=0.48$), or in a 2 by 2 contingency analysis ($X^2=1.84$, $df=1$, $p=0.18$). Only 18% ($N=44$) of all breeding yearlings on removal outcrops failed to wean any young in a season; this did not differ from the percentage of complete failures among yearlings on control outcrops (29% of 63; $X^2=1.52$, $p=0.22$; Figure 5b).

Litter size differences between control and removal yearlings could not be explained by differences in pre-breeding weight or date of birth. Yearlings on removal outcrops did not weigh more than those on control outcrops (control: 261.0±4.7 [47]; removal: 252.9±4.5 [34], $t=1.18$, $p=0.24$), and litter size was correlated with weight among yearlings only on control outcrops (control: see above; removal: $r=-0.22$, $p=0.20$, $N=35$; mean weight by litter size class: LS=0: 262.5g±15.32 [6]; $0>LS\leq 2$: 255.6g±6.23 [17]; $LS>2$: 247.5g±6.44 [12]). Similarly, mean (year-adjusted) dates of birth of all successful litters did not differ between removal classes (control: 158.9±2.7 [55]; removal: 163.1±2.7 [47]), nor did litter size vary significantly with birth dates among yearlings on control (see above) or removal outcrops ($r=-0.05$, $p=0.76$, $N=47$).

Successful Litters

Most females that raised at least 1 offspring to weaning within a breeding season had only 1 successful litter. Of 141 female-years, 41 (29%) raised two successful litters within a season. Only 2 individuals (both on removal outcrops) successfully raised 3 litters within a season (one managed the feat in 2 successive seasons), although 6 others unsuccessfully attempted 3 pregnancies within a season. The relative frequencies of females successfully raising 1 vs. 2 (or 3) litters in a breeding season did not differ between removal or age classes. The MOTHER AGE*REMOVAL term was not significant (p=0.95) in a saturated log-linear model, nor were either of the main effects (REMOVAL: p=0.41, MOTHER AGE: p=0.49), in the appropriate reduced models; Table 9a).

Date of first parturition was a better predictor of the number of successful litters raised in a breeding season than was age or removal class. Females that raised 2 litters initiated, on average, from 7 (control yearlings: p=0.07) to 14 days (control adults: p=0.003; removal yearlings: p=0.002) earlier than those that raised only 1 (Table 9b).

Pre-breeding weights, on the other hand, did not differ between females that had 2 litters and those that had 1, among control yearlings (2 litters: 263.5g±6.90 [13]; 1 litter: 272.6g±7.80 [21]; t=0.77, p=0.44), control adults (2: 315.0g±14.30 [11]; 1: 308.5g±6.40 [24]; t=0.48, p=0.49), or removal yearlings (2: 257.9g±5.55 [7]; 1: 250.5g±5.70 [22]; t=0.69, p=0.49). Small sample sizes precluded statistical analysis among adults on removal outcrops (2: 278.3g±8.33 [3]; 1: 320.0g±10.08 [10]).

Total Weaned Offspring per Season

A female's total reproductive output in a breeding season is the product of the size of her litters and the number of successful litters she produced. Because mean litter sizes varied between removal and age classes, whereas the number of litters raised per individual did not, patterns of variation in total reproductive output reflected those of litter size. A significant REMOVAL*MOTHER AGE term ($F_{(1,117)}=4.83$, $p=0.03$) in the reduced 3-way ANOVA model was explained by significant variation in reproductive output between 1) yearling and adult mothers on control outcrops only, and 2) control and removal outcrops for yearlings only (Tables 10a, 11a).

On control outcrops, reproductive output of adult females exceeded that of yearlings in each of 3 years (Table 10b). Reproductive output varied from 0 to 7. The overall frequency distribution of offspring raised to weaning tended to differ between yearlings and adults ($X^2=8.28$, $df=4$, $p=0.08$; ≥ 4 offspring pooled), and adults raised 4 or more offspring more often ($X^2=3.79$, $df=1$, $p=0.05$), and 0 or 1, less often ($X^2=3.79$, $df=1$, $p=0.05$) than did yearlings (Figure 5a). The results of this analysis do not exclude the possibility that differences in reproductive output between yearlings and adults may be due, in part, to cohort effects (i.e., adults born in a "better" year than yearlings; Albon et al. 1987). However, in a longitudinal sample of 36 individuals that bred as yearlings and adults, reproductive output increased from the first to the second season in 24 cases, showed no change in 8, and decreased in 4, providing strong evidence for a true age effect.

Yearlings on removal outcrops had greater reproductive output within a breeding season than did those on control outcrops, and reproductive output varied among years for all yearlings, with fewest offspring being produced in 1988 (Table 11). The difference between removal classes was consistent among years; yearlings on removal outcrops raised, on average, about 1 more offspring to weaning in every breeding season than did yearlings on control outcrops (Table 11b). Yearling mothers raised from 0 to 8 offspring to weaning within a breeding season, and the overall distribution of reproductive output did not differ between removal classes ($X^2=4.02$, $df=4$, $p=0.40$; ≥ 4 offspring pooled; Figure 5b). The difference in output between removal classes detected by ANOVA was due, in part, to fewer yearlings raising ≤ 1 offspring on removal outcrops than on control outcrops ($X^2=3.41$, $df=1$, $p=0.06$).

Variation in the number of weaned offspring produced in a season was considerable (Figure 5a,b), but was not strongly associated with either pre-breeding weight or date of first parturition. Total reproductive output did not vary significantly with pre-breeding weight within any mother age/removal class ($-0.1 \leq r \leq 0.19$, $p \geq 0.18$, $N=16$-49), although there was a weak association ($r=0.24$, $p=0.02$, $N=91$) between the two variables on control outcrops with age classes pooled. A non-significant covariate term in 1-way (MOTHER AGE) ANCOVA (WEIGHT: $F_{(1,88)}=2.39$, $p=0.13$) suggested that age class was a better predictor of output on control outcrops (MOTHER AGE term with covariate deleted: $F_{(1,112)}=6.54$, $p=0.01$) than was pre-breeding weight.

Total output varied significantly with date of first parturition among yearlings on removal outcrops only ($r=-0.39$, $p=0.02$, $N=36$), although similar trends were evident among adults on removal outcrops ($r=-0.41$, $p=0.13$, $N=15$), and yearlings on control outcrops ($r=-0.28$, $p=0.06$, $N=46$). Reproductive output among adults on control outcrops clearly did not vary with parturition date ($r=-0.02$, $p=0.96$, $N=40$).

Consistent with the interpretation that females competitively exclude others from access to resources on outcrops, reproductive output varied with female density, but only on control outcrops. The per capita production of weaned offspring varied inversely with female densities (r_s= -0.43, p=0.03, N=27) on control outcrops, but there was no relationship between the 2 variables on removal outcrops (r_s= 0.14, p=0.45, N=32). There was variation in mean reproductive output among removal outcrops, however. Although female density (females per unit outcrop length) did not vary with the number of females breeding on removal outcrops (due to the effects of the removals), the mean number of offspring weaned per female was high on outcrops that had only 1 or 2 females breeding on them (1 female: 4.2±0.44 [20]; 2 females: 3.2±1.0 [6]), relative to those with 3 to 5 females on them (1.6±0.26 [37]). Further, 7 of 8 removal females that were reproductively active but failed to wean any young were from outcrops with 3 or more resident females on them.

Sex Ratio

Because litter size at birth is usually 3 or 4, litters that had only 1 or 2 juveniles by date of first capture had probably experienced some loss since birth. I had no way of distinguishing between the several possible sources of loss from birth to date of first capture, which may or may not have included sex ratio adjustment after parturition. Hence, I tested for evidence of sex ratio adjustment before birth by considering data from litters of 3 or 4 only.

None of the overall sex ratios within mother age/removal class (by year, or years pooled) deviated from 50:50 (p>0.10, Table 12). Further, log-linear analysis was unable to detect significant variation in overall sex ratios between removal, age, or year classes. The MOTHER AGE*REMOVAL*YEAR term was not significant (X^2=0.55, df=1, p=0.76) in the saturated log-linear model, nor were any 2-way (p>0.41) or main effect terms in reduced models; sex ratios were independent of removal (REMOVAL: X^2=0.19, df=1, p=0.66), age (MOTHER AGE: X^2=0.16,

$df=1$, $p=0.69$), and year effects (YEAR: $X^2=1.91$, $df=2$, $p=0.39$). However, small observed values within many cells (Table 12) may have restricted the model's ability to detect differences between removal classes. I re-ran the analysis with years pooled within removal class, but sex ratio remained independent of removal (REMOVAL: $X^2=0.74$, $df=1$, $p=0.39$), and age class (MOTHER AGE: $X^2=0.81$, $df=1$, $p=0.37$) in the reduced models. Lastly, that females did not appear to adjust litter sex ratios in response to lowered densities was further supported by the fact that the distribution of litter sex ratios on either control or removal outcrops did not deviate from that expected by chance (Table 12).

However, overall sex ratios did vary with pre-breeding weight, but only among adults. A 2-way (MOTHER AGE, REMOVAL) ANCOVA indicated that the relationship between sex ratio (arcsine-transformed) and pre-breeding spring weight differed between yearling and adult mothers (MOTHER AGE*WEIGHT: $F_{(1,50)}=4.39$, $p=0.04$), but not between removal classes (REMOVAL*WEIGHT: $F_{(1,49)}=0.09$, $p=0.77$, REMOVAL main effect: $F_{(1,49)}=0.00$, $p=0.998$). The non-significant MOTHER AGE*REMOVAL*WEIGHT term ($F_{(1,47)}=1.22$, $p=0.28$) in the saturated model indicated that the way that sex ratio varied with weight within age class did not differ betweeen removal and control outcrops.

Litter sex ratios did not vary with pre-breeding body weight in yearling mothers ($r_s=0.01$, $p=0.998$, $N=30$; Figure 6a), but they were positively correlated with pre-breeding weight of adults ($r_s=0.59$, $p=0.002$, $N=25$; Figure 6b). Further, whereas the distribution of litter sex ratios did not deviate from that expected by chance in light ($\leq$ median weight) yearlings, light adults, or heavy ($>$ median weight) yearlings, heavy adults produced fewer female-biased litters, and more male-biased litters, than expected by chance (Table 13).

If the tendency for heavy (presumably good condition) mothers to produce more males than expected by chance represents an adaptive adjustment of sex ratio, then those males should in turn exhibit enhanced condition, or other measure of reproductive success, relative to males born to light adults. My tests of this prediction are weak, due to the loss of many males from outcrops, and my lack of knowledge of the actual reproductive success of any males. However, I found little evidence to support the prediction. Survival from weaning to autumn did not differ between the 2 groups (heavy mothers: 42% [31]; light mothers: 41% [17]; $X^2=0.20$, $p>0.50$). Males born to heavy adults that survived to the autumn of birth were born, on average, about the same time (158±4.2 Julian days [13]), and weighed the same in the autumn (226.2g±15.82) as males born to light adults (mean birth date: 150±6.4 Julian days; mean autumn weight: 228.6g±23.42; $N=7$). Although sample sizes were small, there was some indication that more sons born to heavy mothers survived the winter interval to become breeding residents on their natal outcrop (5 of 13) than those born to light mothers (1 of 7).

3.3.3 GROWTH

Juvenile Growth

Rates of post-weaning growth (i.e., the slopes of weight on age regressions) of juvenile females born on control outcrops differed between juveniles born to adult and yearling mothers (MOTHER AGE*AGE: $p=0.004$; Table 14). Small sample sizes may have reduced the ability of the saturated ANCOVA model to detect among-year variation; ANCOVA within years showed that slope differences were significant in 1989 only (1987: $F_{(1,37)}=1.40$, $p=0.24$; 1988: $F_{(1,31)}=0.10$, $p=0.76$; 1989: $F_{(1,38)}=4.35$, $p=0.04$), when juveniles of adult mothers grew faster than juveniles of yearlings, although the trend was apparent in 1987 (Table 15a).

A significant MOTHER AGE*YEAR*AGE term in the saturated ANCOVA model for juvenile males born on control outcrops (Table 14a) was explained by 1) slope differences between age classes of mothers in 1989 only (MOTHER AGE*AGE term in ANCOVA by year; 1987: $F_{(1,35)}=0.70$, $p=0.41$; 1988: $F_{(1,36)}=2.56$, $p=0.12$; 1989: $F_{(1,39)}=3.78$, $p=0.06$), when juveniles of yearling mothers grew faster than juveniles of adult mothers (Table 15b), and 2) a tendency for slopes to vary among years for juveniles of adult mothers only (YEAR*AGE term: adults: $F_{(1,62)}=2.61$, $p=0.08$; yearlings: $F_{(1,48)}=1.22$, $p=0.30$). Juveniles of adult mothers appeared to grow more slowly in 1989 than in other years, contributing to the difference in growth rates between yearling and adult mothers in 1989 (Table 15b). However, that slope differences were reversed in 1987 and 1988 suggests a need for caution when interpreting the difference in 1989 as a general phenomenom.

On control outcrops, adults weighed more than yearlings in the spring before the onset of reproductive activity (see section 3.3.2), and in the autumn after reproductive activity had ceased (adults: 331.3g±5.8 [35]; yearlings: 302.9g±4.7 [43]; $t=3.85$, $p=0.0002$). If the mother age effects on post-weaning growth in female juveniles reflected weight differences, then juveniles of heavy mothers should have grown faster than those of light mothers; in other words, juvenile weight, controlled for age, should vary positively with weight of mother. However, neither pre-breeding nor post-breeding weight of mothers varied positively with age-adjusted weight of juvenile females (or males). Growth of juvenile females did vary significantly with pre-breeding weight of yearling mothers, but the relationship was negative ($r=-0.40$, $p=0.02$, $N=32$) and cannot explain the mother age effects on post-weaning growth of juvenile females in terms of mother weight. There were no other significant correlations between pre- or post-breeding weight of mothers and age-adjusted weight of juveniles of either sex, within mother age class, or with age classes pooled ($-0.19 \leq r \leq 0.20$, $p \geq 0.10$, $N \geq 25$).

Low sample sizes of juveniles born to adult mothers on removal outcrops restricted an analysis of removal effects on growth in juveniles to those born to yearling mothers. The reduced ANCOVA model for juvenile females born to yearling mothers indicated that growth rates differed between removal classes (REMOVAL*AGE term: $p=0.02$), and a significant YEAR main effect ($p=0.01$) indicated that weight intercepts at 20 days of age varied among years (Table 14b). Juvenile females grew faster, on average, on removal outcrops than on control outcrops (Table 15a, Figure 7a). ANCOVA and linear regression within years showed that these growth patterns were apparent in 2 of 3 years (REMOVAL*AGE term; 1987: $F_{(1,53)}=4.14$, $p=0.05$; 1988: $F_{(1,23)}=0.00$, $p=0.99$; 1989: $F_{(1,29)}=2.54$, $p=0.12$; Tables 14, 15). The significant year effect in the original ANCOVA model appeared due to depressed pre-weaning and/or early post-weaning growth in 1988, relative to 1987 and 1989; weight intercepts were lowest for juveniles on both control and removal outcrops in 1988 (Table 15a).

The relationship between weight and age in juvenile males did not differ significantly between removal classes or among years, either in slope (REMOVAL*AGE: $p=0.13$, YEAR*AGE: $p=0.51$) or elevation (REMOVAL main effect: $p=0.13$, YEAR main effect: $p=0.34$; Table 14b). The weak tendency ($p=0.13$) for growth rates to differ between removal classes was due to faster growth in juveniles on removal outcrops (Table 15b, Figure 7b), and ANCOVA within years indicated that the difference was most apparent in 1988 (REMOVAL*AGE term; 1987: $F_{(1,48)}=0.91$, $p=0.34$; 1988: $F_{(1,20)}=3.35$, $p=0.08$; 1989: $F_{(1,31)}=0.15$, $p=0.71$;

Table 15b).

Differences in growth of juvenile females born on control outcrops and those born on removal outcrops could not be explained by differences in weight of mothers. Yearlings on removal outcrops did not weigh more than those on control outcrops in the spring (see section 3.2.2), or in the autumn (removal: 302.9g±5.9 [28]; control: 302.9g±4.7 [43]$t=0.01$, $p=0.99$), and age-adjusted weights of juveniles did not vary with pre- or post-breeding weight of mothers on removal outcrops ($p>0.30$, $N\geq25$).

Yearling Growth

Relative weight gain of female woodrats during their first winter differed among years, but not between removal classes (Table 16a). The significant year effect was due to higher relative increases in weight in 1989-1990 than in other years on both control and removal outcrops (Table 16b). The relative increase in body weight during the interval spanning a female's first breeding season did not vary among years or between control and removal outcrops (Table 16a, b).

Pre-breeding spring weights of yearlings varied positively with their weights in the autumn of birth ($r=0.57$, $p=0.0001$, $N=42$). Further, weight of yearlings in the autumn following their first breeding season were strongly correlated with pre-breeding spring weight ($r=0.75$, $p=0.0001$, $N=48$).

3.3.4 SURVIVAL

Juvenile Female Survival

The proportion of juvenile females that survived the weaning to autumn interval on control outcrops did not differ among years (YEAR: $X^2=2.3$, $df=2$, $p=0.32$), or between juveniles born to yearling and adult mothers (adults: 57%, $N=62$; yearlings:

68%, $N=62$; MOTHER AGE: $X^2=1.61$, $df=1$, $p=0.20$; log-linear analysis). Survival from the autumn in the year of birth to the following breeding season also did not differ among years (YEAR: $X^2=0.59$, $df=2$, $p=0.74$), but there was a strong tendency for juveniles born to adult mothers to survive the interval better than those born to yearlings (adults: 71%, $N=35$; yearlings: 50%, $N=42$; MOTHER AGE term: $X^2=3.3$, $df=1$, $p=0.07$). Survival over the entire weaning to breeding interval did not differ among years (YEAR: $X^2=0.39$, $df=2$, $p=0.82$), or between mother age classes (adults: 40% $N=62$; yearlings: 34% of 62; MOTHER AGE: $X^2=0.75$, $df=1$, $p=0.39$). Similarly, the proportion of mothers that were successful in having at least one daughter survive the winter interval on her natal outcrop did not differ between age classes (yearlings: 53%, $N=38$; adults: 61%, $N=33$, $X^2=0.46$, $p=0.50$).

Because some effects of mother age on survival of juvenile females were apparent, and sample sizes of breeding adults on removal outcrops were small, I tested for removal effects on survival of juveniles from yearling mothers only. The proportion of juvenile females surviving the weaning to autumn, autumn to breeding, and the entire weaning to breeding intervals, did not differ significantly among years, or between juveniles from control and removal outcrops (Table 17). However, juveniles from removal outcrops did experience (non-significantly) higher survival in all years over all intervals than did juveniles from control outcrops. The p-value associated with the REMOVAL term in the log-linear model for the entire interval ($p=0.12$; Table 17) reflects this weak trend. The power of the X^2-test to detect the difference (34% vs. 48%) in survival over the entire interval was low (0.32, following Zar [1984], p. 397); there was a 68% chance of accepting a false null hypothesis of no difference in survival between removal and control outcrops. Hence, the data suggest that more juvenile females from removal outcrops survived the entire weaning to breeding interval to become breeding residents on their natal outcrop than did those from control outcrops, although larger sample sizes are needed to validate this assertion. Consistent with this trend is the fact that of those yearlings that raised at least one juvenile female to weaning, only 53% (N=38) of those on control outcrops had a daughter that survived to become a breeding resident on her natal outcrop, whereas 73% (N=33, X^2=3.03, p=0.08) of those on removal outcrops successfully recruited at least one daughter.

There was no evidence that survival of juvenile females over the weaning to autumn interval was related to date of birth. There were no significant interaction terms ($p>0.10$) in a 3-way (MOTHER AGE, REMOVAL, SURVIVAL) ANOVA on (year-adjusted) birth date. The only significant main effect on date of birth was REMOVAL ($F_{(1,208)}=12.4$, p=0.0005); the non-significant SURVIVAL term ($F_{(1,208)}=0.06$, p=0.81) showed that those juveniles that survived from weaning to autumn clearly did not differ in their mean date of birth (control: 156.0±2.2 [81]; removal: 165.0±2.4 [60]) from those juveniles that did not survive the interval (control: 155.0±2.8 [43]; removal: 167.4±5.0 [28]). This analysis would not detect a birth date effect if survival varied with birth date in a non-linear fashion (e.g., low survival in early and late born juveniles). However, no such patterns of survival were evident when I examined the proportion of juveniles born in each quartile of the breeding season that survived from weaning to autumn, on control outcrops (1st quartile: 62%. 2nd: 83%, 3rd: 53%, 4th: 65%; N=124; X^2=6.00, p=0.11), or on removal outcrops (71%, 71%, 75%, 55%, N=88; X^2=2.19, p=0.54).

Survival of juvenile females over the weaning to autumn interval was also not affected by pre-breeding, spring weight of their mothers. The proportion of juveniles surviving the interval did not differ between those born to light mothers and those born to heavy mothers on control outcrops (Yearlings; light: 73% [41]; heavy: 68% [22]; $X^2=0.18$, $p=0.68$; Adults; light: 54% [50]; heavy: 60% [15]; $X^2=0.17$, $p=0.68$), or on removal outcrops (Yearlings: light: 68% [44]; heavy: 88% [17]; $X^2=2.6$, $p=0.11$; Adults: light: 57% [21]; heavy: 67% [6]).

The REMOVAL main effect was the only significant term in a 3-way (MOTHER AGE, REMOVAL, SURVIVAL) ANOVA on autumn weight ($F_{(1,132)}=4.28$, $p=0.04$), indicating that juveniles were heavier in the autumn on control outcrops (215.2g±3.93 [45]) than they were on removal outcrops (202.5g±4.55 [61]). This effect was presumably due to differences in mean dates of birth of juveniles surviving the weaning to autumn interval between removal classes (see above); autumn weight was inversely correlated with date of birth in juvenile females ($r=-0.78$, $p=0.0001$, $N=136$). There was a tendency for juveniles that survived the winter interval to be heavier in autumn (control: 219.0g±5.15 [44]; removal: 206.8g±6.06 [37]) than those that did not survive the interval (control 209.8g±6.05 [31]; removal: 196.0g±6.77 [24]); SURVIVAL main effect: $F_{(1,132)}=2.58$, $p=0.11$). The saturated ANOVA model did not detect the fact that there were no differences in weight between survival classes in juveniles of yearlings on removal outcrops (live: 203.6g±6.88 [28]; "die": 200.3g±8.20 [17]; $p=0.39$; 1-tail t-test), but that autumn weights differed consistently between survival classes in the other 3 age/removal classes (3 classes pooled, controlling for removal class differences; live: 220.7g±4.78 [53]; "die": 207.7g±5.38 [38]; $p=0.04$; 1-tail t-test).

Juvenile Male Survival

High losses of juvenile males from outcrops over the winter interval restricted a statistical appraisal of mother age and removal effects on survival over the weaning to autumn period. Log-linear analysis indicated that survival of juvenile males over the weaning to autumn interval on control outcrops was not dependent on year (YEAR: $X^2=0.01$, $df=2$, $p=0.99$) or age of mother (adults: 40%, $N=72$; yearlings: 49%, $N=59$; MOTHER AGE term: $X^2=0.94$, $df=1$, $p=0.33$). Further, the proportions of juvenile males (born to all mothers) surviving the weaning to autumn period did not differ ($p=0.61$) between control and removal outcrops (Table 18), and the patterns of survival were virtually unchanged for juveniles born to yearlings only (Control: 49%, $N=59$; Removal: 45%, $N=58$). Survival of juvenile males over the autumn to breeding interval, and the re weaning to breeding interval was low, relative to that of females, and is included in Table 18 for descriptive purposes.

Survival over the weaning to autumn interval was not strongly related to date of birth. A significant MOTHER AGE*REMOVAL*SURVIVAL term ($F_{(1,203)}=3.69$, $p=0.05$) in a saturated ANOVA model was explained by the fact that only among juveniles born to adult mothers on control outcrops did date of birth differ between juveniles that survived the interval, and those that did not. Those that survived the interval were born later, on average, (163±3.1 [32]) than those that didn't survive (153±2.6 [41]). The proportion of juvenile males surviving the weaning to autumn interval was independent of the quartile of the breeding season that they were born in for males born on removal outcrops ($X^2=3.45$, $p=0.33$), or those born to yearling mothers on control outcrops ($X^2=1.4$, $p=0.71$). Males born to adults on control outcrops tended to survive better in the later quartiles (1st: 23%, 2nd: 32%, 3rd: 48%, 4th: 65%; $X^2=7.20$, $p=0.07$), as suggested by the ANOVA.

Pre-breeding spring weight of mothers did not affect survival of male juveniles from weaning to autumn. Juveniles born to light mothers survived as well as those born to heavy mothers, among juveniles born on control outcrops to yearlings (light:

50% [40]; heavy: 53% [17]; $X^2=0.04$, $p=0.84$) and adults (light: 32% [38]; heavy: 39% [33]; $X^2=0.47$, $p=0.49$), as well as those born on removal outcrops to yearlings (light: 44% [45]; heavy: 46% [13]; $X^2=0.01$, $p=0.91$) and adults (light: 44% [16]; heavy: 40% [5]).

In order to consider the influence of autumn weight on survival of male juveniles over the winter interval, I pooled data among mother age classes within removal class (due to low numbers of males surviving the interval). There were no significant terms ($p>0.13$) in a 2-way (REMOVAL, SURVIVAL) ANOVA on autumn weight. The SURVIVAL term in the main effects model ($F_{(1,90)}=2.37$, $p=0.13$), indicated that, like females, there was a weak tendency for males that survived the autumn to breeding interval to be heavier in the autumn (248.5g±8.65 [24]) than those that disappeared during the interval (230.7g±6.11 [69]). Autumn weight of all juveniles that survived from weaning to autumn were, on average, virtually identical between removal classes (control: 235.8g±6.69 [57]; removal: 234.6g±7.94 [36]).

Yearling and Adult Survival

The proportion of yearling females surviving from their first breeding season to the beginning of their second did not vary significantly among years ($p=0.20$) or between control and removal outcrops ($p=0.09$; Table 19a). Yearling females from removal outcrops did, however, survive better than those from control outcrops in 1987-88 (2 by 2 contingency analysis; $X^2=3.91$, $df=1$, $p=0.05$), and the direction of the difference was consistent in 1988-89 and 1989-90 (Table 19a). Further, the power to detect a true difference in survival between removal treatments in the overall (years pooled) X^2-test was low (power=0.35, following Zar [1984], p.397), suggesting that the marginally significant ($p=0.09$) difference in overall survival between control and removal outcrops may reflect a real difference that could only be detected statistically with larger sample sizes.

Yearlings that survived the winter interval were heavier in the autumn (311.1g±4.2 [59]) than those that did not survive the interval (295.9g±4.5 [33]; $F_{(1,89)}=6.09$, $p=0.02$), and the difference did not vary with removal class (REMOVAL*SURVIVAL: $F_{(1,88)}=0.08$, $p=0.78$; REMOVAL: $F_{(1,89)}=1.88$, $p=0.17$). Year differences could not be detected with this analysis (data were pooled among years). However, a cursory examination of the data among years revealed that the weight effect was apparent in 2 of 3 years; the differential between survival classes was 27g, 16g, and 0g, in 1987 ($N=40$), 1988 ($N=25$), and 1989 ($N=28$), respectively.

There was no evidence that overwinter survival was related to reproductive output in yearling females. Measures of reproductive output differed between removal classes only (<u>litter size model</u>: $F_{(1,104)}=5.25$, $p=0.02$; <u>total weaned model</u>: $F_{(1,104)}=5.79$, $p=0.02$). None of the terms in the ANOVA models that partitioned variation between survival classes was significant (<u>litter size model</u>; REMOVAL*SURVIVAL: $F_{(1,103)}=0.83$, $p=0.36$; SURVIVAL: $F_{(1,104)}=0.04$, $p=0.84$; <u>total weaned model</u>; REMOVAL*SURVIVAL: $F_{(1,103)}=0.81$, $p=0.37$; SURVIVAL: $F_{(1,104)}=0.23$, $p=0.63$).

Among yearling males, differences in overwinter survival between control and removal outcrops were not consistent among years, as indicated by a marginally significant REMOVAL*YEAR term ($p=0.06$) in a log-linear analysis (Table 19a). Yearlings from removal outcrops tended to survive better than those from control outcrops in 1987 (2 by 2 contingency analysis; $X^2=2.31$, $df=1$, $p=0.13$), but more poorly in 1989 ($X^2=2.86$, $df=1$, $p=0.09$), and survival tended to vary among years on control outcrops only (3 by 2 contingency analysis; Control: $X^2=5.16$, $p=0.07$;

Removal: $X^2=2.37$, $p=0.31$).

Given that small samples precluded a statistical analysis of survival of adults from the end of their second breeding season to the start of their third, no major differences among years or between control and removal outcrops within either sex were obvious, and adults generally survived as well as yearlings (Table 19b).

3.3.5 LIFETIME REPRODUCTIVE SUCCESS (LRS)

Lifetime output of weaned offspring (LRS1) in females on control outcrops varied from 0 to 13, and the distribution was skewed to the right; most (77%) individuals produced ≤ 4 offspring (mean=3.4±3.11 [SD], median=3, $N=64$; Figure 8a). There was no association between LRS1 and mean date of first parturition (PDATE), but LRS1 varied positively with maximum (lifetime) pre-breeding (PRE) and post-breeding (POST) weights, and with the number of years that an individual was reproductively active (YEARS) (Table 20a). However, PRE and POST were both postively correlated with YEARS ($r=0.44$, and 0.29, respectively), and LRS1 did not vary with either PRE or POST when YEARS was held constant in a partial correlation analysis (Table 20a). Thus, YEARS was the only independent predictor of LRS1. One-year breeders produced, on average, 1.8±1.65(SD) (median=1.0, $N=33$), 2-year breeders, 4.0±2.60(SD) (median=3.5, $N=22$), and 3-year breeders, 8.0±3.54(SD) (median=8.0, $N=9$). Females that lived to breed in more than one year did not wean more young (2.1±0.27 [31]) *in their first year* than females that bred for one year only (1.8±0.29 [33]; $t=0.63$; $p=0.53$), but they were heavier, both in the spring prior to their first breeding season (2,3-year breeders: 287.2g±6.86 [18]; 1-year breeders: 261.0g±5.45 [25]; $t=3.03$, $p=0.004$), and in the following autumn (2,3-year: 323.3g±5.93 [30]; 1-year: 299.4g±5.46 [26]; $t=2.93$; $p=0.005$).

Lifetime output of weaned offspring in females on removal outcrops did not vary with YEARS, PRE, POST, or PDATE. LRS1 was similar between removal classes (control: see above; removal: 3.7±3.36 [SD], median = 3, N=31; p=0.66, U-test), as was the overall frequency distribution (0-1, ≥5 offspring pooled, X^2=4.3, df=4, p=0.37; Figure 8a). However, there was a tendency for females on removal outcrops to have 2 or 3 offspring more often (45% of 31) than females on control outcrops (27% of 64; X^2=3.29, p=0.07). The reproductive responses of yearlings to the removal experiment were apparently such that they had a significant impact on lifetime production of weaned offspring, even relative to that of 2-year breeders on both removal and control outcrops. The lack of association between LRS1 and YEARS on removal outcrops was due to the fact that LRS1 was similar between 1-year breeders (3.1±1.70 [SD], median=3.0, N=18) and 2-year breeders (4.4±4.96 [SD], median=3.0; N=12, p=0.93, U-test). This may not be particularly meaningful, as some of the 2-year breeders on removal outcrops bred as yearlings before the removal experiment was begun. Further, many adults that bred as yearlings on removal outcrops were subsequently removed at the start of their 2nd or 3rd year. Their LRS would be expected to exceed that of 1-year breeders had they been allowed to breed beyond their first year. More interesting, however, is the fact that LRS1 did not differ between 1-year breeders on removal outcrops and 2-year breeders on controls outcrops (p=0.34; U-test).

There was little variation in the number of philopatric daughters that a female produced in her lifetime (LRS2). Only 2 of 94 females had more than 2 daughters that became breeding residents on their natal outcrop (Figure 8b). On control outcrops, mean LRS2 was 0.7±0.88(SD), but the median was 0; 56% (N=64) failed to raise any philopatric daughters to breeding age during their lifetime. LRS2 did not vary significantly with PRE or POST. However, LRS2 did vary positively with YEARS, and inversely with PDATE (Table 20b). One-year breeders produced, on average, 0.4±0.66(SD) philopatric daughters (median=0; N=33), 2-year breeders, 0.7±0.77(SD) (median=1; N=22), and 3-year breeders, 1.8±1.16(SD) (median=2; N=9). Females that bred for 2 or 3 years on control outcrops produced the same number of philopatric daughters in their first year (0.5±0.77 [SD]; N=31) as did 1-year breeders (0.4±0.66 [SD]; N=33; p=0.75, U-test).

The correlation between PDATE and LRS2 was not due to variation between PDATE and YEARS; LRS2 varied significantly with PDATE, after controlling for YEARS (r_{partial}=-0.37, p=0.01). Mean date of first parturition varied from 159.3±3.1 (N=23), to 150.3±3.7 (15), and 145.0±3.5 (12), among females that raised 0, 1, and ≥ 2 philopatric daughters, respectively. The importance of date of first parturition in this analysis may have been related to 2 factors: 1) lifetime production of daughters to weaning was inversely related to mean date of first parturitions (r=-0.27, p=0.05, n=51), and positively correlated with LRS2 (r=0.74, p=0.0001, N=63), and 2) weight of juveniles in the autumn of birth was inversely related to parturition date (r=-0.78, p=0.0001, N=38), and juveniles that survived to become philopatric daughters were heavier in the autumn than those that did not survive (see section 3.2.4).

Lifetime production of philopatric daughters did not vary with YEARS, PRE, POST, or PDATE among females on removal outcrops. PDATE did vary consistently with LRS2 (LRS2=0: 166.1±6.1 [10], LRS2=1: 158.9±3.4 [14]; LRS2=2: 154.5±11.3 [4]), but sample sizes (and presumably power to detect an association between variables) were low. Females on removal outcrops produced, on average, the same number of philopatric daughters (0.7±0.69 [SD], median=1, N=31) as those on control outcrops ($p=0.55$, U-test), and the frequency distributions of LRS2 did not differ between removal classes (2-3 daughters pooled, $X^2=4.51$, $df=2$, $p=0.11$; Figure 8b). However, like LRS1, LRS2 in 1-year breeders on removal outcrops was high (0.7±0.67 [SD], median=1.0, $N=18$); it did not differ from that of 2-year breeders on either removal outcrops (0.6±0.67 [SD], median=0.5, $N=12$, $p=0.57$, U-test) or control outcrops ($p=0.98$, U-test).

3.3.6 DISPERSAL AND IMMIGRATION

In this section, I consider the influence of density of resident females (i.e., a removal effect) on the patterns of movement of those individuals that left their natal outcrop, and were captured at least once on another outcrop.

Females

Of 212 female woodrats born on the control and removal outcrops, only 6 were known to have dispersed from their natal outcrop to become a breeding resident on another outcrop. Only 5 others were ever captured off their natal outcrop. Each of these 5 were caught once on an outcrop adjacent to their natal outcrop; 2 as juveniles and 3 as breeding yearlings. Five of the 6 dispersers moved between outcrops before they became reproductively active as yearlings; 1 of these moved with her mother after the mother's first breeding season on her natal outcrop. Four of the dispersal events occurred between adjacent outcrops separated by less than 200 metres, whereas 2 involved larger distances (1 km, 10 km) spanning several outcrops. All 6 of the dispersers moved from a control outcrop into a removal outcrop, suggesting that immigration of female woodrats may have been limited by the density of resident females. Consistent with this interpretation is the fact that more immigrants (of unknown origin) appeared on removal outcrops than on control outcrops as juveniles during the breeding season (removal: $N=17$; control: $N=9$). Further, twice as many immigrants established residency on removal outcrops ($N=34$) than on control outcrops ($N=17$) during the autumn to spring interval, and immigrants constituted a greater proportion of breeding females on removal outcrops (44%, $N=93$) than on control outcrops (28%, $N=71$; $X^2=4.37$, $df=1$, $p<0.05$).

Males

There were 6 cases of known dispersal among the 212 juvenile males born on the study outcrops. In all cases, dispersal occurred sometime during the autumn to spring interval. Three of the dispersers moved between control outcrops, 1 between removal outcrops, 1 from a control to a removal outcrop, and 1 from a removal to a control outcrop. Movements were from the natal outcrop into the nearest adjacent outcrop in 3 cases (0.5, 0.8, and 1.0 km); the other 3 moved 1.5, 2.0, and 3.0 km between non-adjacent outcrops. Five other males of known origin were caught once on a non-natal outcrop (mean distance from natal outcrop: 3.6 km, range: 1.0 - 10.0 km), and never caught again; they may or may not have been successful dispersers. Four males were resident on different (adjacent) outcrops between years. Two moved from a removal outcrop, and all 4 moved into a control outcrop. In addition, 17 males were resident on 2 adjacent outcrops within a breeding season, and another 17 were caught once, usually early in the breeding season, on an outcrop adjacent to the one that they were a resident on. There were 16 different outcrops used by these 34 males (9 control, 7 removal).

These inter-outcrop movements suggest that the immigration of male woodrats was not affected by the density of resident females. That 1) the same number of immigrant juvenile males (*N*=32) was caught on control and removal outcrops during the breeding season, and 2) the proportion of breeding residents that were immigrants did not differ between control and removal outcrops (control: 79% [*N*=65]; removal: 84% [*N*=61]; $X^2=0.54$, *df*=1, $p>0.40$) provides further evidence for the lack of a (female) removal effect on immigration of male woodrats.

Table 2. Number of female and male non-juvenile woodrats resident[1] on a) unmanipulated (control) and b) experimental (removal) rock outcrops in 1987-1990.

	Females				Males			
	1987	1988	1989	1990	1987	1988	1989	1990
a) Control Outcrops								
Aspen	-	-	5	6	-	-	5	5
Elbow	-	2	2	4	-	2	2	4
Fire	2	2	3	3	2	2	4	5
Hidden	3	4	4	3	4	3	3	4
Marmot	12	10	8	12	3	3	5	7
Mud-1	3	2	2	2	2	2	2	1
Pika	6	8	4	3	5	4	2	1
Power	1	1	2	2	2	1	2	1
Ranger	2	3	2	4	1	2	2	2
Raven	-	6	5	6	-	6	5	4
Shady	2	2	-		3	1	-	-
Slippery	3	-	-	-	2	-	-	-
Wedge	3	1	1	3	2	2	1	1
Total	37	41	38	48	26	28	32	35

	Females							Males			
	1987		1988		1989		1990	1987	1988	1989	1990
b) Removal Outcrops											
Barrier	8[b]	3[a]	9[b]	5[a]	8[b]	4[a]	8	5	9	13	6
Beaver	3	1	2	1	1	1	1	3	1	1	0
Bridge	4	2	1	1	1	1	2	2	1	1	1
Dusty	2	1	3	1	0	0	1	3	2	0	0
Gulch	6	3	11	5	6	3	4	2	3	3	3
Kel's	9	4	9	4	3	3	6	8	7	4	4
Mossy	2	1	2	1	2	1	1	1	2	2	1
Mud-2	4	2	3	1	0	0	0	1	3	0	1
Rocks	2	1	1	1	2	1	4	1	1	2	0
S[illegible]le	2	1	0	0	1	1	2	1	0	1	1
Shady	-	-	-	-	2	1	2	-	-	3	2
Sibbald	2	1	2	1	1	1	2	1	1	2	1
Slippery	-	-	6	3	2	2	2	-	1	3	2
Total	44	20	49	24	29	19	36	29	31	33	22

[1]: Residents were individuals caught in at least 3 trap sessions (see text) per year in 1987-89, and 2 sessions in 1990. Some males were resident on 2 outcrops in a year.

[b]: Before removal. [a]: After removal.

Table 3. Variation in mean date of parturition of first successful litter of year on control outcrops among years and between yearling and adult mothers. a) 2-way ANOVA table for reduced main effects model. Interaction term was not significant ($F_{(1,82)}=1.01$, $p=0.37$). b) Mean Julian dates ± standard error. Sample sizes in parentheses.

a)

Source	*df*	*F*	*p*
Error	83	-	-
Model	3	8.70	0.0001
Mother Age	1	5.77	0.02
Year	2	12.16	0.0001

b)

Year	Yearlings	Adults
1987	147±3.5 (22)	136±5.4 (8)
1988	160±5.7 (9)	146±3.3 (17)
1989	163±2.8 (14)	160±4.3 (17)

Table 4. Variation in mean date of parturition of first successful litter of year for yearling mothers among years and between control and removal outcrops. "Captives" were females permanently removed from experimental outcrops. a) 2-way ANOVA table for reduced main effects model. Interaction terms were not significant ($p \geq 0.49$). b) Mean Julian dates ± standard error. Sample sizes in parentheses.

a)

	Without captives			With captives		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	79	-	-	107	-	-
Model	3	12.70	0.0001	3	12.20	0.0001
Removal	1	0.20	0.66	1	0.36	0.55
Year	2	24.90	0.0001	2	24.30	0.0001

b)

Year	Control	Removal	Removal, with captives
1987	147±3.5 (22)	145±4.2 (15)	146±3.3 (23)
1988	160±5.7 (9)	161±3.1 (12)	153±2.4 (27)
1989	163±2.8 (14)	167±4.3 (11)	163±3.7 (15)

Table 5. Variation in mean date of parturition of first successful litter of year for adult mothers among years and between control and removal outcrops. "Captives" were females permanently removed from experimental outcrops. a) 2-way ANOVA table for reduced main effects model. Interaction terms were not significant ($p \geq$ 0.69; b) Mean Julian dates ± standard error. Sample sizes in parentheses.

a)

	Without captives			With captives		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	53	-	-	72	-	-
Model	3	9.00	0.0004	3	9.90	0.0002
Removal	1	3.70	0.06	1	1.50	0.23
Year	2	14.90	0.0003	2	19.60	0.0001

b)

Year	Control	Removal	Removal with captives
1987	136±5.4 (8)	146±13.3 (3)	144±3.9 (10)
1988	146±3.3 (17)	157±11.7 (6)	150±5.2 (14)
1989	160±4.3 (17)	172±11.6 (5)	164±7.6 (9)

Table 6. Variation in litter size at weaning among years and between yearling and adult mothers, by removal class. Only yearlings that bred once were included. a) 2-way ANOVA tables for reduced main effects models. Interaction terms were not significant ($p \geq 0.71$). b) Mean litter size ± standard error. Sample sizes in parentheses.

a)

	Control Outcrops			Removal Outcrops		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	115	-	-	60	-	-
Model	3	3.23	0.02	3	0.42	0.74
Mother Age	1	6.93	0.01	1	1.12	0.29
Year	2	2.24	0.11	2	0.03	0.97

b)

	Control Outcrops		Removal Outcrops	
Year	Yearling	Adult	Yearling	Adult
1987	1.5±0.31(17)	1.8±0.47(10)	2.1±0.48(8)	1.4±0.51(5)
1988	0.8±0.32(12)	1.6±0.26(28)	1.7±0.43(11)	1.7±0.49(11)
1989	1.4±0.22(25)	2.2±0.27(27)	2.1±0.32(18)	1.6±0.39(11)
1987-89	1.3±0.16(54)	1.9±0.17(65)	2.0±0.22(37)	1.6±0.26(27)

Table 7. Variation in litter size at weaning among years and between control and removal outcrops, by age class. a) 2-way ANOVA tables for reduced main effects models. Interaction terms were not significant ($p \geq 0.56$). b) Mean litter size ± standard error. Sample sizes in parentheses.

a)

	Yearlings			Adults		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	151	-	-	88	-	-
Model	3	3.07	0.03	3	0.73	0.54
Removal	1	4.77	0.03	1	0.78	0.38
Year	2	2.26	0.11	2	0.70	0.50

b)

	Yearlings		Adults	
Year	Control	Removal	Control	Removal
1987	1.6±0.22(39)	1.9±0.29(28)	1.8±0.47(10)	1.4±0.51(5)
1988	0.9±0.22(25)	1.6±0.31(19)	1.6±0.26(28)	1.7±0.49(11)
1989	1.4±0.22(25)	2.1±0.32(18)	2.2±0.27(27)	1.6±0.39(11)
1987-89	1.4±0.13(89)	1.8±0.17(65)	1.9±0.17(65)	1.6±0.26(27)

Table 8. Percentages of reproductive attempts that failed between removal and age classes. An attempt was considered as failed if a female was captured in advanced pregnancy or during lactation, but there were no offspring at weaning associated with the attempt. Reproductive attempts within individuals (within years) were considered independent. Number of litters in parentheses.

	Yearlings		Adults	
Year	Control	Removal	Control	Removal
1987	26(38)	29(28)	17(12)	20(5)
1988	54(24)	32(19)	32(38)	31(13)
1989	24(25)	22(18)	19(27)	17(12)
Pooled	33(87)	28(65)	25(77)	23(30)

Table 9. a) The influence of removal and mother age effects on the percentage of females raising 2 (vs. 1) successful (≥ 1 offspring to weaning) litters in a breeding season. Breeding events between years within individuals were assumed to be independent. The REMOVAL*MOTHER AGE term was not significant (X^2=0.00, df=1, p=0.95) in the log-linear analysis. Sample sizes in parentheses. b) Mean adjusted Julian dates of first parturition (±SE [N]) of females raising 1 vs. 2 successful litters per season, by age and removal class. Dates were adjusted to 1988 mean for each age/removal class, and years (87-89) pooled. p is the probability that dates within age/removal class differ by chance (2-tailed t-test).

a)

	% 2 Litters (N)		Log-linear Analysis			
Mother Age	Control	Removal	Source	X^2	df	p
Yearling	31 (45)	25 (36)[a]	Removal	0.70	1	0.41
Adult	38 (43)	29 (17)[b]	Mother Age	0.48	1	0.49

[a] includes 2 females that raised 3 successful litters

[b] includes 1 female that raised 3 successful litters

b)

Outcrop	Age	1 Litter	2 Litter	t	p
Control	Yearling	162±2.4(32)	155±4.2(14)	1.88	0.07
	Adult	151±3.2(24)	137±2.7(16)	3.14	0.003
Removal	Yearling	164±2.3(26)	150±3.5(10)	3.39	0.002
	Adult	160±7.3(10)	155±13.3(5)	-	-

Table 10. Variation in number of offspring raised to weaning between yearling and adult mothers, by removal class. Only yearlings that bred once were included. a) 2-way ANOVA tables for reduced main effects models. Interaction terms were not significant ($p \geq 0.55$). b) Mean ± standard error. Sample sizes in parentheses.

a)

	Control Outcrops			Removal Outcrops		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	76	-	-	37	-	-
Model	3	3.01	0.04	3	0.43	0.74
Mother Age	1	8.18	0.01	1	0.50	0.48
Year	2	1.03	0.36	2	0.37	0.69

b)

	Control Outcrops		Removal Outcrops	
Year	Yearling	Adult	Yearling	Adult
1987	2.2±0.5(12)	3.0±0.8(6)	4.3±0.3(4)	2.3±1.3(3)
1988	1.1±0.5(9)	2.7±0.4(17)	2.4±0.5(11)	2.7±1.3(7)
1989	2.0±0.3(18)	3.0±0.4(20)	3.1±0.6(12)	2.4±0.8(7)
1987-89	1.9±0.3(39)	2.8±0.3(43)	3.0±0.4(24)	2.5±0.6(17)

Table 11. Variation in number of offspring raised to weaning between control and removal outcrops, by age class. a) 2-way ANOVA tables for reduced main effects models. Interaction terms were not significant ($p \geq 0.66$). b) Mean ± standard error. Sample sizes in parentheses.

a)

	Yearlings			Adults		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	103	-	-	56	-	-
Model	3	5.42	0.002	3	0.11	0.96
Removal	1	8.88	0.004	1	0.25	0.62
Year	2	4.27	0.02	2	0.03	0.97

b)

	Yearlings		Adults	
Year	Control	Removal	Control	Removal
1987	2.2±0.3(28)	3.1±0.5(17)	3.0±0.8(6)	2.3±1.3(3)
1988	1.3±0.3(17)	2.0±0.4(15)	2.7±0.4(17)	2.7±1.3(7)
1989	2.0±0.3(18)	3.1±0.6(12)	3.0±0.4(20)	2.4±0.8(7)
1987-89	1.9±0.2(63)	2.7±0.3(44)	2.8±0.3(43)	2.5±0.6(17)

Table 12. a) Percentage of juvenile males at weaning in litters of 3 or 4, between control and removal outcrops, by age class. None differed from 50:50 ($p > 0.10$). Number of juveniles in parentheses. b) Observed and expected (binomial) frequency distributions of litter sex ratios within removal class. Years and mother age classes pooled. *p* is the probability that litter sex ratios within removal class were determined by chance.

a)

Age	Year	Control Outcrops	Removal Outcrops
Yearling	1987	61 (41)	50 (38)
	1988	56 (9)	42 (19)
	1989	50 (10)	65 (26)
	1987-89	58 (60)	53 (83)
Adult	1987	55 (11)	0 (3)
	1988	49 (39)	50 (14)
	1989	56 (39)	60 (10)
	1987-89	53 (89)	48 (27)

b)

	Control Outcrops			Removal Outcrops		
% Males	Obs.	Exp.	Cell X^2	Obs.	Exp.	Cell X^2
0-0.25	6	8.19	0.59	7	6.29	0.08
0.33	13	10.88	0.41	4	8.25	2.19
0.50	4	5.63	0.47	5	4.13	0.18
0.67	8	10.88	0.76	10	8.25	0.37
0.75-1.0	13	8.19	2.82	7	6.29	0.08
X^2			5.05			2.90
p			> 0.10			> 0.50

Table 13. Observed and expected (binomial) frequency distributions of percentage of juvenile males at weaning in litters of 3 or 4, among light (≤ median pre-breeding [spring] weight), and heavy (> median) mothers within age class. Sex ratio categories were combined to create expected frequencies ≥ 5 where possible. *p* is the probability that litter sex ratios were determined by chance.

	Light			Heavy		
% Males	Obs.	Exp.	Cell X^2	Obs.	Exp.	Cell X^2
YEARLINGS						
0-0.33	6	7.25	0.22	5	6.50	0.35
0.50	2	1.50	0.17	0	1.50	1.50
0.67-1.0	8	7.25	0.08	9	6.50	0.96
X^2			0.46			2.81
p			> 0.50			> 0.10
ADULTS						
0-0.33	9	6.10	1.38	1	4.75	2.96
0.50	0	0.75	0.75	2	2.25	0.03
0.67-1.0	4	6.10	0.72	9	4.75	3.80
X^2			2.85			6.79
p			> 0.10			< 0.05

Table 14. ANCOVA of post-weaning growth between a) juveniles born to yearling and adult mothers on control outcrops, and b) control and removal outcrops for juveniles of yearling mothers. "AGE" term is juvenile age in days (covariate). "MOTHER" term partitioned variance between yearling and adult mothers. p-values for terms not shown were ≥ 0.13 in reduced models.

a) Mother Age Effect	Juvenile Females			Juvenile Males		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Error	112	-	-	110	-	-
Model	5	124.33	0.000	11	101.27	0.000
Age	1	608.02	0.000	1	717.37	0.000
Mother	1	10.31	0.002	1	0.20	0.66
Year	2	1.98	0.14	2	0.73	0.48
Mother*Age	1	8.51	0.004	1	0.18	0.67
Year*Age	-	-	-	2	0.02	0.98
Mother*Year	-	-	-	2	1.08	0.34
Mother*Year*Age	-	-	-	2	3.18	0.05

b) Removal Effect	Juvenile Females			Juvenile Males[a]		
Error	111	-	-	106	-	-
Model	5	102.18	0.000	4	206.84	0.000
Age	1	497.96	0.000	1	790.99	0.000
Removal	1	8.51	0.004	1	2.33	0.13
Year	2	4.49	0.01	2	1.10	0.34
Removal*Age	1	5.77	0.02	1	2.29	0.13
Year*Age	-	-	-	2	0.68	0.51
Removal*Year	-	-	-	2	0.15	0.86
Removal*Year*Age	-	-	-	2	1.03	0.36

[a] F value of 3-way term from saturated model. Other F values from appropriate reduced models (eg., F=2.29 for REMOVAL*AGE term from model: Weight= REMOVAL · AGE · REMOVAL*AGE).

Table 15. Least-squares linear regression for juvenile post-weaning growth. Weight (g) was regressed on (Age-20 days) to generate weight intercepts close to weaning age. *a*=intercept, *b*=slope. All regressions were significant ($p<0.0001$).

a) Juvenile Females

	Control Outcrops								Removal Outcrops			
	Adults				Yearlings				Yearlings			
Year	*a*	*b*	r^2	*N*	*a*	*b*	r^2	*N*	*a*	*b*	r^2	*N*
1987	92.3	1.94	0.93	10	119.3	1.55	0.76	31	95.5	2.03	0.86	26
1988	93.8	2.03	0.91	25	96.6	1.95	0.88	10	84.6	1.94	0.80	17
1989	87.1	2.08	0.89	26	108.1	1.56	0.80	16	92.0	2.02	0.89	17
87-89	91.2	2.02	0.90	61	113.4	1.59	0.77	57	92.7	1.96	0.83	60

b) Juvenile Males

	Control Outcrops								Removal Outcrops			
	Adults				Yearlings				Yearlings			
Year	*a*	*b*	r^2	*N*	*a*	*b*	r^2	*N*	*a*	*b*	r^2	*N*
1987	95.1	2.67	0.96	10	100.6	2.39	0.89	29	98.6	2.66	0.87	23
1988	89.5	2.85	0.91	30	103.1	2.29	0.93	10	91.5	2.93	0.92	14
1989	93.3	2.24	0.85	28	83.4	2.83	0.90	15	90.7	2.69	0.86	20
87-89	87.0	2.77	0.90	68	97.3	2.46	0.89	54	93.1	2.75	0.88	57

Table 16. Variation in proportional weight gain among females during their first 1) winter, and 2) breeding season, between control and removal outcrops. a) 2-way ANOVA tables for reduced main effects models. Interaction terms were not significant ($p \geq 0.69$). Proportional weight gains were arcsine-transformed prior to ANOVA. b) Mean (untransformed) proportional weight gains ± standard error. Sample sizes in parentheses.

a)

	Winter Interval			Breeding interval		
Source	*df*	*F*	*P*	*df*	*F*	*p*
Error	63	-	-	67	-	-
Model	3	6.98	0.004	3	0.35	0.79
Removal	1	0.53	0.47	1	0.73	0.40
Year	2	10.43	0.0001	2	0.15	0.86

b)

	Winter Interval			Breeding Interval	
Year	Control	Removal	Year	Control	Removal
87-88	0.16±0.04(12)	0.18±0.04(13)	1987	0.17±0.23(14)	0.18±0.03(9)
88-89	0.14±0.03(12)	0.18±0.06(10)	1988	0.17±0.02(13)	0.20±0.03(10)
89-90	0.33±0.06(16)	0.43±0.07(6)	1989	0.17±0.02(16)	0.19±0.02(9)
Pooled	-	-	Pooled	0.17±0.01(43)	0.19±0.02(28)

Table 17. The influence of removal and year effects on the percentages of juvenile females born to yearling mothers that survived from 1) weaning to autumn, 2) autumn to the following breeding season, and 3) weaning to breeding. The REMOVAL*YEAR term was not significant ($p > 0.89$) in any of the log-linear models. Number of juveniles in parentheses.

		% Surviving		Log-linear Analysis			
Interval	Year	Control	Removal	Source	X^2	*df*	*p*
Weaning to Autumn	1987	67 (33)	77 (26)				
	1988	60 (10)	71 (17)	Removal	1.05	1	0.31
	1989	74 (19)	78 (18)	Year	0.80	2	0.67
	Pooled	68 (62)	75 (61)				
Autumn to Breeding	1987-88	50 (22)	65 (20)				
	1988-89	50 (6)	67 (12)	Removal	1.42	1	0.23
	1989-90	50 (14)	57 (14)	Year	0.16	2	0.92
	Pooled	50 (42)	63 (46)				
Weaning to Breeding	1987-88	33 (33)	50 (26)				
	1988-89	30 (10)	47 (17)	Removal	2.41	1	0.12
	1989-90	37 (19)	44 (18)	Year	0.05	2	0.98
	Pooled	34 (62)	48 (61)				

Table 18. The influence of removal and year effects on the percentages of juvenile males born to all mothers that survived from 1) weaning to autumn, 2) autumn to the following breeding season, and 3) from weaning to breeding. Small sample sizes restricted statistical analysis to the first interval only. The REMOVAL*YEAR term in log-linear model was not significant ($X^2=0.31$, $df=2$, $p=0.86$). Number of juveniles in parentheses.

		% Surviving		Log-linear Analysis			
Interval	Year	Control	Removal	Source	X^2	*df*	*p*
Weaning to Autumn	1987	46 (41)	38 (29)				
	1988	43 (42)	44 (25)	Removal	0.26	1	0.61
	1989	44 (48)	41 (27)	Year	0.01	2	0.99
	Pooled	44 (131)	41 (81)				
Autumn to Breeding	1987-88	42 (19)	27 (11)				
	1988-89	39 (18)	58 (11)				
	1989-90	14 (21)	0 (11)				
	Pooled	31 (58)	27 (33)				
Weaning to Breeding	1987-88	20 (41)	11 (29)				
	1988-89	17 (42)	24 (25)				
	1989-90	6 (48)	0 (27)				
	Pooled	14 (131)	11 (81)				

Table 20. Correlates of measures of lifetime reproductive success in female woodrats. For non-significant (NS) correlations: $0.20 < p < 0.90$. Pre^{P} and Post^{P} are partial correlations, controlling for Years; all others are Pearson correlations. a) Number of offspring produced to weaning age (LRS1). b) Number of female offspring that became breeding residents on natal rock outcrop (LRS2).

Outcrop		Years	Pre	Pre^{P}	Post	Post^{P}	Pdate
a) LRS1							
Control	*r*	0.59	0.44	0.09	0.29	0.02	-0.18
	p	0.0001	0.001	NS	0.03	NS	NS
	N	64	50	50	56	56	51
Removal	*r*	0.08	0.16	-	-0.13	-	-0.26
	p	NS	NS		NS		NS
	n	31	26		24		28
b) LRS2							
Control	*r*	0.40	0.26	0.13	0.18	0.003	-0.41
	p	0.001	0.07	NS	NS	NS	0.003
	N	63	49	49	55	55	50
Removal	*r*	0.01	0.20	-	0.10	-	-0.17
	p	NS	NS		NS		NS
	n	31	26		24		28

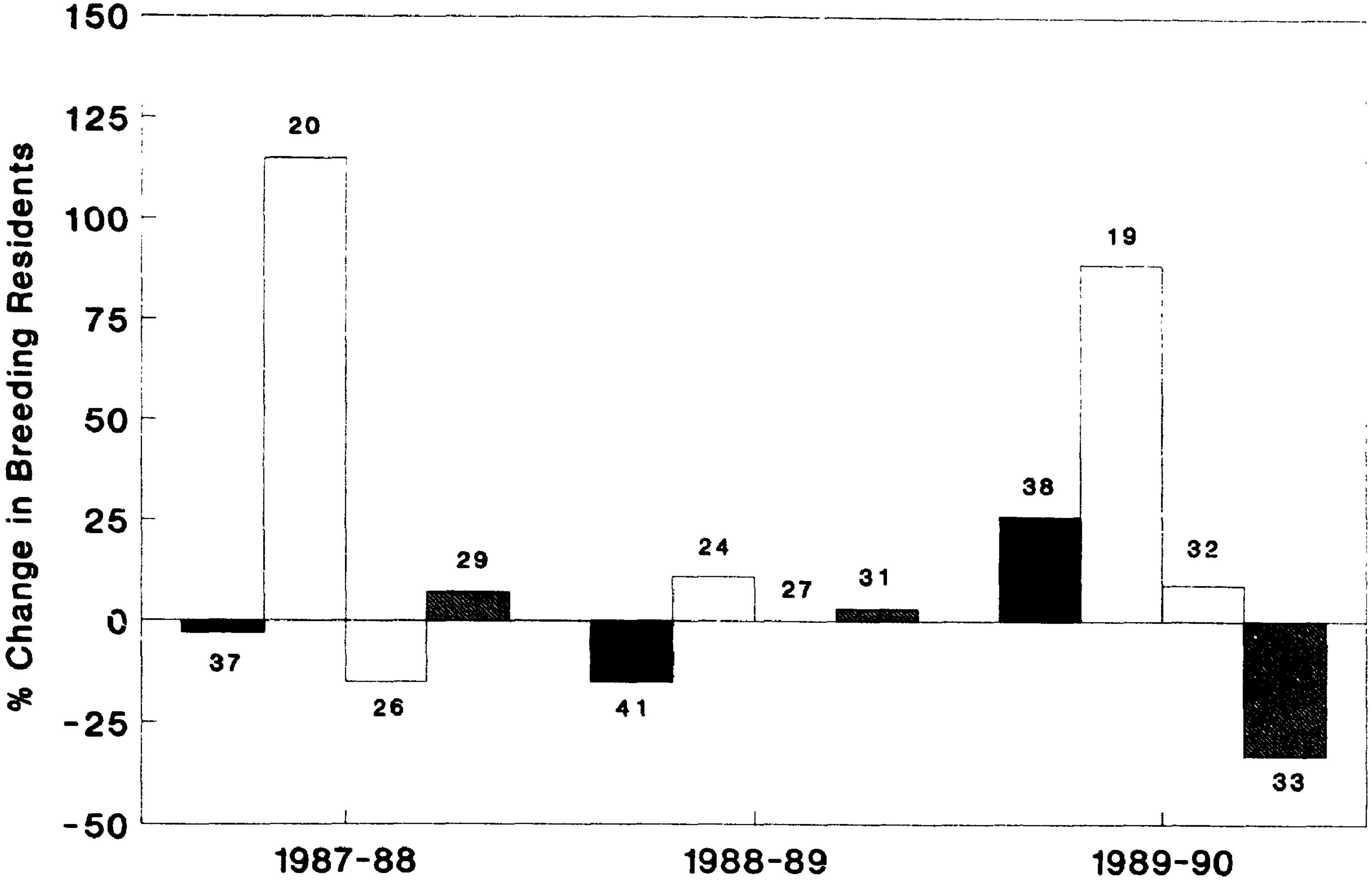
Years: number of breeding seasons alive.
Pre: maximum pre-breeding (spring) weight.
Post: maximum post-breeding (autumn) weight.
Pdate: mean date of first parturitions.

Table 20. Correlates of measures of lifetime reproductive success in female woodrats. For non-significant (NS) correlations: $0.20 < p < 0.90$. Pre^P and Post^P are partial correlations, controlling for Years; all others are Pearson correlations. a) Number of offspring produced to weaning age (LRS1). b) Number of female offspring that became breeding residents on natal rock outcrop (LRS2).

Outcrop		Years	Pre	Pre^P	Post	Post^P	Pdate
a) LRS1							
Control	*r*	0.59	0.44	0.09	0.29	0.02	-0.18
	p	0.0001	0.001	NS	0.03	NS	NS
	N	64	50	50	56	56	51
Removal	*r*	0.08	0.16	-	-0.13	-	-0.26
	p	NS	NS		NS		NS
	n	31	26		24		28
b) LRS2							
Control	*r*	0.40	0.26	0.13	0.18	0.003	-0.41
	p	0.001	0.07	NS	NS	NS	0.003
	N	63	49	49	55	55	50
Removal	*r*	0.01	0.20	-	0.10	-	-0.17
	p	NS	NS		NS		NS
	n	31	26		24		28

Years: number of breeding seasons alive.
Pre: maximum pre-breeding (spring) weight.
Post: maximum post-breeding (autumn) weight.
Pdate: mean date of first parturitions.

Figure 3. Percentage change in numbers of breeding residents between breeding seasons (1987-90) on all outcrops. For removal outcrops, changes in numbers are from post-removal in one year to the initiation of the breeding season (pre-removal) in the next year. Control females: closed bars; Removal females: open bars; Control males: stippled bars; Removal males: hatched bars. Sample sizes above/below bars.


150
125
100
75
50
25
0
-25
-50
% Change in Breeding Residents
20
26
29
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41
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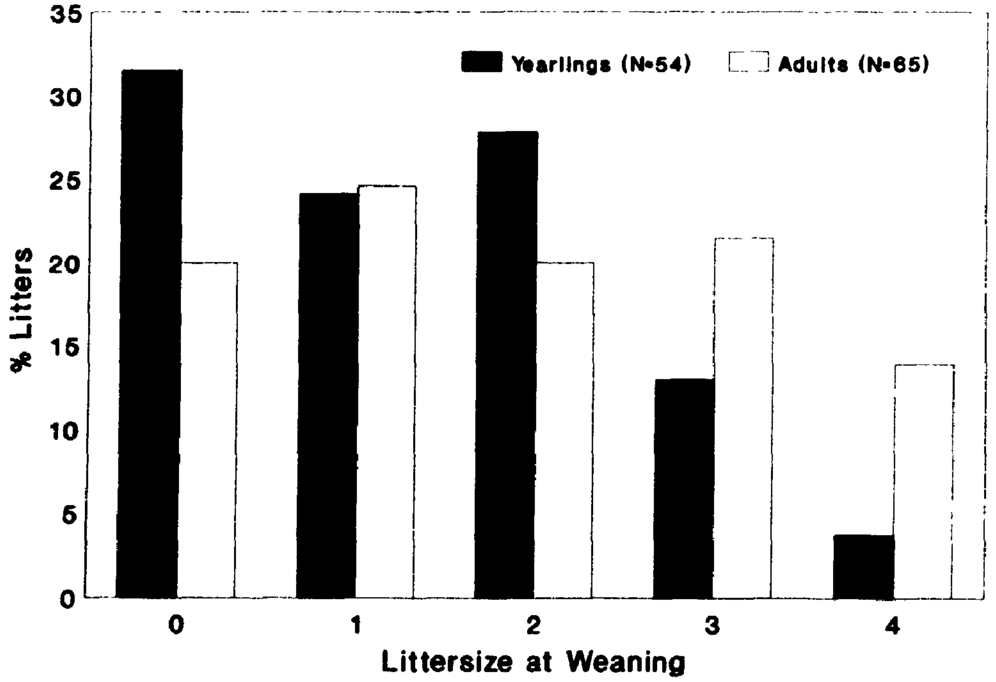
31
38
19
32
33
1987-88
1988-89
1989-90

Figure 4. Distribution of litter sizes. Years (1987-89) pooled. a) Control outcrops. Distributions did not differ between age classes ($p=0.15$), but adults had more litters of 3 than did yearlings ($p=0.03$). b) Yearling mothers only. Distributions did not differ between removal classes ($p=0.10$), but there were more litters of 3 on removal outcrops than on control outcrops ($p=0.03$).

a) Control Outcrops



b) Yearling Mothers

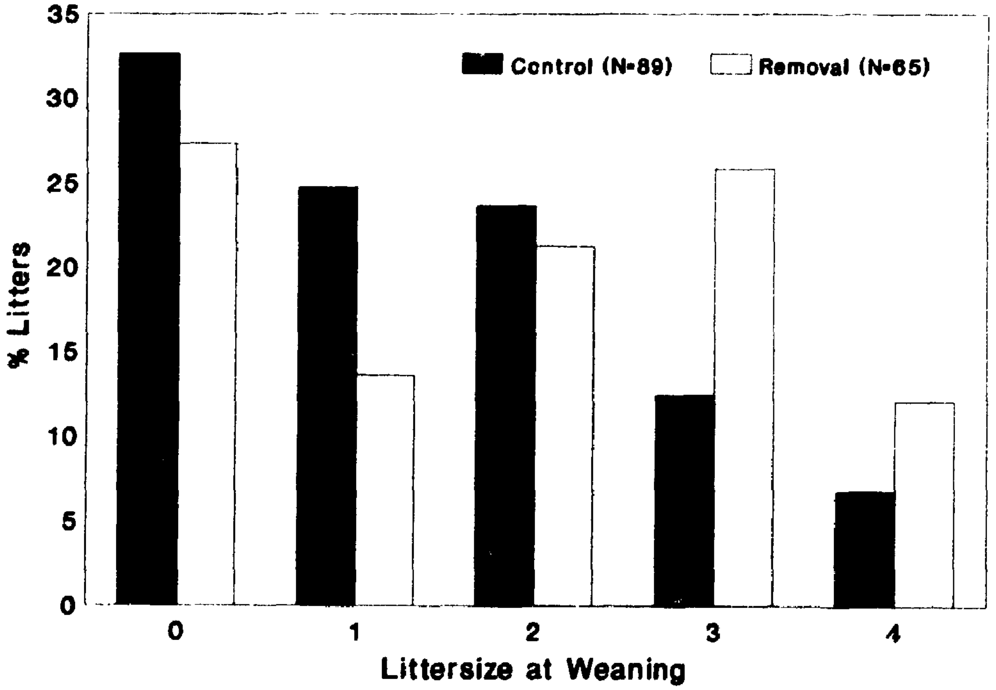
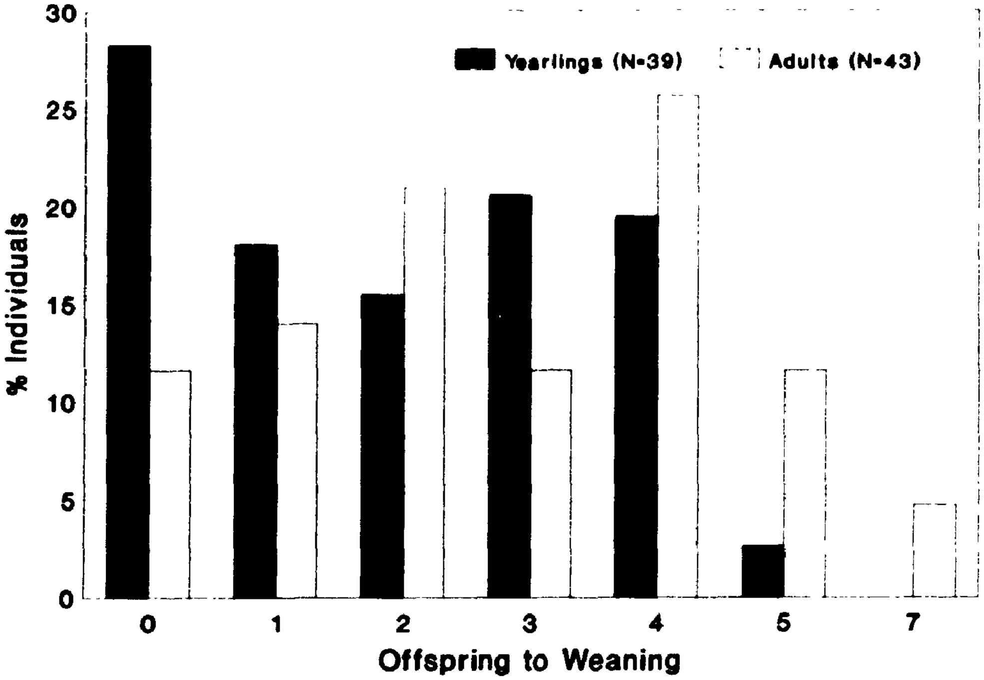


Figure 5. Distribution of number of offspring raised to weaning per season. Years (1987-89) pooled. a) Control outcrops. Distributions tended to differ between age classes ($\geq$4 offspring pooled; p=0.08), and adults raised $\geq$ 4 offspring more often (p=0.05), and $\leq$ 1 offspring less often (p=0.05), than yearlings. b) Yearling mothers only. Distributions did not differ between removal classes ($\geq$ 4 offspring pooled; p=0.40), but yearlings on removal outcrops tended (p=0.06) to raise $\leq$ 1 offspring less often than those on control outcrops.

a) Control Outcrops



b) Yearling Mothers

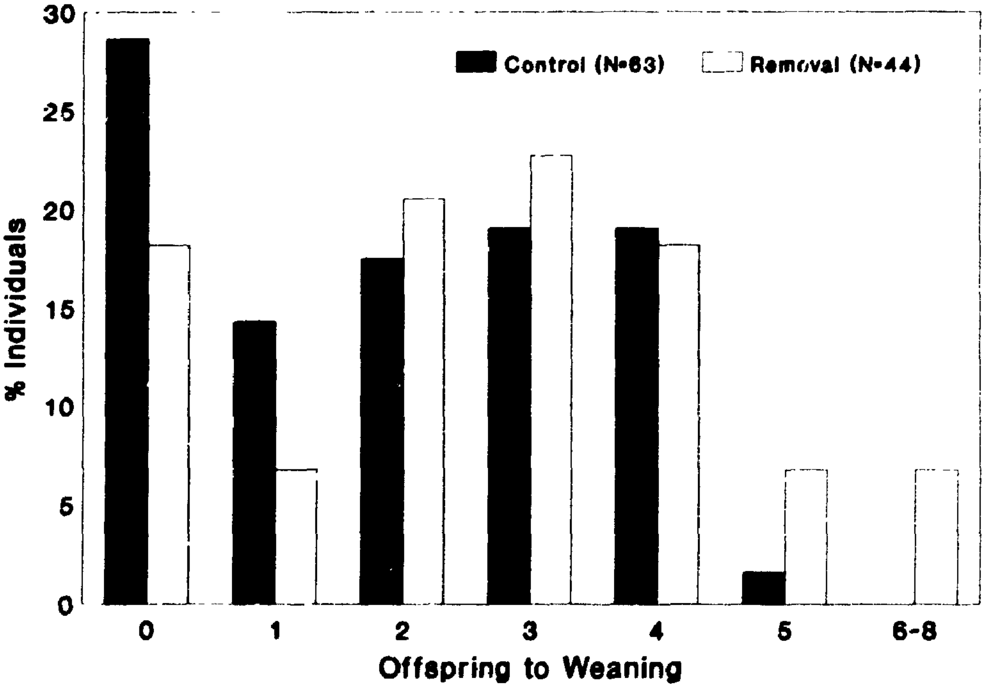
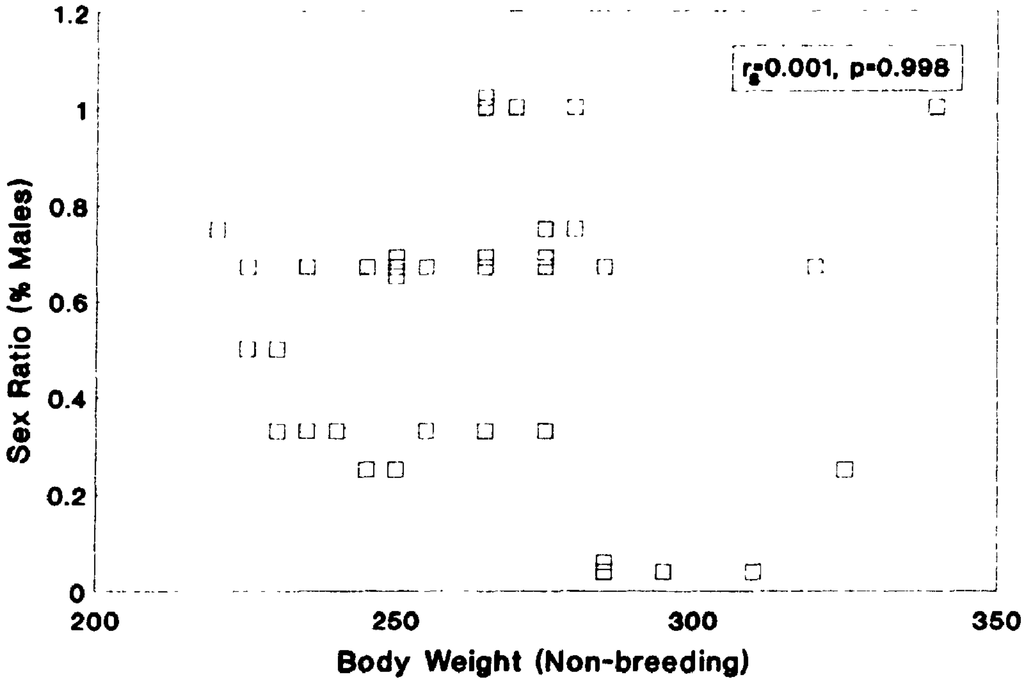


Figure 6. Association between litter sex ratios and maximum spring pre-breeding weight in a) yearling and b) adult mothers. Only litters of 3 or 4 offspring at weaning (i.e., complete litters) included. Years (1987-89 for control, 1988-89 for removal) and removal classes pooled. r_s is Spearman rank correlation coefficient.

a) Yearlings



b) Adults

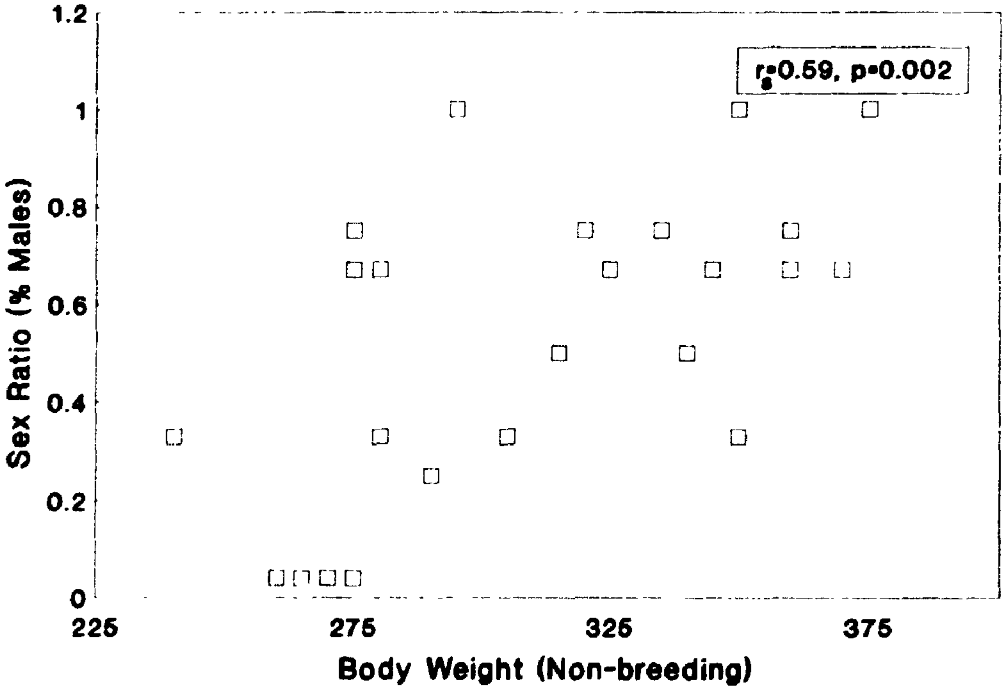
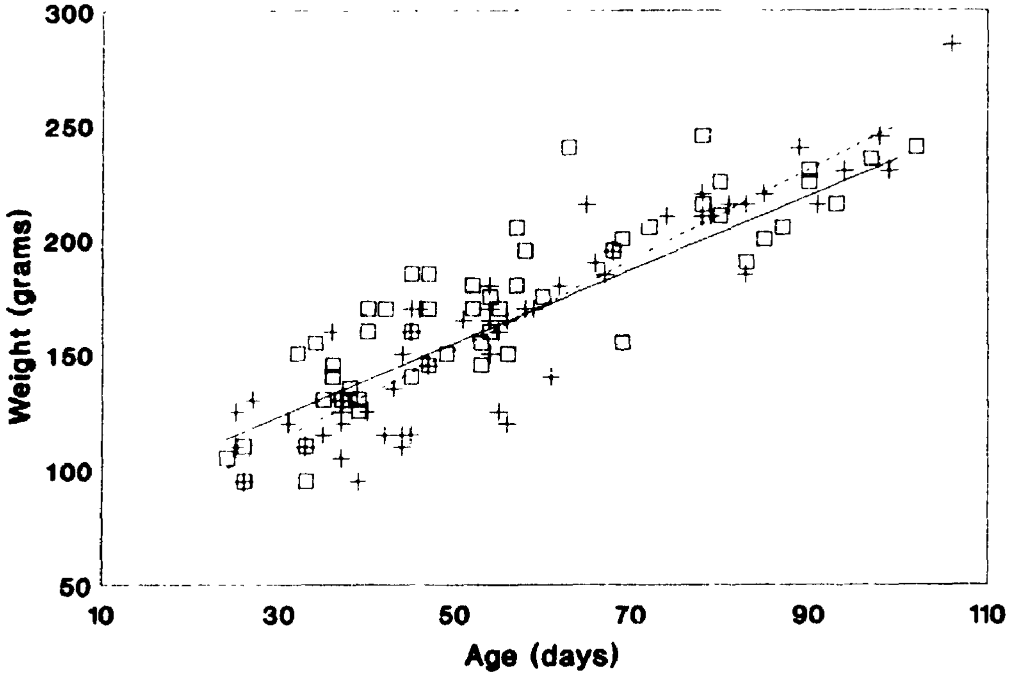


Figure 7. Post-weaning growth in juveniles born to yearling mothers, by removal class. Weight was regressed on (Age-20 days) to generate intercepts near weaning age. Lines are least-squares regression lines.

a) Juvenile females. For control outcrops (open boxes, solid line), $\text{Weight}=113+1.6(\text{Age}-20)$, $r^2=0.77$, $P=0.0001$, $N=57$. For removal outcrops (crosses, dashed line), $\text{Weight}=93+2.0(\text{Age}-20)$, $r^2=0.83$, $P=0.0001$, $N=60$. Slopes were not homogeneous ($P=0$ 02).

b) Juvenile males. For control outcrops (open boxes, solid line), $\text{Weight}=97+2.5(\text{Age}-20)$, $r^2=0.86$, $P=0.0001$, $N=54$. For removal outcrops (crosses, dashed line), $\text{Weight}=93+2.8(\text{Age}-20)$, $r^2=0.88$, $P=0.0001$, $N=57$. Slopes did not differ significantly ($P=0.13$).

a) Females



B) Males

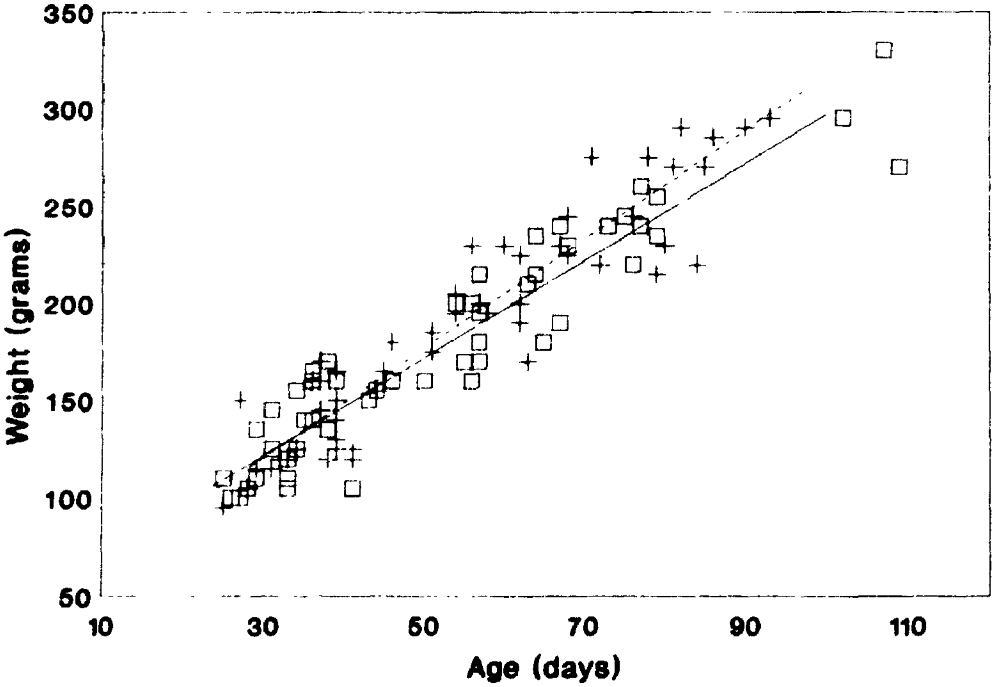
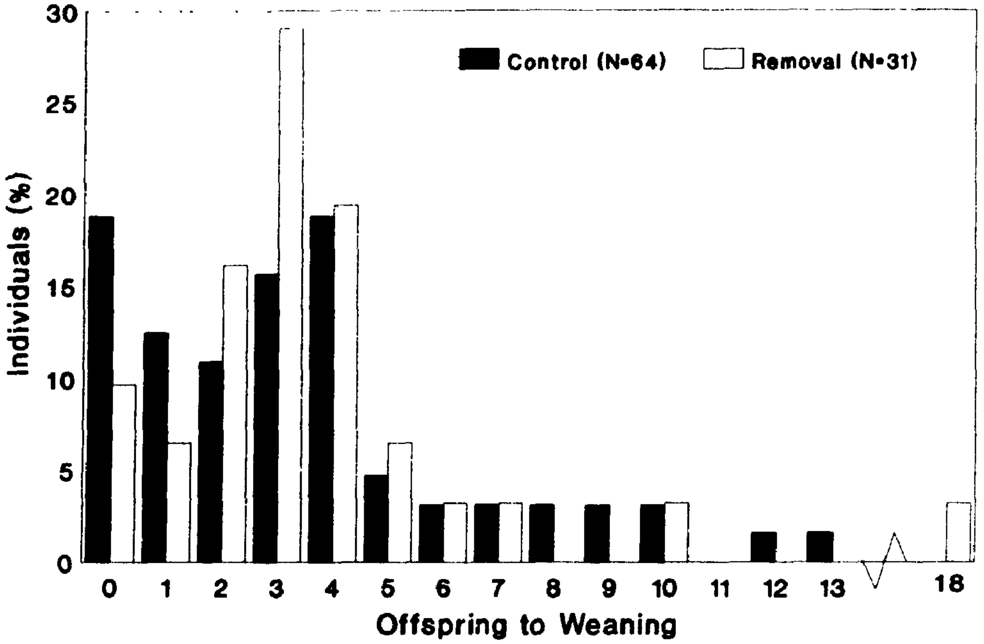


Figure 8. Frequency distributions of measures of lifetime reproductive success in females. On control outcrops, there were 33 (53%) 1-year breeders, 22 (34%) 2-year breeders, and 9 (14%) 3-year breeders. On removal outcrops, 18 (56%) bred in 1 year, 12 (39%) in 2 years, and 1 (3%) bred in 3 years.

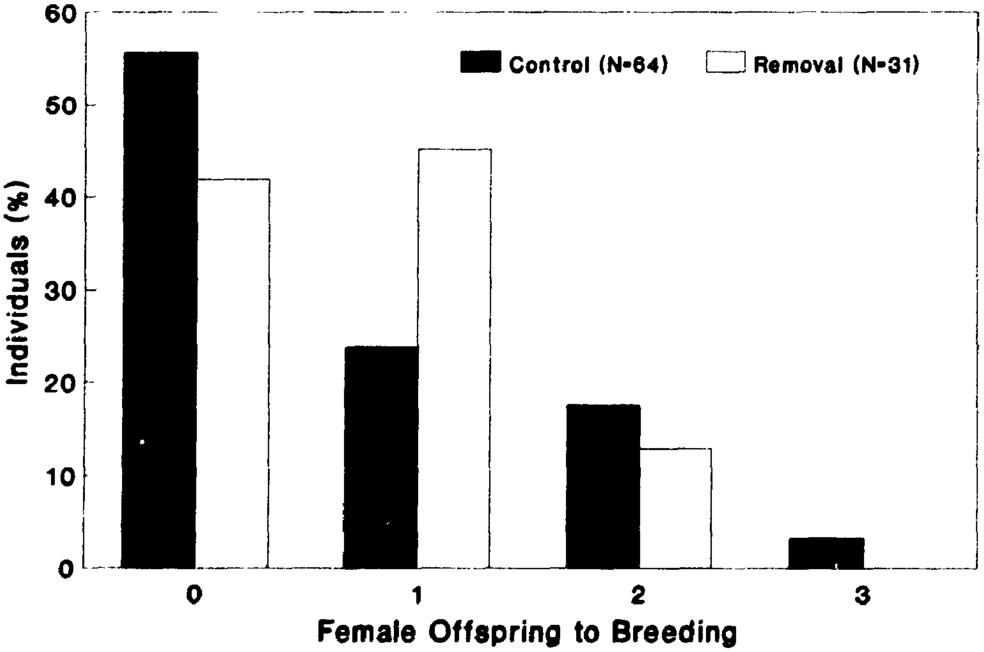
a) LRS1. Lifetime production of weaned offspring. Distributions did not differ between removal classes ($\leq$ 1, $\geq$ 5 offspring pooled; p=0.37), but females on removal outcrops tended (p=0.07) to produce 2 or 3 offspring more often than those on control outcrops.

b) LRS2. Number of female offspring that became breeding residents on natal rock outcrop. Distributions did not differ between removal classes ($\geq$ 2 pooled; p=0.11).

a)


Control (N=64)
Removal (N=31)
Individuals (%)
0
5
10
15
20
25
30
0
1
2
3
4
5
6
7
8
9
10
11
12
13
18
Offspring to Weaning

b)


Control (N=64)
Removal (N=31)
Individuals (%)
0
10
20
30
40
50
60
0
1
2
3
Female Offspring to Breeding

3.4 DISCUSSION

Individuals "strive" to contribute the most genetically to future generations relative to the contributions made by conspecifics. Female behaviour that reduces reproductive success of conspecifics may have the same net effect on individual fitness as those that enhance individual reproductive success; a female's competitive ability relative to conspecifics may be the most influential factor affecting her relative reproductive success (Begon 1983; Hrdy and Williams 1983; Clutton-Brock and Albon 1985, Clutton-Brock 1988a). Competitive relationships among conspecifics are not restricted to asocial species. On the contrary, that there is evidence of competition among conspecifics in cooperative breeding (Hannon et al. 1985) and eusocial species (Reeve and Sherman 1990; Seger 1991) suggests that opportunities for females to enhance their fitness at the expense of others may be widespread.

Results of this study indicate that competition among female bushy-tailed woodrats affects aspects of both fecundity and survival, and impacts significantly on lifetime reproductive success. On unmanipulated outcrops, most females bred for only 1 or 2 seasons, and yearlings generally exhibited lower reproductive success than did adults. The differences were not trivial. Relative to yearlings, adults initiated reproduction earlier, and raised larger litters and more offspring to weaning per season. In addition, juvenile females born to adults exhibited faster post-weaning growth, and tended to survive the winter better, than those born to yearlings. Two measures of lifetime reproductive success (lifetime production of weaned offspring, and of daughters that survived to breed on the natal outcrop) were higher in adults than in yearlings that bred in one season only. Adults appeared to adjust the primary sex ratios of their litters in relation to condition (weight), but yearlings did not. Yearlings and adults did not differ in the number of litters that they raised to weaning in a season, nor were there any detectable differences in the survival of their daughters over the summer months, or in the growth or survival of their male offspring. Annual survival of yearlings and adults was similar.

Differences in reproductive output between yearling and adult animals have been noted in many species (Reiter et al. 1981), and may reflect asymmetries in size (Gross and Sargent 1985; Howard 1988), experience (Harvey et al. 1988; Ollason and Dunnet 1988), or condition (Michener 1989), as well as competitive abilities (Slade and Balph 1974; Dublin 1983; Wasser and Barash 1983; Clutton-Brock and Albon 1985; Clutton-Brock 1988a; Dunbar 1988). The results of my removal experiment indicated that age-based asymmetries in reproductive success in bushy-tailed woodrats clearly did not reflect physiological constraints; reproductive success of yearlings breeding on outcrops on which densities of breeding females had been experimentally reduced ("removal" outcrops) generally exceeded that of yearlings on unmanipulated ("control") outcrops.

Relative to yearlings on control outcrops, those on removal outcrops raised more offspring to weaning in a season, their female offspring exhibited faster post-weaning growth, and both the yearlings themselves and their daughters tended to exhibit higher annual survival. In a cohort of yearlings that were known to have bred in one year only, those on removal outcrops produced more offspring to weaning and more daughters to breeding (i.e., in their lifetime) than did yearlings on control outcrops. Indeed, most measures of reproductive success in yearlings on removal outcrops were similar to those of adults on control outcrops, indicating that yearling bushy-tailed woodrats experience significant socially-mediated fitness costs. Further, that fewer immigrant females successfully recruited to control outcrops than to removal outcrops suggests that competitive interactions among females may completely exclude some individuals from access to critical resources. Some measures of reproductive success did not respond to the removal experiment. Yearlings on removal outcrops did not initiate reproduction earlier, or raise more litters per year than yearlings on control outcrops. Further, litter sex ratios, and growth and survival of male offspring were unaffected by reduced densities of breeding females on experimental outcrops.

I now consider a detailed examination of some of these components of reproductive success to more clearly illustrate the nature and effects of competition among female bushy-tailed woodrats on reproductive success.

Initiation of Reproduction

Mean date of first parturition varied among years, and appeared to be inversely related to winter and spring temperatures, consistent with the interpretation that initiation of reproduction in bushy-tailed woodrats is generally regulated by the availability of spring forage (Hickling 1987; Hickling et al. 1991), as it is with many seasonal breeders (Armitage 1988). However, date of first parturition also exhibits considerable variation among conspecifics within years. Hickling et al. (1991) found that initiation of reproduction in bushy-tailed woodrats varied inversely with age and weight. Because body fat varied positively with weight, (Hickling et al. 1991) suggested that woodrats in good condition are better able to withstand unpredictable nutritional environments expected to occur early in the spring, and thus initiate earlier, than those in poor condition. I found that adults initiated earlier than yearlings in 2 of 3 years, although date of parturition did not vary with pre-breeding spring weight within either age class. Adults were much heavier, on average, than yearlings; weight differences between age classes may reflect differences in mean condition. However, female bushy-tailed woodrats meet most (≈ 80%) of their energetic demands of reproduction from exogenous sources (Hickling et al. 1991), and I suggest that an equally plausible alternative explanation for the difference in initiation dates among conspecifics is that heavier, older females have access to better food resources (i.e., food caches) in the spring than others. Whether date of first parturition varies with fat levels or quality of food resources is unknown, but it is clear that it varies with availability of food resources over the autumn to spring interval; woodrats provided with supplemental food over the winter initiated reproduction earlier than did unmanipulated woodrats (Hickling 1987). However, that date of first parturition did not respond to my removal experiment suggests that socially-mediated exclusion of access to food resources among conspecifics does not influence initiation of reproduction. That is, food resources in the autumn may not be limiting per se; adults may simply be more experienced and efficient food hoarders than yearlings. However, the removal experiment may have been a weak test in this regard. If differential access to resources affects initiation of reproduction in the spring, then competition for resources during the autumn and winter is likely to be the most important determinant of initiation. Because densities of females were maintained at low levels on removal outcrops during the spring and summer only, the level of resource competition among philopatric and immigrant females over the autumn and winter may not have differed between removal and control outcrops.

Number of Litters

The number of litters that females weaned in a season also failed to respond to the removal experiment. It is equally difficult to interpret this lack of response, because the number of litters that a female weaned in a season was apparently closely tied to date of first parturition. Females that weaned 2 litters in a season initiated reproduction earlier than those that weaned only 1 (this study; Hickling 1987). Further, a greater proportion of females weaned 2 litters when they initiated reproduction early in response to food supplementation (Hickling 1987). Thus, the lack of response to the removal experiment may indicate that the factors affecting the number of litters that a female weans (i.e., affecting initiation) is not influenced by intraspecific competition, or, alternatively, that the removal experiment did not manipulate competition for food resources during the critical period (i.e., autumn-winter). In addition, the removal of early initiating females from experimental outcrops may have further reduced the ability of the experiment to detect a potential response (i.e., if females that were removed were most likely to have had 2 litters).

It is interesting to note that the proportion of females that weaned 2 litters did not differ between age classes, even though adults initiated earlier, on average, than yearlings. Similar results were presented by Hickling (1987). This appeared to be due to the fact that the length of the breeding seasons did not differ between age classes; yearlings generally started and finished later than adults. The consistency among years of the date of termination of reproduction in yearlings suggests that the ability of yearlings to prolong the period of reproductive activity is constrained. Winter and spring temperatures were generally milder than normal during this study; it is possible that a difference in the proportion of adult and yearling females weaning 2 litters would be more apparent in years when initiation of reproductive is delayed by "late springs".

Production of Weaned Offspring

Survival of juveniles from birth to weaning is a component of reproductive success that may be particularly susceptible to the effects of intrasexual competition. Mothers must balance the need to acquire energy for the heavy demands of lactation, and the need to provide thermoregulation and protection from predators and aggressive conspecifics to her dependent young. Physical harassment, or exclusion from high quality food resources, of pregnant or lactating females by conspecifics would be expected to negatively affect the number of offspring that are successfully weaned. In addition, direct killing of dependent young by conspecifics occurs in many species (Hausfater and Hrdy 1984), and may represent a significant source of juvenile mortality in some populations (Sherman 1981; Hoogland 1985; Packer et al. 1988).

Litter size at weaning exhibited considerable variation among females bushy-tailed woodrats, and part of that variation could be explained by intraspecific competition. Because most litters of *N. cinerea* conceived in the wild and born in captivity were litters of 3 (64%) or 4 (27%), I assumed that size of litters born in the wild exhibited little variability at birth, and that variation in litter size at weaning (i.e., first capture) represented differential survival from birth to weaning. Litters born to adults were larger at weaning than were those born to yearlings. Adult females were heavier, on average, than were yearlings, and litter size at weaning varied with pre-breeding weight, especially among yearling mothers. Thus, differential survival of juveniles from birth to weaning may simply reflect physiological constraints of the mother associated with body weight, rather than the effects of intraspecific competition. That per capita production of weaned offspring and pre-breeding weight of females increased on food-supplemented outcrops (Hickling 1987) is consistent with this interpretation. Similar findings have been reported for several other mammalian species that have been subjected to food supplementation experiments (see Boutin 1990). To the extent that mothers rely on endogenous reserves to sustain their offspring through lactation, a positive correlation between weight of mother and pre-weaning survival of juveniles may reflect physiological (condition) constraints on this measure of reproductive success (Myers and Master 1983; Murie and Dobson 1987). However, an alternative explanation for the relationship between weight and litter size in species that rely on exogenous reserves of energy to raise their offspring to weaning is that heavy mothers are socially dominant, and are better able to gain access to high quality resources (e.g., food, shelter) and defend their dependent young against intruders. Yearling woodrats on removal outcrops weighed the same in the spring as did yearlings on control outcrops, and yet they raised more offspring to weaning in all 3 years of this study. Therefore, the most plausible explanation for the observed variance in litter size at weaning between yearling and adult woodrats is that it reflects differential competitive abilities of females within outcrops. Whether pre-weaning loss is due to socially-induced, differential access to high quality foraging areas or food caches, infanticide, predation, or a combination of these, is unknown.

Because most bushy-tailed woodrats successfully weaned only 1 litter in a year, and less than half of all yearlings survived to breed in a second year, variation in litter size at weaning had a strong effect on both annual and lifetime production of weaned offspring. Adults on control outcrops consistently produced more offspring to weaning within a season than did yearlings. The annual production of weaned offspring by yearlings on removal outcrops similarly exceeded that of yearlings on control outcrops in all years; indeed, it appeared not to differ from that of adults on control outcrops. The patterns of variation in the lifetime production of weaned young were similar. That females breeding in one year on removal outcrops produced, on average, as many weaned offspring (in their lifetime) as those that bred on control outcrops in 2 successive seasons clearly illustrates the major effects that variation in early juvenile survival can have on reproductive success in a short-lived species with limited reproductive output. Consistent with the interpretation that variation in annual production of weaned offspring reflects competition among breeding females was 1) the observed negative correlation between mean annual per capita production of offspring and the density of breeding females on control outcrops (Hickling 1987; this study), and 2) the lack of any relationship between the two variables on removal outcrops.

Socially-induced, age-based asymmetries in the production of weaned young have been demonstrated in several species of large, diurnal mammals; post-partum mortality is often directed toward juveniles of young, subordinate mothers (Reiter et al. 1981; Silk 1983; Wasser and Barash 1983; Clutton-Brock and Albon 1985; Dunbar 1988). In some cases, post-partum mortality may be the major cause of variation in lifetime reproductive success in females (LeBouef and Reiter 1988). Quantification of individual reproductive output is generally less tractable in rodents than in large, diurnal species, and relatively little is known of the role of socially-induced mortality of juveniles and it's effect on individual reproductive output in this group. However, some evidence suggests that my findings (i.e., that adult females suppress weaning success in yearlings) may reflect a general phenomenon in rodents that requires further investigation. In an experiment that was conceptually similar to mine, Rodd and Boonstra (1988) found that yearling meadow voles (*Microtus pennsylvanicus*) raised more young from birth to weaning on an experimental grid from which adult females had been removed, than when they bred in the presence of adults on an unmanipulated grid. Similarly, weaning success in female red-backed voles (*Clethrionomys rutilus*) that were breeding in their year of birth was highest when they bred in the absence of older females on an experimental grid (Gilbert et al. 1986). Reproductive output in small mammals is typically estimated by dividing the number of juveniles appearing on a study area by the number of reproductively-active females. This technique lacks the resolution to differentiate between immigration and natality of resident females, and is unable to detect variation in reproductive output among individuals. Unfortunately, in neither of the studies above was natality of resident females unambiguously differentiated from immigration; high weaning success on experimental grids may have reflected increased immigration of young juveniles in response to lowered densities. However, studies that have employed techniques capable of quantifying individual reproductive output indicate considerable variation in weaning success among individuals, often based on age, in several species (*Microtus pennsylvanicus*: Ostfeld et al. 1988; *Peromyscus leucopus*: Goundie and Vessey 1986; *Sciurus vulgaris*: Wauters and Dhondt 1989; various ground-dwelling squirrels: Snyder and Christian 1960; Armitage and Downhower 1974; Murie et al. 1980; Sherman and Morton 1984; Dobson and Kjelgaard 1985). Further experiments designed to test the hypothesis that variation in weaning success reflects differential competitive abilities among conspecific females may be rewarding.

Sex Ratios

Litter sex ratios have been shown to vary with maternal condition, age, and/or social dominance in many species (see Clutton-Brock and Iason 1986; Armitage 1987, for reviews). The direction of the shift in sex ratio (i.e., in response to elevated condition) differs among species, and presumably reflects the sex that benefits most from an increase in maternal investment (Trivers and Willard 1973; Gomendio et al. 1990). If the large degree of sexual size dimorphism in bushy-tailed woodrats reflects a selective advantage in large males associated with procuring mates, then one would expect that an incremental increase in a male offspring's condition would fetch greater inclusive fitness benefits to a mother than would a similar increase in a daughter's condition (Trivers and Willard 1973). Consistent with the Trivers/Willard hypothesis (Trivers and Willard 1973), I found that pre-birth litter sex ratios in bushy-tailed woodrats varied with body weight. Heavy adult females on control outcrops gave birth to more males than expected by chance. In view of this, it is surprising that Hickling (1987) was unable to detect variation in overall sex ratios in female woodrats on food-supplemented outcrops, even though females were heavier on supplemented outcrops than on unmanipulated outcrops. Hickling tested for evidence of sex ratio variation by examining potential deviations from a 50:50 ratio in all juveniles produced by all females on supplemented outcrops, relative to those on unmanipulated outcrops. My analysis suggests that a stronger test more capable of detecting a potential effect would have been provided had Hickling been able to examine sex ratios of individual litters of females within outcrops. McClure (1981) found that food-restricted eastern woodrats (*Neotoma floridana*) selectively reduced their litters at the expense of their sons, in accordance with the Trivers/Willard hypothesis. Food-restricted golden hamsters (*Mesocricetus auratus*) responded similarly (Labov et al. 1986).

Few studies have investigated the effects of varying competition on sex ratio adjustment experimentally (but see Dickman 1988), although the predictions from theory are clear. If there was an increase in female condition in response to the removal experiment, the Trivers/Willard hypothesis would predict that females breeding on removal outcrops should bias their litters toward males. The local resource competition hypothesis (Clark 1978; Silk 1983), on the other hand, would predict that, if the removal of some females from outcrops lowered the level of intrasexual competition among females, and the cost of sharing a natal area with a daughter, then females on removal outcrops should preferentially invest in daughters. However, I detected no change in weight (condition) among females on removal outcrops, nor was there any evidence of facultative sex ratio adjustment by females on removal outcrops. I conclude that woodrats may adjust their pre-birth sex ratios in favour of sons, but only in response to an elevated nutritional plane. This does not imply that intrasexual competition may not affect sex ratios in bushy-tailed woodrats. Resource competition among females may cause significant variation in condition (and thus adjustment of sex ratios), but my experiment was unable to test this.

Growth

Post-weaning growth in the wild is often proximately limited by food availability; food addition studies commonly report enhanced growth of juveniles and adults (Boutin 1990). Post-weaning growth in bushy-tailed woodrats is similarly affected; juveniles of both sexes exhibited accelerated growth when provided with supplemental food (Hickling 1987). I found that daughters of adults grew faster from weaning to the autumn of birth than did daughters of yearlings, indicating that either 1) adult mothers provide their daughters access to superior food resources (and possibly deny it to daughters of yearling mothers), or 2) the daughters of adult mothers are themselves superior competitors for food resources, relative to daughters of yearlings. Daughters of yearling mothers on removal outcrops grew faster than those on control outcrops, supporting the assertion that asymmetries in post-weaning growth in juveniles on control outcrops were caused by competitive exclusion from food resources. It is interesting to note that the difference in post-weaning growth rates of female juveniles on control outcrops (1.6 g/day) and those on removal outcrops (2.0 g/day) was similar to the difference between growth rates of juveniles on control outcrops (1.7 g/day), and those on food-supplemented outcrops (2 [illegible] g/day) reported by Hickling (1987; [rates estimated for growth from day 30 to 100]). There are, presumably, fitness advantages accruing to mothers that raise fast-growing offspring; juveniles that survived the winter interval were heavier in the autumn of their birth than those that did not survive (this study; Hickling 1987).

It is interesting that growth of juvenile males was unaffected by their mother's age, or by the density of breeding females on an outcrop, and yet Hickling (1987) found that post-weaning growth in juvenile males responded strongly to food supplementation. This suggests that mothers exert little influence on the growth of juvenile males. Although little is known of the spatial or foraging dynamics of mothers and offspring in bushy-tailed woodrats, it is apparent that space use of mothers and daughters on an outcrop may overlap to a large degree (Escherich 1981; this study, Chapter 4), providing a social environment that is conducive to post-weaning investment in daughters. I was unable to quantify space use between mothers and sons because sons appeared to utilize many trap sites throughout an outcrop soon after weaning (Chapter 4). Bushy-tailed woodrats exhibit male-biased dispersal, and low survival (residency) among juvenile males during the breeding season, relative to females, suggests that some males disperse at this time. Hence, it is likely that there is little opportunity for post-weaning maternal investment in sons. However, more detailed information on space use of mothers and offspring during the breeding season is needed.

Although it is usually assumed that females (and their offspring) compete for access to food resources (Emlen and Oring 1977; Silk 1983; Clutton-Brock and Albon 1985; Ostfeld 1985; Cheney and Seyfarth 1987), few studies have tested the possibility that juvenile growth may vary with the competitive abilities of their mothers. Dittus

(1977) reported that juveniles of subordinate toque macaques (*Macaca sinica*) were literally starved to death because they were denied access to quality foraging sites by breeding females, so the relationship between growth and competitive interference at least is clear in this case. Similarly, daughters of dominant Japanese macaque (*Macaca fuscata*) mothers had access to the best food resources, and grew faster than daughters of subordinate mothers (Mori 1979). Some studies have tested for competitive effects on post-weaning growth in small mammals by investigating the relationship between post-weaning growth and group density, but results are generally inconclusive. Cowan and Garson (1985) found that post-weaning growth in juvenile rabbits (*Oryctolagus cuniculus*) was inversely related to group density, and similar results were reported for snowshoe hares (*Lepus americanus*; Keith and Windberg 1978). Boonstra (1978) reported that growth of juvenile male *Microtus townsendii* varied inversely with density of adult males, but other studies have found no density effects on juvenile growth (Redfield et al. 1978; Porter and Deuser 1986; Rodd and Boonstra 1988). In species in which there may be an opportunity for mother-offspring interactions to affect post-weaning growth, it is possible that an investigation of a density effect *per se* is too course-grained an approach to detect variance in post-weaning growth among conspecifics.

Survival

Woodrats would be expected to "accept" fecundity and growth costs associated with sharing an outcrop with others if 1) there are survival benefits of grouping that outweigh the costs (survival would be higher in the presence of conspecifics than in their absence), or 2) there are no survival benefits of grouping, but opportunities for breeding solitarily are limited (survival would be enhanced in the absence of conspecifics). The results of my removal experiment are most consistent with the second alternative. That I detected no decreases in survival of juveniles, yearlings, or adult bushy-tailed woodrats when group sizes of breeding females on outcrops were experimentally reduced indicates that the presence of several females on an outcrop does not confer net survival benefits to individuals residing on outcrops. Rather, juvenile and yearling females tended to experience greater annual survival on removal outcrops than on control outcrops, suggesting that females compete for limited resources necessary for extended residency on rock outcrops. The movement of all known dispersing females from control outcrops to removal outcrops, and the increase in the number of female immigrants that established residency on removal outcrops, relative to control outcrops, provides additional evidence that some females exclude others from access to limited resources necessary for overwinter survival on outcrops.

Although the differences in the proportions of juvenile females surviving on control and removal outcrops were generally not statistically significant, they were consistent during both the summer and winter intervals in all 3 years of the study, and they impacted significantly on reproductive success of yearlings. Yearlings on removal outcrops were more successful in producing at least one daughter that survived to become a breeding resident on their natal outcrop than were those on control outcrops. In fact, the lifetime production of philopatric daughters by 1-year breeders on removal outcrops did not differ from that of 2-year breeders on control outcrops. The enhanced annual survival of yearlings on removal outcrops suggests even greater fitness costs to yearlings breeding on control outcrops; both my measures of lifetime reproductive success were positively correlated with annual survival among females on control outcrops. Lastly, because densities of females were reduced on experimental outcrops during spring and summer only, the survival effects detected by the experiment may be a minimum estimate of overwinter survival costs of intraspecific competition in bushy-tailed woodrats.

The reliance of female bushy-tailed woodrats on the use of highly clumped rock outcrops, and on a limited number of established, traditional den (shelter and food cache storage) sites within outcrops is expected to favour philopatry over dispersal, and yet create a potentially competitive environment within outcrops (Waser and Jones 1983; Waser 1988; Emlen 1991). The cracks, crevices, and caves in rock outcrops that serve as den sites for *N. cinerea* are permanent structures that are used over many generations. Hence, woodrats cannot enhance the availability of den sites, and competition for access to this limited resource should be strong. Several lines of evidence suggest that the availability of den sites limits the number of females that are able to breed on an outcrop. First, the number of females breeding on any given outcrop is generally stable among years (Hickling 1987; this study), suggesting that some unchanging ecological factor(s) may be setting an upper limit on the density of breeding females. Second, Hickling (1987) found that breeding densities were not food limited; enhanced reproductive output of woodrats on food-supplemented outcrops resulted in elevated summer densities, but neither immigration nor overwinter survival were affected by food supplementation, and spring to spring densities remained unchanged. Lastly, that more immigrant females became breeding residents on my removal outcrops than on my control outcrops indicates the presence of "surplus" females, and suggests that stable densities are not due to a lack of potential recruits. Hence, the evidence strongly suggests that den sites are a limiting resource for female bushy-tailed woodrats, and I suggest that overwinter survival of juveniles and yearlings was enhanced on my removal outcrops due to an increased availability of den sites. Various *Neotoma* species exhibit high levels of aggression toward conspecifics in laboratory and enclosure settings (Egoscue 1962; Cameron 1971; Boggs 1974; Escherich 1981; Wallen 1982), and I found that wild female *N. cinerea* were highly agonistic in the autumn and spring when paired with non-kin in a neutral arena (Chapter 4). Thus, spacing behaviour maintained by overt aggression is a possible proximate mechanism affecting immigration and residency (i.e., den site ownership) on rock outcrops. Those juveniles and yearlings that survived overwinter on control outcrops were heavier in the autumn than those that did not survive, as was also noted by Hickling (1987). A similar relationship between weight and overwinter survival exists in some hibernating species (Murie and Boag 1984; Sauer and Slade 1987), where weight presumably reflects endogenous reserves critical for hibernation (Murie and Boag 1984). Bushy-tailed woodrats do not hibernate, however, and heavy individuals may survive better because they are superior competitors for critical resources. It is interesting to note that the weight effect was not apparent among juvenile females on removal outcrops; perhaps light individuals were not disadvantaged, relative to heavy ones, when competition for resources was relatively low.

Females of most *Neotoma* species utilize some type of elaborate den or house (Finley 1958; Newton 1990), and experimental evidence suggests that competition for access to these sites may be a general feature of *Neotoma* ecology. Removal experiments have shown that adult females exclude competitors from access to den sites in several *Neotoma* species (Dial 1988; Newton 1990), and the addition of artificial sites increased breeding densities in *N. albigula*, clearly illustrating the limiting nature of the resource (Newton 1990). Similarly, banner-tailed kangaroo rats (*Dipodomys spectabilis*) and pikas (*Ochotona princeps*) utilize patchily distributed den and food cache sites. The availability of sites regulates overwinter survival of philopatric juveniles in both of these species, and appears to limit (maximum) densities of breeding animals (Smith and Ivins 1983; Jones 1986; Smith 1988; Waser 1988). Experimental removal studies conducted on various other small mammal species (see Introduction for references) have demonstrated the general pervasiveness of intrasexual competition in females [illegible] its effect on survival; survival of juveniles (and often adults) is generally enhanced on removal areas, relative to unmanipulated areas. However, virtually none of these studies has quantified reproductive success among individual conspecifics. The question of how the social environment affects individual fitness in small mammals will remain unanswered until reproductive output of individuals is more carefully monitored.

General Discussion

One of the strengths of my study was its emphasis on quantifying reproductive output among individuals over a significant proportion of their lifetime. It allowed me to demonstrate that relatively small effects of intrasexual competition on (primarily) litter size at weaning and juvenile and yearling annual survival, caused significant fitness costs, particularly to yearlings. One should expect a similar impact of small, socially-induced decreases (or increases) in fecundity and/or survival on lifetime reproductive success in other species that also exhibit low reproductive output and a short lifespan. This may apply to many *Neotoma* species (Finley 1958; Goertz 1970; Vaughan and Czaplewski 1985), if not small mammals in general, particularly those existing close to carrying capacity. Haigh (1987) presents an interesting hypothesis that states that, in species in which reproductive output is constrained at a low level (i.e, when females are physiologically unable to increase their own reproduction), selection should favour behaviour in females that reduces the reproductive output of their conspecific competitors. Haigh (1987) presented this hypothesis as a general explanation for the evolution of reproductive inhibition in *Peromyscus*, but it could be applied equally well to any behavioural interactions that act to suppress reproductive output of conspecifics, such as those that I have inferred occur in *N. cinerea*. I suggest that competitive interference will be most strongly favoured in species that exhibit low lifetime reproductive output, due to the added impact that small decreases in reproductive output have on lifetime reproductive success in these species.

Despite substantial fitness costs associated with sharing an outcrop with conspecifics, female bushy-tailed woodrats are strongly philopatric (over 70% of all females breeding on control outcrops bred on the outcrop that they were born on), suggesting that opportunities for dispersal and successful establishment on non-natal outcrops are rare, and even more costly, than philopatry. The intensity of competition for den sites (or other critical resources) experienced by philopatric females is generally a function of the number of den sites available per competitor. The availability of sites in turn depends on several factors, such as population turnover rates, reproductive output of conspecifics, and the prevalence of other limiting density-independent factors (Waser and Jones 1983). My data suggest that, on average, the net effect of these factors is such that there are fewer available sites than there are competitors; bushy-tailed woodrats compete for access to them. However, philopatry need not necessarily lead to a strictly competitive sociality. Indeed, philopatry is considered a necessary (although not sufficient) condition for the evolution of cooperative breeding (Smith 1990; Emlen 1991) and cooperative socialities in general (Waser and Jones 1983; Waser 1988). The potential for the evolution of cooperative interactions should depend in part on the extent to which philopatry leads to spatial aggregations of close kin (i.e., mother-offspring), and the relative costs and benefits accruing to mothers willing to share resources (e.g., den sites) on the natal range with their philopatric offspring (Hamilton 1964; Waser 1988; Anderson 1989). I did not control for the effects of kinship in the analyses presented here. Hence, they remain as a potential confounding variable. I consider the effects of kinship on survival and reproductive output in Chapter 4. However, it is clear that among all females on an outcrop, there were strong effects of competition on reproductive success.

That 1) I was unable to detect any decreases in measures of reproductive success in yearlings on removal outcrops, relative to those on control outcrops, and 2) annual per capita reproductive output varied inversely with density of females on control outcrops, suggests that interactions among conspecific females on an outcrop do not provide net fitness benefits, and is consistent with the interpretation that the association of several females on rock outcrops represents a response to an ecological constraint (i.e., clumped distribution of limited, critical resources) that forces, rather than permits, females to aggregate and interact (Alexander 1974; Vehrencamp 1979; Emlen 1991).

On this general level, the socioecology of bushy-tailed woodrats appears to be similar to that of yellow-bellied marmots (Armitage 1981; 1984; 1988), and perhaps black-tailed prairie dogs (*Cynomys ludovicianus*; Hoogland 1981a). Both species have been referred to as cooperative breeders (Hoogland 1981a; Armitage 1988), but only in the sense that non-reproductive yearlings assist in the detection of predators. Marmots are more obviously restricted to clumped, limited resources (den sites and hibernacula on rock outcrops) than are prairie dogs, although burrow sites are likely to be limiting for prairie dogs at times (Stockrahm and Seabloom 1988). Although amicable relationships between group members have been documented in both species (Hoogland 1981a; Armitage and Johns 1982), fitness benefits of grouping has not been convincingly demonstrated for either marmots or prairie dogs. In fact, yearlings of both species may not reproduce at all, and infanticide is a major source of infant mortality in prairie dogs (Hoogland 1985). Further, per capita reproductive output is maximized in small groups of prairie dogs (Hoogland 1981a), and in solitary females in marmots (Armitage 1988). Female sociality would appear largely competitive in both of these sciurid rodents, and a reasonable hypothesis would seem to be that yearlings experience fitness costs associated with intraspecific competition, which they are presumably unable to avoid, due to limited availability of critical resources. However, manipulative removal experiments have not been conducted in either of these species; the alternative that females living in large groups are phenotypically "inferior", and incapable of enhanced reproductive success, relative to those in small groups, cannot be discounted.

CHAPTER 4

MOTHER-OFFSPRING ASSOCIATIONS:
SPACE USE, BEHAVIOUR, AND REPRODUCTIVE SUCCESS

4.1 INTRODUCTION

Philopatry, or the tendency for young to remain in their natal area, may lead to the spatial association of close kin (i.e., mother and offspring), which in turn increases the potential for the evolution of cohesive social interactions (Hamilton 1964). Certainly, most mammalian social groups are composed of closely related, philopatric individuals (Vehrencamp 1979; Michener 1983; Wrangham and Rubenstein 1986; Waser 1988), but philopatry is not a *sufficient* cause for the development of a cohesive sociality. Many mammals are philopatric, but sociality in philopatric mammals varies from solitary to highly gregarious (Waser and Jones 1983). The realization of the potential for cohesive relationships created by philopatry depends, in part, on the costs and benefits accruing to mothers willing to share resources on the natal range with their philopatric offspring (Waser 1988; Anderson 1989).

Generally, if access to critical resources outside the natal area is limited for emigrating offspring, then mothers should tolerate or encourage philopatry of her offspring, to the extent that it does not lower her residual reproductive value (Waser 1988; Anderson 1989). However, females compete for resources necessary for raising offspring, and competition among philopatric females may be particularly intense when they are reproductively active. Because mothers are not expected to engage in behaviour that enhances the production of grandoffspring at the expense of the production of her own offspring (Hamilton 1964; Trivers 1974; Rubenstein and Wrangham 1980), intense competition between reproductively active mothers and daughters may not favour the maintenance of cohesive relationships. An inverse relationship between intragroup resource competition and group cohesion among breeding females has been noted in many social vertebrates, including cooperative breeding birds (Curry and Grant 1990), many primates (Clutton-Brock and Albon 1985), red deer (Clutton-Brock et al. 1982), and large diurnal rodents (Festa-Bianchet and King 1984; Armitage 1986; Hoogland 1986; Barash 1989). Hence, philopatric species may or may not exhibit a cohesive sociality, and, in those that do, cohesive relationships may not necessarily be stable.

I have shown in Chapter 3 that, in spite of effects of intrasexual competition on measures of fitness, female (and to some extent male) bushy-tailed woodrats exhibit philopatry (defined as residing or breeding on the rock outcrop on which one was born). In addition, because virtually all individuals breed in the first year after birth, and some females breed for 2 or 3 successive years, philopatry should often lead to mothers and daughters (and to a lesser extent, sons) breeding simultaneously on the same outcrop. The purpose of this chapter is to address the following question: Do stable, cohesive relationships exist between mothers and philopatric offspring, and, if so, is there evidence that the relationships confer fitness benefits tnat outweigh the costs the intrasexual competition? I have attempted to do this in 3 ways.

First, I describe the use of space within outcrops by breeding females in general. Then, for cases where adult mothers bred simultaneously with a yearling daughter, I quantified distances maintained between mothers and daughters during the breeding season. Because I was unable to meaningfully quantify distances maintained between non-kin, I did not test whether close kin maintain different spatial relationships than non-kin. Rather, I simply attempted to determine whether adult mothers and yearling daughters are spatially associated when they are reproductively active.

Secondly, to test whether mother-offspring relationships were more cohesive than those of adult females and non-kin, I quantified behavioural interactions in mother/offspring and adult female/non-kin dyads in a neutral arena during 1) the autumn when offspring were immature, and 2) the following breeding season when all dyad members were reproductively active. If woodrat sociality is shaped primarily by the effects of competition for limited resources, behavioural interactions among associated conspecifics would be expected to be typified by agonism, regardless of kinship of dyad members. Further, agonism among females would be especially prevalent during the breeding season. However, if mother-offspring associations are able to buffer the costs of resource competition (i.e., via inclusive fitness benefits), then kin-based behavioural asymmetries, with non-kin interacting agonistically and kin interacting amicably, should be evident.

Finally, I tested for evidence of fitness benefits of mother-daughter associations by comparing measures of reproductive success (reproductive output, growth, and survival) between philopatric daughters that shared an outcrop with their mother, and yearlings that resided on an outcrop without their mother. If behavioural interactions observed in a neutral arena reflect adaptive social relationships, then any observed patterns of variation in behavioural interactions should reflect similar patterns of variation in fitness.

4.2 METHODS

4.2.1 SPATIAL DISPERSION OF BREEDING FEMALES

The configuration of trap sites on many outcrops was 3 dimensional, and an estimate of space use based on capture locations on these outcrops was not feasible. However, 4 outcrops (2 control, 2 removal) could be conceptualized as linear habitat patches with trap sites arranged along the outcrop on one plane. I mapped the location of trap sites on these outcrops using a transfer stereoscope on aerial photographs (series 82-176c, line 2659-2660, Alberta Ministry of Energy and Natural Resources) that were enlarged to 1:2000 from 1:20,000 scale. Hickling (1987) determined that this technique was accurate to ± 2m for distances ≤ 100m, and ± 5m for distances over 100m. I considered the first trap site on each outcrop to be at 0m. I measured distances between successive trap sites on the outcrop maps to the nearest mm, and converted them to metres from the zero position. I then plotted frequencies of all captures (recorded April-September, 1988 and 1989) of each resident female against the location of the captures to describe space use among females on each of the 4 outcrops. In addition, I considered 2 standard deviations from an individual's mean capture location to be a crude quantification of home range for that individual. I calculated home ranges for all woodrats that were resident on the 4 outcrops in 1988 and/or 1989. For individuals that were residents on an outcrop in both years, I used the mean of the yearly estimates.

In order to quantify the use of space by a yearling in the breeding season, relative to that of her mother, I estimated minimum straight line distances (from aerial photos, as above) between "most utilized trap sites" (defined as the trap site at which ≥ 50% of all captures of an individual within a year occurred) of all philopatric yearlings and their mothers. If a mother survived to breed as an adult, I used capture locations in the breeding season that mother and daughter bred simultaneously (i.e., in the year that the mother bred as an adult) to estimate most utilized trap sites. If a mother did not survive the winter to become an breeding adult, I used capture locations during the year that both females bred as yearlings (i.e., year X for mother, year X+1 for daughter) to estimate most utilized trap sites. If a mother had more than 1 daughter that survived to breed on her natal outcrop, I only included data from the daughter that settled closest to her mother. Individuals that were captured in less than 3 trap sessions (i.e., non-residents) were not included in this analysis, nor were data from outcrops ≤ 50 m in length. For individuals that were permanently removed from experimental outcrops (see Chapter 2), I used capture locations for that individual and her mother/daughter up to and including the date of removal. Some juvenile males born on the study outcrops became philopatric residents as yearlings. However, few were captured at any one site often enough to calculate a most utilized trap site. Hence, males were not considered in this analysis.

4.2.2 BEHAVIOURAL TRIALS

Woodrats were temporarily taken from outcrops for use in dyadic behavioural trials over two sampling periods. From 25 August to 11 September 1988, post-breeding adult females and juveniles of both sexes were removed from 14 different outcrops (7 control, 7 removal). Kin dyads were composed of an adult female and her juvenile daughter or son. Non-kin dyads included an adult female and an unrelated juvenile female or male.

The second sampling period, from 4 May to 26 May 1989, occurred during the early part of the breeding season. Individuals were sampled from 16 different outcrops

(8 control, 8 removal) during this period. Kin dyads consisted of an adult female and her yearling daughter or son. Non-kin dyads consisted of an adult female and an unrelated female or male yearling. Twelve of 13 adult females, and 13 of 16 yearling females were in early or mid-pregnancy during the trials. The remaining 4 females were not pregnant. All 10 males had scrotal testes when the behavioural trials were conducted. In all cases (for both sampling periods), members of kin dyads were from the same outcrop, whereas members of non-kin dyads were not necessarily from the same outcrop.

Maternal descent of members of non-kin dyads was ultimately traced to two females inhabiting different outcrops and of unknown relatedness (e.g., woodrats born in 1986 or earlier). In the unlikely event that these individuals were either littermate sisters with the same father, or mother and daughter, coefficients of relatedness for members of non-kin dyads would be 1/4 for three cases and 1/8 to 1/16 for 29 cases. However, because females inhabiting different outcrops are not expected to be closely related, true coefficients of relatedness for members of non-kin dyads were likely much lower than these estimates.

Animals used in the trials were removed from the site of capture in a covered live trap, and transported to a holding facility at the Kananaskis Centre for Environmental Research within 2 hr. Animals were transferred to a covered holding cage (40 x 70 x 20 cm) and maintained on ad libitum laboratory rat chow, fresh herbaceous plants, and water, under ambient temperature and light regimes. Olfactory contact was reduced among subjects until the beginning of a trial by maintaining at least 3 m between holding cages.

Trials were conducted for both sampling periods between 2300 and 0430 hours, during the second or third night after the morning of capture, in a neutral arena (110 x

60 x 50 cm) in a windowless room adjoining the holding facility. The arena was constructed of darkly painted wood with a wire mesh (2 cm) front, and was separated into two compartments by a sliding partition. The arena was wiped clean (with dilute acetic acid) and dried between trials.

Each member of a dyad was removed from its holding cage, weighed, had a small portion of its tail dipped in a non-toxic coloured powder to ensure proper identification of individuals, and then placed in one half of the arena for a 10 min pre-trial acclimation period. I then withdrew the partition from behind a black curtain 2.5 m from the front of the arena. Lighting was provided by one 25 Watt red bulb suspended above the arena.

Each adult female was paired with a kin and a non-kin (i.e., with a juvenile in the non-breeding period, and a yearling in the breeding period) that were of the same sex and the same approximate body weight. These two dyads (with a common adult female) were observed in succession. The order in which the pairs of dyads were observed was randomly assigned by an assistant; I was, as the observer, "blind" to relatedness during all trials.

Frequencies of all identifiable interactions were recorded for 15 min on a tape recorder. Most interactions were of short (< 15 sec) duration. In order to prevent potential under-representation of interactions that occurred continuously for over 30 sec, they were scored once every 30 sec. Because no published ethograms are available for this species, I became acquainted with the behavioural repertoire of *N. cinerea* by observing 15 dyads of unknown kinship under similar conditions in May 1988. All interactions that were recorded during the trials are described in Appendix 2. Each animal was returned to its holding cage upon completion of the trial, and to its location of capture at first light the next morning.

To avoid subjective, *a priori* categorization of individual interactions, frequencies of interactions from all trials ($N=64$) were subjected to a factor analysis (SAS; PROC FACTOR). Factors were extracted by a principal component analysis of the correlation matrix, and the first five factors, each of which had an eigenvalue > 1.0, and explained $\geq 10\%$ of the total variation in the data, were rotated by the Varimax method. Varimax rotation maintained independence of factors, and created readily interpretable factors, with most interactions loading high on one factor only.

Multivariate analyses on small matrices, or those with a small ratio of sample size to number of variables, may generate unstable coefficients of limited value (Gibson et al. 1984; Williams and Titus 1988). I tested the stability of factor loadings with a modified jackknife technique. I randomly sampled approximately 75% of the data set 25 times, and did a factor analysis on each new data set to generate a mean and standard error for each loading.

Because each adult female was used in two successive trials within a season, events occurring in these two trials were not independent. Hence, I used the *difference* between factor scores (for each factor) generated by the paired trials as a response variable to test for effects of season (post-breeding, breeding) and sex of juvenile/yearling in a 2-way ANOVA. Further, the effect of kinship on variation in factor scores was assessed for each factor with a paired comparisons ANOVA, blocking by adult female. Mean frequencies of individual interactions were compared between treatments with 2-tailed *t*-tests, or Mann-Whitney *U*-tests if variances were unequal. Restrictive sample sizes required the use of the same adults between seasons in 9 cases. I was unable to control for this lack of independence statistically, and assume that the effects that trial events in August/September 1988 may have had upon those occurring eight months later would have been minimal.

4.2.3 MOTHER-OFFSPRING ASSOCIATIONS AND REPRODUCTIVE SUCCESS

I defined philopatric yearling females that shared an outcrop with their adult mother as "matrilineal", and those whose adult mothers were not present on their natal outcrop as "non-matrilineal". I compared measures of 1) survival, 2) growth, and 3) reproductive output, between matrilineal and non-matrilineal yearlings. General methodology followed that described in Chapter 3, sections 3.2.1-3.2.4.

I tested for the possibility that the presence of a juvenile's mother on the natal outcrop over the winter interval may have affected that juvenile's chance of surviving the interval to become a breeding resident as a yearling. I compared relative frequencies of survivors between juveniles of mothers that overwintered on their natal outcrop and juveniles of mothers that did not survive the winter interval, using log-linear analysis. All juveniles that were born in 1987-1989 were included in this analysis.

I tested the hypothesis that yearlings that were associated with their mothers exhibited faster growth than those that were not, by comparing proportional weight gains from 1) the autumn in the year of birth to the following spring (winter interval), and 2) the spring prior to the first breeding season (the end of the winter interval) to the following autumn (breeding interval). Only non-reproductive weights were used for females. Most males had scrotal testes when first captured in the spring; I used weight at first capture of the year to mark the end of the winter interval, and the start of the 2nd interval, in yearling males. All juveniles that were born in 1987, 1988, or 1989, and bred as philopatric yearlings in 1988, 1989, or 1990, respectively, (and for which appropriate weight data were available), were included in this analysis. Proportional weight gains over the winter interval in females were adjusted to the 1988-89 mean to control for year differences (see Chapter 3, section 3.2.3).

The measures of reproductive output that I considered were mean number of offspring raised to weaning age, the proportion of individuals that had 2 (vs 1) successful litters, and the proportion of reproductive attempts that failed (i.e., advanced pregnancies that produced no weaned offspring). Because only 2 yearlings bred simultaneously with their mothers on removal outcrops (i.e., several mothers were permanently removed from the outcrops), this analysis included data from yearlings on control outcrops only. All females that were born in 1987 or 1988 on control outcrops (and bred as philopatric yearlings in 1988 and 1989) were included.

4.3 RESULTS

4.3.1 SPATIAL DISPERSION OF BREEDING FEMALES

Two trends are readily apparent in the descriptive analysis of capture locations among breeding females on 4 outcrops: 1) females were captured at few trap sites, relative to the number available on the outcrop, and 2) some females showed a high degree of overlap in capture locations (Figure 9, 10). Data from one breeding season only is presented in Figures 9 and 10 for illustrative purposes, but patterns of space use on these outcrops appeared similar in 1988 and 1989. During these 2 years, mean home ranges (2 standard deviations from mean capture location) of resident females encompassed a small proportion of the total outcrop length on the 4 outcrops (Barrier: 40 m [12% of total length]; Kel's: 54 m [16%]; Marmot: 25 m [9%]; Raven: 38 m [14%]; Table s1). Resident males were generally caught over a much greater range of trap sites than were females. On 3 of the 4 outcrops, capture locations of resident males spanned, on average, at least twice as much of the outcrop as did capture locations of females (Table 21).

Some females exhibited extreme overlap in capture locations, especially on control outcrops. Some cases of overlapping females occurred between adult mothers and yearling daughters (Figures 9, 10). This apparent tendency for mothers and daughters to breed in proximity was clearly reflected in the analysis of distances between "most utilized trap sites" among mothers and daughters on all outcrops. There were 40 cases of adult mothers breeding on the same outcrop in the same year with at least 1 daughter. I could calculate a most utilized trap site for 29 of these. The mean distance between mother-daughter dyads on control outcrops was only 15.1 m (SD=19.02, N=18), and 15.4 m (SD=25.91, N=11) on removal outcrops. Further, mothers and daughters shared the same trap site in 48% (14) of these cases.

The tendency for yearlings to use the same part of an outcrop as their mother was also apparent in those cases where the mother did not survive to become an adult. The trap site most utilized by these philopatric yearlings was, on average, 11.4 m (SD=22.50, *N*=13 [9 control, 4 removal]) from the trap site that their mother had most used in the previous year. The most utilized trap site was identical between mother and daughter in 77% (10) of these cases.

4.3.2 BEHAVIOURAL TRIALS

The first five factors extracted by factor analysis explained 71.5% of the total variation in the behaviour frequency data. I examined the variables with the highest positive structural coefficients on each factor (Table 22), and interpreted Factor 1 as being typified by amicable behaviour, Factors 3 and 5 by agonistic behaviour, and Factor 2 by investigative behaviour. Factor 4 was difficult to interpret after the original factor analysis, but jackknifing indicated that it was dominated by variation in 'box' and 'stand'; thus I interpreted Factor 4 as an additional agonistic factor. Jackknifing further indicated that my interpretation of Factors 1, 2, 3, and 5 from my original analysis was sound (Table 22). Although most mean factor loadings generated by jackknifing were lower than those from the original analysis, their relative values within each factor generally coincided with the original loadings. The highest mean loading for any variable not included in Table 22 was 0.12; the average was -0.06 (SE=0.02).

If woodrats were able to recognize kin in a neutral arena, and if behavioural asymmetries consistent with a kin-based cohesive sociality occurred among woodrats, then I would predict that kin dyads would have higher scores on Factor 1, and/or lower scores on Factors 3, 4, and 5, than would non-kin dyads. Analysis of variance largely supported this prediction. The interaction of sex and season failed to explain a significant amount of variation in (the differences of kin and non-kin) scores on any factor ($P \geq 0.29$), as did sex and season in the resultant main effects model (Table 23). Hence, I pooled seasons and sexes, and tested for kinship effects directly in a paired comparisons ANOVA. There was more variation in factor scores between kin and non-kin dyads than within either group for Factors 1, 3, and 5 (Table 24), where kin scored highest on Factor 1 (mean scores: kin = 0.31, non-kin = -0.31,), and lowest on Factors 3 (kin = -0.38, non-kin = 0.38) and 5 (kin = -0.32, non-kin = 0.32).

To facilitate a more descriptive analysis of individual interactions, I compared mean frequencies of each amicable and agonistic interaction within treatments. I first compared mean frequencies between sexes. Although mean frequencies of all amicable interactions within seasons were greater among female-female kin dyads than among female-male dyads, the differences were not significant; there were no differences ($p \geq 0.1$) in mean frequencies between males and females for any combination of kinship and season for 15 of the 16 designated interactions. 'Nose-nose' occurred more often ($p = 0.01$) in non-kin dyads with male juveniles (i.e., post-breeding period) than in those with female juveniles. However, 'nose-nose' was a relatively unimportant interaction among non-kin (comprising, on average, 3.6% ± 0.01 of designated interactions); hence I pooled sexes to examine differences in interactions between seasons within kinship.

Behavioural interactions within both kin and non-kin dyads varied little between the post-breeding and breeding seasons. Although most amicable and agonistic interactions occurred less often among kin in the breeding season than in the post-breeding season (Table 25), the differences were not significant ($p \geq 0.2$). Among non-kin, 'stand' tended ($p = 0.08$) to occur more often in the post-breeding season, and 'fight' occurred most often ($p = 0.02$) in the breeding season. No other agonistic interaction varied between seasons ($p \geq 0.1$). 'Nose-neck' was the only amicable interaction that varied between seasons among non-kin ($p = 0.04$). It occurred only in the breeding season, and comprised 3.4% (± 0.02) of interactions at that time (Table 25).

As suggested by the ANOVA on factor scores, differences in mean frequencies of individual interactions were most evident between kin and non-kin. Within seasons, and with seasons pooled, kin exhibited more of each amicable interaction ($p \leq 0.005$) and less of 6 of the 8 agonistic interactions ($p \leq 0.001$) than did non-kin. Only 'box' and 'stand' did not differ ($p \geq 0.23$) between kinship treatments.

There were distinct behavioural asymmetries based on kinship evident in the data. However, each kin dyad consisted of woodrats that were closely associated with each other on the same rock outcrop, whereas members of some non-kin dyads were sampled from different outcrops. Hence, it is possible that these asymmetries simply reflect a tendency for familiar individuals, independent of kinship, to interact amicably. If this were the case, and if degree of familiarity varied among non-kin, then familiar non-kin should interact more amicably and/or less agonistically than unfamiliar non-kin. Although I had no direct measure of familiarity between members of non-kin dyads, I assumed that non-kin dyads taken from the same outcrop ($N = 9$) were more familiar than those taken from different outcrops ($N = 23$).

Familiar non-kin dyads did not interact differently than unfamiliar non-kin dyads. There were no differences ($p > 0.1$) in mean frequencies of any amicable or agonistic interaction between the 2 groups (Table 26). Further, familiarity did not explain a significant amount of variation ($p > 0.32$) between the 2 non-kin groups in any factor score from the original factor analysis, nor did sex, season, and all interactions ($p > 0.24$) in a 3-way ANOVA.

4.3.3 MOTHER-OFFSPRING ASSOCIATIONS AND REPRODUCTIVE SUCCESS

Survival of juvenile females over the winter interval appeared to be influenced by the presence or absence of their mothers on the natal outcrop, although the effect differed between control and removal outcrops. The MOTHER AGE*MOTHER PRESENCE*REMOVAL term in a saturated log-linear model was significant ($X^2=7.43$, $df=2$, $p=0.02$), and log-linear analysis within removal class showed that 1) only juveniles on control outcrops were more likely to survive the winter interval in the presence of their mother than in her absence ($p=0.005$), and 2) the effect tended to be more obvious in juveniles of adult mothers than in juveniles of yearling mothers ($p=0.06$; Table 26). Juveniles on removal outcrops, however, were as likely to survive without their mothers, as they were with them ($p=0.59$; Table 26). The MOTHER AGE*MOTHER PRESENCE term in the log-linear model for removal outcrops suggested ($p=0.07$) that the effect of a mother's presence on the survival of her offspring differed between yearling and adult mothers. However, the interaction term appears driven by higher survival of juveniles born to adult mothers when their mothers were absent than when they were present (Table 26), and small sample sizes warrant caution in interpreting this effect. In any case, it is clear that the absence of a mother did not appear to reduce the chances of overwinter survival of juveniles on removal outcrops.

Overwinter survival of juvenile females on control outcrops was related to autumn weight (Chapter 3) and the presence or absence of their mothers. However, the "mother presence effect" was not due to differences in autumn weights of juveniles. Autumn weights were not heavier in juveniles whose mothers were present for the winter interval (208.1g±7.43 [40]) than in those juveniles whose mothers were not present for the interval (207.0g±5.14 [44]; $t=0.12$, $p=0.91$).

In order to consider the influence of mother presence effects on survival of male juveniles over the winter interval, I pooled data among mother age classes within removal class (due to low numbers of males surviving the interval). Log-linear analysis showed that survival of male juveniles over the winter interval was not dependent on the presence or absence of their mothers on the natal outcrop on either control or removal outcrops (MOTHER PRESENCE*REMOVAL: $p=0.13$; MOTHER PRESENCE: $p=0.23$; Table 26). However, small sample sizes may have restricted the ability of the log-linear model to detect differences between removal classes; 2 by 2 contingency analysis within removal class revealed that there was a strong tendency for juveniles on control outcrops to survive the winter interval better if their mothers were present than if they were absent ($p=0.06$), whereas the presence or absence of mothers clearly had no effect on overwinter survival of male juveniles on removal outcrops ($p=0.62$; Table 26). The mother presence effect on control outcrops appeared independent of weight in the autumn; juveniles whose mothers survived the winter interval were not heavier in the autumn (220.0g±10.55 [28]) than those whose mothers did not survive (226.9g±9.62 [29]; $t=0.48$, $p=0.63$).

There was little evidence that matrilineal yearlings grew faster than non-matrilineal yearlings during the winter or breeding intervals. Proportional increase in weight from the autumn of birth to the following spring did not differ between the 2 groups on control or removal outcrops ($p \geq 0.26$; Table 27). Proportional change in weight over the breeding interval was clearly not higher in matrilineal females on control outcrops (0.15±0.02 [9]) than in non-matrilineal females on control outcrops

(0.21±0.03 [10], Table 27). The permanent removal of many mothers in the spring prohibited a consideration of weight change over the breeding interval, with respect to the presence or absence of mothers, on removal outcrops.

Given that sample sizes of philopatric yearling males were low, I was unable to detect any significant differences ($p \geq 0.26$) in proportional weight gains between those that shared an outcrop with their mothers and those that did not (Table 27).

Mean date of first parturition did not differ between matrilineal (159±3.4 [9]) and non-matrilineal yearlings (164±3.3 [7]; $t=0.97$, $p=0.35$). Matrilineal yearlings weaned more offspring (1.9±0.40, $N=12$) than those that bred in the absence of their mother (1.0±0.30, $N=14$; $t=1.88$, $p=0.04$). Some of this variation was due to a strong trend for non-matrilineal females to experience more reproductive failures (56% of 18 litters) than matrilineal females (25% of 16 litters; $X^2=3.27$, $p=0.07$). It is interesting to note that the reproductive output of immigrant yearlings (0.9±0.35 [8] weaned offspring; 4 of 8 litters failed) was similar to that of non-matrilineal yearlings. Among yearlings that successfully weaned at least one offspring, those that were matrilineal still weaned more, on average (2.7±0.29, $N=9$) than those whose mothers did not survive to breed as adults (2.0±0.22, $N=7$, $t=1.75$, $p=0.05$). A statistical appraisal of numbers of litters produced was not possible; few yearlings produced more than 1 successful litter, regardless of their association with their mothers (with mother: 3 of 12 [25%] had 2 litters; without mother: 1 of 17 [7%]). Of further interest is the fact that adult mothers (that bred simultaneously with their yearling daughters) did not appear to incur costs in terms of reduced reproductive output. They weaned, on average, 3.0±0.55 [10] offspring, compared to an overall mean produced by adults of 2.8±0.30 [43]; Chapter 3, Table 10).

Table 21. Estimates of home range on 4 rock outcrops by resident woodrats from April-September, 1988-1989. Home range is 2 standard deviations of mean capture location, in metres (see text). For individuals that were alive in both years, the mean of yearly estimate was used. Marmot and Raven were control outcrops, Barrier and Kel's were removal outcrops.

	Females			Males		
Outcrop	Mean	Range	*N*	Mean	Range	*N*
Marmot	25.1	0.0-49.0	13	126.3	68.6-190.5	8
Raven	38.0	0.0-92.0	8	78.5	13.9-138.6	11
Barrier	40.4	0.0-82.8	7	80.7	0.0-172.4	17
Kel's	53.5	3.0-77.4	6	88.7	49.0-174.9	10

Table 22. Varimax rotated factor pattern from frequencies of all behaviour observed in 64 dyadic trials

	Factor 1			Factor 2			Factor 3			Factor 4			Factor 5		
	Load	Mean	SE	Load	Mean	SE	Load	Mean	SE	Load	Mean	SE	Load	Mean	SE
Allogroom	0.92	0.70	0.07												
Huddle	0.88	0.65	0.07												
Follow	0.82	0.74	0.04							0.34	0.09	0.05			
Nose-neck	0.73	0.70	0.03	0.38	0.30	0.06				0.32	0.05	0.06			
Nose-gen[1]	0.36	0.38	0.03	0.35	0.20	0.05									
Move toward				0.87	0.41	0.09									
Investigate				0.74	0.42	0.06									
Move away	0.48	0.58	0.03	0.74	0.41	0.07									
Vocalize				0.57	0.30	0.06									
Nose-ab[2]	0.54	0.62	0.02	0.55	0.30	0.07									
Nose-nose	0.32	0.47	0.03	0.53	0.23	0.07				0.48	0.07	0.08			
Groom				0.52	0.29	0.06									
Flee							0.91	0.60	0.08						
Lunge							0.91	0.59	0.08						
Avoid							0.65	0.49	0.05						
Fight							0.61	0.36	0.07						
Foot drum															
Box										0.87	0.39	0.08			
Stand										0.85	0.37	0.09			
Face													0.89	0.40	0.09
Tooth chatter							0.34	0.21	0.04				0.76	0.33	0.08
Variance explained	18.8%			16.9%			14.4%			11.6%			9.8%		

Factor loadings $\leq$ 0.30 not included. Means and SE's were generated by jackknifing ($N=25$; see text).

Nose-gen[1]: Nose-genital. Nose-ab[2]: Nose-abdomen.

Table 23 a). Probabilities associated with 2-way ANOVA on factor score differences (KIN-NONKIN) within adult females.

Source	Factor1 (Amicable)		Factor2 (Investigative)		Factor3 (Agonistic)		Factor4 (Agonistic)		Factor5 (Agonistic)	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Sex	0.22	0.64	0.85	0.36	1.16	0.29	1.52	0.23	2.56	0.12
Season	3.20	0.08	0.00	0.98	0.58	0.45	0.33	0.57	0.02	0.89

Degrees of freedom: Model=2, Error=29. Interaction term was not significant ($p \geq 0.29$) in any saturated model.

Table 23 b). Probabilities associated with 2-way paired comparisons ANOVA on factor scores.

Source	Factor1 (Amicable)		Factor2 (Investigative)		Factor3 (Agonistic)		Factor4 (Agonistic)		Factor5 (Agonistic)	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Kinship	6.92	0.01[a]	3.12	0.09	11.48	0.0002[b]	0.03	0.87	7.20	0.01[b]
Adult	1.11	0.39	1.53	0.12	1.14	0.36	2.22	0.01	0.95	0.55

Degrees of freedom: Kinship=1, Adult=31, Error=31.

[a] KIN scored highest. [b] NON-KIN scored highest.

Table 24. Mean frequencies of amicable and agonistic interactions recorded during dyadic encounters of kin and non-kin in post breeding (1988) and breeding (1989) season. Numbers of dyads in brackets. SE=standard error. Dyads were female-female, or female-male (sexes pooled within kinship).

	Kin				Non-Kin			
	Post Breeding (19)		Breeding (13)		Post Breeding (19)		Breeding (13)	
Behaviour	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Amicable								
Allogroom	3.6	1.47	1.2	0.93	0.0	0.00	0.0	0.00
Huddle	8.9	2.46	4.4	1.74	0.2	0.21	0.1	0.08
Follow	4.8	1.71	1.5	0.60	0.2	0.12	0.9	0.66
Nose-neck	6.1	2.02	5.0	1.48	0.0	0.00	0.9	0.50
Nose-genital	2.3	0.79	2.4	0.89	0.1	0.07	1.3	0.73
Move away	16.9	2.59	12.8	2.54	8.1	0.77	9.9	2.28
Nose-abdomen	4.8	1.53	3.6	0.98	0.2	0.12	0.8	0.52
Nose-nose	10.7	2.07	10.8	1.89	2.2	0.74	2.3	1.05
Total amicable	58.2	12.21	41.7	7.76	10.9	1.25	16.2	5.02
Agonistic								
Flee	2.5	1.13	2.5	1.19	12.9	3.82	8.5	3.09
Lunge	2.9	0.81	1.8	0.64	12.7	3.63	10.5	2.91
Avoid	7.3	2.10	6.2	2.04	14.8	2.77	13.9	3.79
Fight	0.6	0.24	0.2	0.17	1.1	0.39	4.6	1.34
Box	0.7	0.29	0.9	0.59	0.3	0.18	0.9	0.59
Stand	2.5	0.96	1.1	0.69	1.4	0.60	1.6	0.90
Face	7.6	2.24	7.1	3.22	16.3	3.22	19.5	4.55
Tooth chatter	5.9	1.94	5.8	1.75	27.4	3.86	5.8	1.75
Total agonistic	30.1	5.71	25.6	6.84	86.7	11.36	79.0	12.48

Table 25. Mean frequencies of amicable and agonistic interactions recorded during dyadic encounters of familiar and unfamiliar non-kin in post breeding (1988) and breeding (1989) season. Dyads were female-female, or female-male. Sexes and seasons pooled. Number of dyads in brackets. SE = standard error.

	Familiar Non-kin (9)		Unfamiliar Non-kin (23)	
Behaviour	Mean	SE	Mean	SE
<u>Amicable</u>				
Allogroom	0.0	0.00	0.0	0.00
Huddle	0.0	0.00	0.2	0.18
Follow	0.2	0.22	0.6	0.38
Nose-neck	0.0	0.00	0.5	0.29
Nose-genital	0.1	0.11	0.8	0.43
Move away	9.1	1.50	8.7	1.32
Nose-abdomen	0.0	0.00	0.6	0.31
Nose-nose	1.8	0.64	2.4	0.81
Total amicable	11.2	2.01	13.8	2.93
<u>Agonistic</u>				
Flee	10.0	3.86	11.6	3.31
Lunge	12.3	3.63	11.6	3.12
Avoid	16.9	3.85	13.5	2.71
Fight	0.6	0.29	3.3	0.86
Box	0.0	0.00	0.7	0.36
Stand	1.1	0.99	1.6	0.60
Face	19.1	5.68	17.0	2.98
Tooth chatter	31.3	6.26	21.3	2.71
Total agonistic	91.3	13.21	80.6	10.48

Table 26. The influence of the presence or absence of a mother on the overwinter survival of her a) female, and b) male offspring. For female juveniles, the MOTHER AGE*MOTHER PRESENCE*REMOVAL term in the saturated log-linear model was significant ($X^2=7.43$, $df=2$, $p=0.02$). and subsequent analysis was within removal class. The MOTHER AGE*MOTHER PRESENCE term was not significant ($X^2=3.16$, $df=2$, $p=0.21$) in the saturated model for control outcrops. For males, mother ages were pooled, and the REMOVAL*MOTHER PRESENCE term was not significant ($X^2=2.31$, $df=1$, $p=0.13$) in the saturated model. Number of juveniles alive in autumn in brackets.

		% Surviving		Log-linear Analysis			
Outcrop	Age	Absent	Present	Source	X^2	*df*	*p*
a) FEMALES							
Control	Yearling	36 (22)	65 (20)	Age[a]	3.57	1	0.06
	Adult	53 (19)	94 (16)	Presence	7.82	1	0.005
	Pooled	44 (41)	78 (36)				
Removal	Yearling	60 (15)	65 (31)	Age*Pres	5.32	2	0.07
	Adult	83 (6)	60 (10)	Age	0.21	1	0.64
	Pooled	67 (21)	62 (42)	Presence	0.14	1	0.71
b) MALES							
Control	Yearling	25 (12)	47 (17)				
	Adult	17 (18)	36 (11)				
	Pooled	20 (30)	43 (28)[b]	Presence	1.46	1	0.23
Removal	Yearling	10 (10)	25 (16)	Removal	0.14	1	0.71
	Adult	67 (6)	0 (1)				
	Pooled	31 (16)	24 (17)[c]				

[a]: Age = Mother Age.

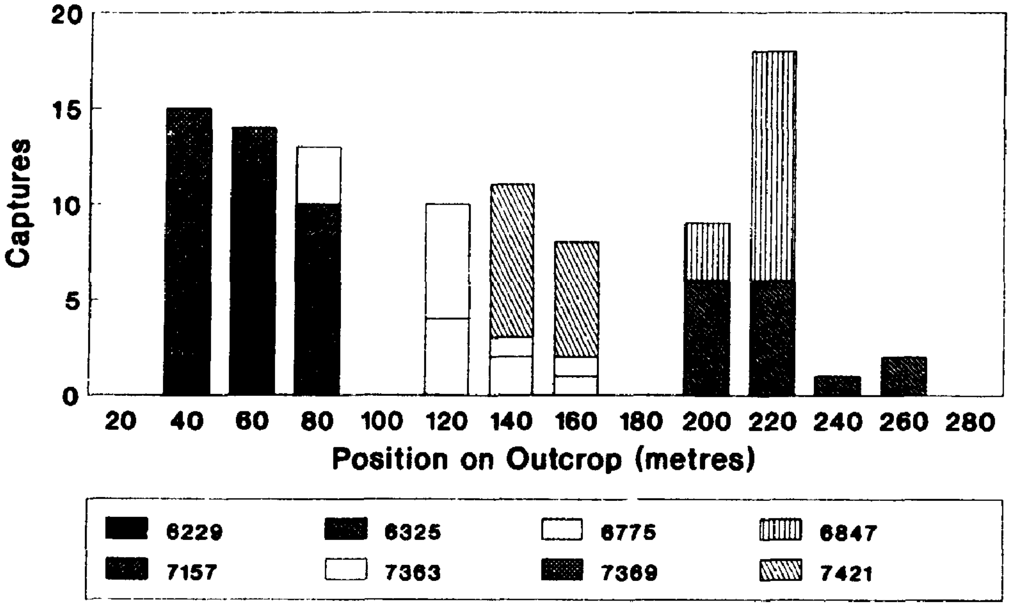
[b,c]: 2 by 2 contingency analysis; [b] $X^2=3.53$, $p=0.06$; [c] $X^2=0.25$, $p=0.62$

Table 27. Proportional weight gains in yearlings during their first 1) winter, and 2) breeding season, with respect to the presence or absence of their mothers. Mean (untransformed) proportional weight gains ± SE. Number of yearlings in brackets. Proportional weight gains were arcsine-transformed prior to *t*-tests.

Sex	Outcrop	Interval	Present	Absent	*t*	*p*
Female	Control	Winter	0.21±0.06 (17)	0.14±0.04 (19)	1.15	0.26
		Breeding	0.15±0.02 (9)	0.21±0.03 (10)	1.79	0.09
	Removal	Winter	0.14±0.03 (10)	0.18±0.05 (12)	0.68	0.50
Male	Control	Winter	0.34±0.05 (11)	0.24±0.08 (6)	1.05	0.32
		Breeding	0.17±0.05 (11)	0.07±0.05 (6)	1.17	0.26
	Removal	Winter	0.19±0.06 (4)	0.23±0.04 (5)	0.55	0.60

Figure 9. Frequency distribution of capture locations of all resident females on 2 control outcrops in 1989. The position of first trap site on outcrop was 0 metres; successive sites were pooled within 20 m intervals. Woodrat 7369 was a yearling daughter of 6629, and 7363 was a yearling daughter of 6775 (Marmot outcrop). 7466 and 7468 were both yearling daughters of 6675 (Raven outcrop). Relatedness among other females was unknown.

a) Marmot



b) Raven

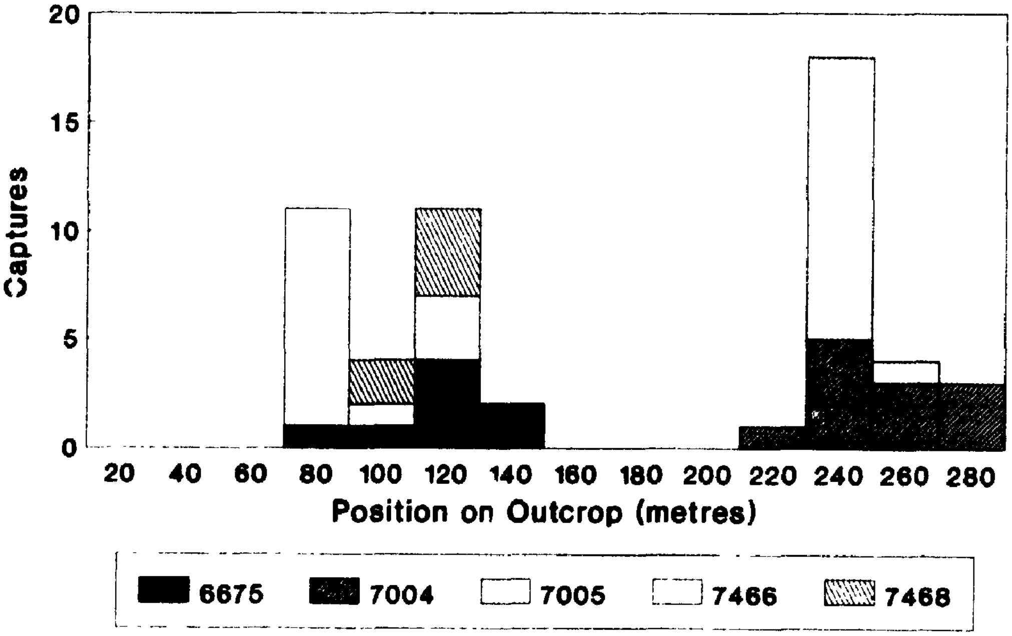
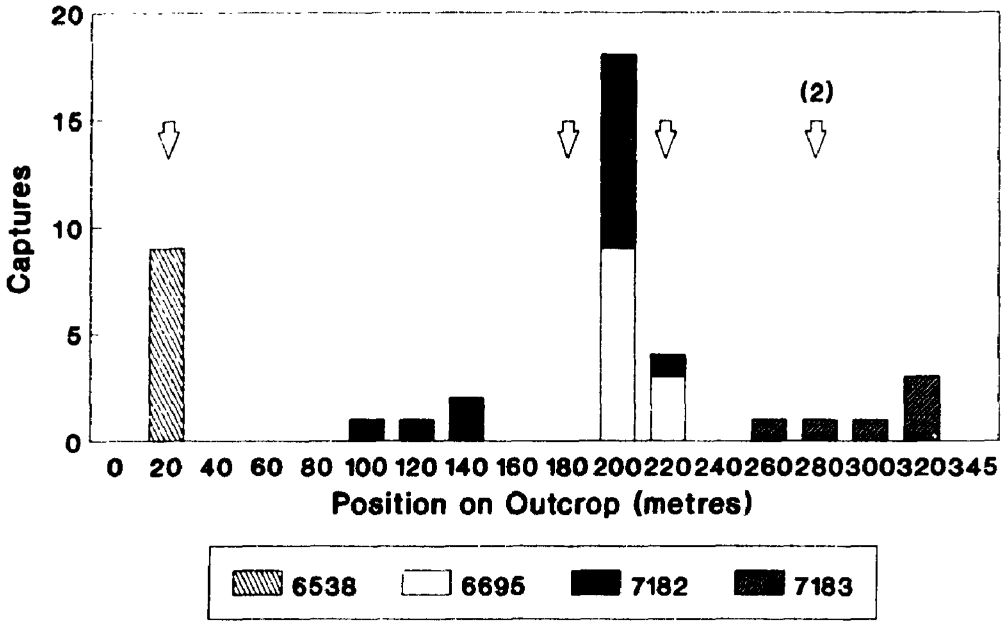
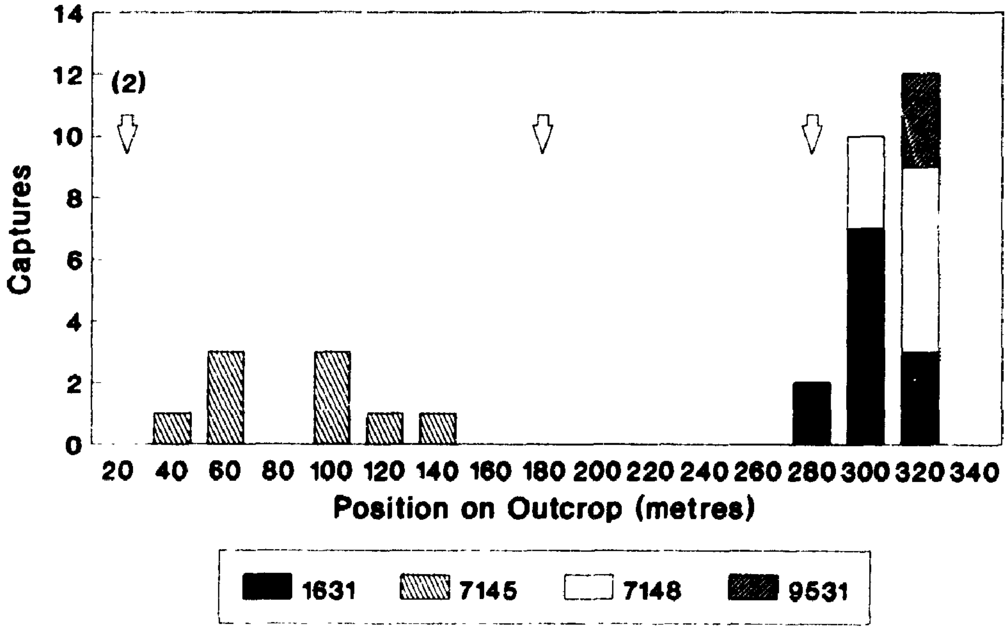


Figure 10. Frequency distribution of capture locations of all resident females on 2 removal outcrops (Kel's in 1988; Barrier in 1989). The position of first trap site on outcrop was 0 metres; successive sites were pooled within 20 m intervals. Woodrat 1631 was a yearling daughter of 7148 (Barrier). Relatedness among other females was unknown. Arrows indicate trap sites from which residents were permanently removed. One resident removed per site, unless noted: (2).



a) Kel's



a) Barrier

4.4 DISCUSSION

Most adult female rodents are essentially sedentary, and juveniles tend to remain on or near their natal area for some time after independence (Waser and Jones 1983; Anderson 1989). This tendency for female-biased philopatry creates the potential for conflict. Because female-biased philopatry often leads to the spatial association of close kin, it may create a social environment that favours the evolution of cohesive relationships (Hamilton 1964). Alternatively, it may act to intensify resource competition among associated females, particularly during the breeding season, such that cohesive relationships cannot be maintained. A female must attempt to balance the need to provide her philopatric daughters with resources necessary for their successful reproduction against her own requirements necessary for maximizing future reproductive output.

In Chapter 3, I demonstrated that competition among female bushy-tailed woodrats within rock outcrops negatively affects reproductive success in some residents, and totally excludes other individuals from gaining access to critical resources on outcrops. In contrast, the results presented here indicate that, within this competitive sociality, strongly cohesive relationships are maintained among overlapping generations of breeding females (i.e., mothers and daughters). Analysis of space use, behavioural relationships, and measures of reproductive success were all consistent with this interpretation.

Space Use

The spatial dispersion of bushy-tailed woodrats is poorly understood. Based on limited information gathered from a small sample of radio-collared woodrats after a breeding season in California, Escherich (1981) suggested that male home ranges were larger than those maintained by females, and that home ranges of some females exhibited considerable overlap within outcrops. Because Escherich (1981) noted that some juvenile females remained on their (putative) natal outcrop in the autumn after their birth, he speculated that those females exhibiting a large degree of overlap may be closely related. Hickling's (1987) calculation of home ranges in *N. cinerea* based on distances between successive trap captures corroborated Escherich's suggestion that adult males maintain larger home ranges than do females, as did my quantification of space use of breeding residents on four outcrops. The relative sizes of male and female home ranges are of general interest only to this investigation. More pertinent to the question of space use and relatedness is the fact that, like Escherich (1981), I found small groups of females that exhibited clumped, highly overlapping distributions of capture locations within outcrops. My results also support Escherich's speculation that these groups are in some cases comprised of (reproductively-active) mothers and daughters. Not only did juvenile females tend to remain on their natal outcrop as breeding yearlings, but they shared their natal range with their adult mother. Indeed, in 14 of 29 cases where a yearling daughter and her adult mother bred simultaneously on the natal outcrop, they were most often captured at the very same trap location (i.e., within 5 m). It is not clear whether mothers and daughters actually shared the same den sites, but they were obviously associated in space, and, presumably, in a position to interact with one another. Many species of woodrats are not known to share houses with non-juvenile conspecifics (Finley 1958; Kelly 1989; Newton 1990). However, unlike other woodrats, *N. cinerea* are unable to modify the availability of permanent den sites on rock outcrops; it is possible that constraints unique to *N. cinerea* may favour sharing of den sites. In any case, it is likely that non-matrilineal yearlings inherited the use of the maternal den site; they were captured most often at the same location that their mothers had been in the previous year in 10 of 13 cases.

Because I did not have sufficient data to quantify space use between non-related or distantly related woodrats, it is unknown whether close kin maintain closer spatial relationships than non-kin. Considering that behavioural interactions between close kin were far more amicable than those between non-kin, it seems reasonable to suggest that non-kin would at least attempt to maintain more exclusive home ranges than would close kin. However, den sites may be economically undefendable, due to their clumped distribution and limited availability (Emlen and Oring 1977; Wittenberger 1981), such that some non-kin may be "forced" to breed in proximity at times. Indeed, it may be under these very conditions when competitive interference between conspecifics is most intense, and reproductive success most adversely affected by the social environment (Chapter 3). A more detailed investigation of space use and reproduction, with respect to relatedness, would be of great value.

The prevalence of philopatry among juvenile females, and the patterns of space use among mothers and daughters suggest that the inheritance of maternal resources on the natal outcrop is an important element of female sociality in bushy-tailed woodrats. The inheritance of maternal resources by philopatric young should be particularly advantageous when the accessibility of critical resources outside the natal area is low (Waser 1988; Anderson 1989). This should certainly apply to *N. cinerea*, in which the costs of emigration include those associated with dispersal between non-contiguous outcrops, and competition for a limited number of den sites with agonistic residents on non-natal outcrops. Although some females were successful immigrants (28% of breeding females on control outcrops were immigrants; Chapter 3, section 3.3.6), my removal experiment (Chapter 3) indicated that other potential immigrants were excluded from access to resources on non-natal outcrops. It would be interesting to know the proportion of emigrating individuals that were unsuccessful in their attempt to recruit to a non-natal outcrop.

Most *Neotoma* species rely on the use of elaborate dens or houses (Finley 1958; Newton 1990), and the use of the maternal house by philopatric juveniles has been noted in several species (*N. albigula*: Newton 1990; *N. floridana*: Fitch and Rainey 1956; *N. fuscipes*: Linsdale and Tevis 1951; Kelly 1989; *N. micropus*: Raun 1966). Further, in some cases when a female breeds in two successive seasons, it is apparent that she may facilitate philopatry by 1) maintaining and defending an extra house that a juvenile eventually settles in (Newton 1990), or 2) moving to a vacant house, and abdicating her house to her philopatric young (Linsdale and Tevis 1951; Fitch and Rainey 1956). Abdication of maternal resources by a female to her offspring may be viewed as a form of maternal investment (Armitage 1988; Anderson 1989), and has been observed in other rodent species that rely on refugia and/or food caches for survival (*Dipodomys spectabilis*: Jones 1984; 1986; *Spermophilus columbianus*: Harris and Murie 1984; *Tamiasciurus hudsonicus*: Price et al. 1986).

In bushy-tailed woodrats, reproductively-active mothers and daughters maintained a large degree of spatial overlap throughout the breeding season. Although overlapping home ranges of female woodrats have been recorded in several species (*N. cinerea*: Escherich 1981, *N. floridana*: Goertz 1970, *N. fuscipes*: Linsdale and Tevis 1951; Kelly 1989, *N. lepida*: Bleich and Schwartz 1975), only Kelly (1989) noted that neighbouring females in *N. fuscipes* were close kin in some cases. More work employing techniques that facilitate the quantification of relatedness in woodrats is badly needed to determine if matrilineal associations are typical in the genus.

Behavioural trials

Cohesive social relationships should only be maintained as long as the fitness benefits of sociality exceed costs. My results from the behavioural trials clearly indicate that dyads of adult female woodrats and non-kin interacted agonistically, while those of adult females and their offspring interacted amicably. That interactions among adult females and non-kin were strongly agonistic regardless of reproductive status and familiarity (i.e., shared residency on a rock outcrop) is consistent with the hypothesis presented in Chapter 3 that 1) there is competitive interference among conspecific females on an outcrop (that negatively affects reproductive output and survival), and 2) woodrats competitively exclude potential immigrants from access to limited resources. However, that adult females and their offspring interacted amicably suggests that close kin reduce costs of competition, and presumably accrue fitness benefits, by maintaining cohesive relationships. Although intragroup competition among females is expected to be particularly intense during the breeding season (Trivers 1972; Clutton-Brock and Albon 1985; Hoogland 1986), cohesive relationships between adult females and their philopatric offspring of both sexes were maintained into the breeding season when offspring were reproductively active as yearlings.

I cannot exclude the possibility that the behavioural asymmetry that I quantified was due, in part, to the use of a neutral arena. The arena, by definition, does not contain a source of competition, and close kin may interact aggressively in the wild when in the presence of a limited resource. However, that non-kin dyads interacted aggressively in the arena suggests that arena interactions at least reflect relationships in the wild.

Intraspecific competition may be manifested in many ways, and it does not necessarily follow that cohesive mother-offspring relationships lack competitive elements and associated costs. A kin-based sociality may represent the only, rather than the best, alternative available to some of its members, and may entail costs such as reproductive suppression (Wasser and Barash 1983), delayed reproductive maturity (Armitage 1981; 1988; Barash 1989), increased incidence of reproductive failure, and reduced fecundity (Armitage 1984; 1986; Clutton-Brock and Albon 1985; Hoogland 1985). However, bushy-tailed woodrats clearly do not experience costs associated with reproductive suppression or delayed maturity (all females first breed as yearlings), and amicability among close kin may indeed represent a beneficial sociality in spite of strong resource competition.

I suggest that a cohesive, kin-based sociality in bushy-tailed woodrats confers at least two important benefits to its members. First, I have shown that natal philopatry leads to mothers and daughters settling and breeding in proximity, and suggest that amicability among kin dyads reflects a tendency for adult females to promote access to limited, critical resources on the natal area (e.g., den sites, food caches) among their offspring. Access to den sites and associated food caches in the autumn would likely improve overwinter survival of philopatric young of both sexes (although it is unknown whether offspring overwintered in proximity to their mothers). Competitive interests are expected to diverge between sexes when individuals become reproductively active; males should strive to maximize access to mates while females are expected to compete for resources necessary for successful rearing of offspring (Trivers 1972). The potential role of a mother-son relationship affecting a male's ability to compete for mates is rarely considered (but see Anderson 1989), probably because lasting mother-son relationships are not often encountered. In woodrats, some males are philopatric. Hence, there is some opportunity for mothers to enhance the reproductive success of their sons if they could promote their sons' settlement on or near the natal area (thereby insuring access to other resident females) by providing an amicable social environment. Most yearling males (71%), however, were not philopatric, suggesting that either male-male competition or non-enforced dispersal may be more important determinants of philopatry in male woodrats than are mother-son relationships.

In addition to promoting access to, and possibly sharing of, critical resources for survival and breeding among female kin, I suggest that cohesive social relationships among breeding females enhance vigilance and defense against interfering conspecifics. Although I have little evidence that competitive interactions intensified among females from autumn to the onset of pregnancy (only 'fight' increased significantly among non-kin dyads in the breeding season), interactions among non-kin were clearly agonistic when females were pregnant, suggesting that female sociality among non-kin is competitive at this time. Aggression between adult females and non-group members or non-residents is a common feature of many rodents, and generally acts to limit settlement of potential intruders (Boonstra 1984; Holekamp 1984; Brody and Armitage 1985; Armitage 1988; Anderson 1989; Barash 1989). An amicable social environment among close kin could provide an effective buffer against aggression from intruders, especially for behaviourally subordinate individuals (Armitage 1984; Barash 1989), and may help to reduce the negative effects of competition on reproductive output among yearlings (Chapter 3).

There have been several attempts to describe behavioural interactions in various *Neotoma* species (Egoscue 1962; Cameron 1971; Boggs 1974; Dial 1988; Kinsey 1976; 1977; Fleming 1979; Escherich 1981; Wallen 1982; Kelly 1990). Unfortunately, few provide any meaningful quantification, and only Kelly (1990) mentioned the relatedness of the subjects. Kelly (1990) reported that pairs of members of matrilines (presumably mother-daughter, or sister-sister) in *N. fuscipes* "behaved affiliatively" in 5 behavioural trials conducted at the initiation of a breeding season, although there was no attempt to describe or quantify the interactions further, and no trials were conducted between non-kin. There is clearly room for further investigation of behavioural relationships in the genus, especially in those where it appears that neighbouring females may in some cases be closely related (e.g., *N. fuscipes*: Kelly 1989; *N. albigula*: Newton 1990).

It is generally recognized that social organization in large, diurnal rodents is based largely on clusters of close kin, particularly of mother and offspring (Armitage 1981; 1988; Michener 1983). Close kin in these species tend to share space and resources on the natal area, and generally interact more amicably toward group members than toward non-kin (Michener 1983; Davis 1984a; Armitage 1986). However, there is some indication that a decrease in social cohesiveness among mothers and philopatric daughters coincides with the daughters' reproductive maturity in marmots (Armitage 1981; Barash 1989) and other ground-dwelling squirrels (Festa-Bianchet and King 1984), suggesting that sociality is favored only when asynchronous breeding (reproductive suppression) among group members reduces the costs of intra-group competition (Armitage 1981).

There is a growing recognition that sociality in many species of small, nocturnal mammals may also be based on groups of closely related females (Boonstra et al. 1987; Kawata 1990; Lambin and Krebs 1991a). It has been suggested that closely related, breeding females may overlap in space in many of these species (McShea and Madison 1984; Kawata 1987; Boyce and Boyce 1988; Ims 1989; Ylönen 1990;

Lambin and Krebs 1991a, 1991b). Although it is commonly assumed that interactions among closely related females will be amicable and beneficial (Boonstra et al. 1987; Lambin and Krebs 1991a), there is little work that has examined behavioural relationships between breeding female kin and non-kin in the wild. Ferkin (1988) demonstrated that neighbouring female meadow voles (of unknown relatedness) in breeding condition interacted less agonistically than strangers. To the extent that neighbouring voles are closely related, this work provides some evidence for a kin-based behavioural asymmetry. More work is clearly needed to address this question. It would seem to be a particularly pertinent one to address, as costs of intrasexual competition among females on immigration, reproduction, and survival have been well documented in several species (see Chapter 3). In a paper where Boonstra (1984) illustrated that adult female meadow voles behave aggressively toward strange (unrelated) young, he recognized the need for researchers to address "the crucial question of how adult microtines respond to their own young (and) how this response varies as a function of the sexual maturity of the young" (p.129). He further noted that only Halpin (1981) had investigated how adult (*Peromyscus maniculatus*) female respond to their own young, but the young were only 3-5 weeks of age at testing. To my knowledge, no one has responded to Boonstra's appeal in writing.

Reproductive Success

The ratio of the number of studies that has documented behavioural asymmetries based on kinship to the number that has tested for fitness asymmetries based on kinship approaches infinity. Needless to say, the adaptive value of relationships between females maintaining overlapping home ranges and/or between matrilineal females in woodrats has not been investigated, to my knowledge, before this study. If the behavioural relationships observed in the neutral arena represent adaptive behaviour, then fitness benefits should accrue to offspring that share an outcrop with their mother, relative to those that do not. The results of my analyses were clearly consistent with this interpretation. Female (and to a lesser extent, male) offspring were more likely to survive the winter interval on their natal outcrop to become breeding yearlings if their mother likewise survived to become a breeding adult, suggesting that the presence of a juvenile's mother enhances the probability of that juvenile surviving (and/or not dispersing) over winter. A female could accomplish this if she were able to facilitate the access of her offspring to a suitable den site, perhaps her own, as suggested above. There is an alternative, non-adaptive explanation for the observed asymmetries in overwinter survival. If predation were an important source of overwinter mortality, and all female bushy-tailed woodrats tended to share their dens with their offspring (e.g., for thermoregulation through huddling), then all individuals sharing a den site may tend to disappear together. Offspring would not survive without their mothers simply because they died simultaneously of a common cause. However, that overwinter survival of juveniles on removal outcrops (where den site availability was presumably relatively high) was independent of the presence or absence of an adult mother is most consistent with the former hypothesis.

Perhaps one of the most interesting findings of this investigation of mother-offspring associations is that, in spite of potentially intense competition between mothers and daughters breeding in proximity, the number of weaned offspring in yearling daughters was enhanced, relative to that of philopatric and immigrant yearlings breeding in the absence of their mother. Because the number of weaned offspring was the component of reproductive output in yearlings that was negatively affected by competition among females on an outcrop (Chapter 3), it seems reasonable that cohesive relationships maintained between mothers and daughters may afford a protective environment for the yearling against agonistic intruders, as was suggested by the results of the behavioural trials. In the same way that a small difference in reproductive output was shown to have a large impact on lifetime reproductive success in bushy-tailed woodrats (Chapter 3), this socially-induced increase in reproductive output is expected to enhance lifetime reproductive success of yearlings. The fitness benefits accruing to matrilineal yearlings are obvious. However, fitness benefits of helping to produce grandoffspring accruing to adults must be weighed against potential costs to the production of their own offspring (Trivers 1974; Clutton-Brock 1991). Matrilineal adults, however, did not appear to incur a direct reproductive cost; they produced as many weaned offspring as did the overall adult population. Hence, matrilineal associations are clearly advantageous to both mothers and philopatric daughters.

These data were not experimental. As such, I cannot exclude the possibility that non-matrilineal yearlings were poor quality individuals (perhaps due to poor quality mothers) that may not have exhibited enhanced reproductive output even in the presence of their mother. An appropriate experiment to test whether my results reflect a true sociality effect would be to compare reproductive output of yearlings from whom their adult mothers were removed at the start of a breeding season to that of yearlings in unmanipulated matrilines. Experimental yearlings would be expected to exhibit depressed reproductive output, relative to unmanipulated yearlings. However, if one considers the general agreement of the patterns of space use, behavioural interactions, and reproductive success, I believe that they constitute compelling evidence for the existence of stable, cooperative relationships among mothers and offspring in bushy-tailed woodrats.

I investigated relationships maintained between mothers and offspring only.

Amicable relationships between sibs and more distantly-related individuals are known to occur in some rodents (Sherman 1980; Hoogland 1981a; Armitage 1988). However, the mortality patterns and low reproductive output experienced by bushy-tailed woodrats generally limit the relationships among reproductively-active kin to those of mother-daughter, and to a lesser extent, sister-sister. There were very few cases of individuals with a coefficient of relatedness of 0.25 sharing an outcrop during any breeding season in my study. Littermate and non-littermate sister pairs shared breeding outcrops in 12 cases (some in the presence of their mother), and it is possible that amicable relationships are maintained in these cases. However, mothers and daughters shared breeding outcrops in some 40 cases, and I suggest that mother-daughter relationships form the basis of cohesive sociality in bushy-tailed woodrats.

Little is known of how reproductive success may vary with relatedness of neighbouring females in other rodents. Armitage (1986) showed that the production of weaned offspring by 2-year old yellow-bellied marmots was greater in the absence of their adult mother, than when mothers and daughters bred in proximity, consistent with the hypothesis that sociality in marmots is competitive, and directed at the maximization of direct fitness (Armitage 1988). In contrast, Davis (1984b) manipulated the relatedness of groups of Richardson's ground squirrels (*Spermophilus richardsonii*), a species in which females first bred as yearlings, and found that production of weaned young was enhanced in a group of close kin, relative to that in a group of non-kin. Recently, Charnov and Finerty (1980) proposed a model to explain fluctuations in vole populations, based on the assumption that closely related females interact more amicably and have higher reproductive success than non-kin. Despite the paucity of information on how kin and non-kin interact in the wild in microtines, several researchers (Kawata 1987; Boonstra and Hogg 1988; Ylönen et al. 1990) have attempted to test the model by creating groups of close kin and non-kin in enclosures, and monitoring the recruitment of young in the two groups. Results have been mixed. No kin effects were detected by Kawata (1987) or Boonstra and Hogg (1988), but Ylönen et al. (1990) found that kin groups did indeed exhibit enhanced production and survival of juveniles, relative to the non-kin groups. Although data are disparagingly uncommon, there is some evidence that close kin in other rodent species are able to buffer the costs of intrasexual competition by maintaining cohesive relationships. However, until far more data are accumulated, it will be difficult to understand, let alone predict, the conditions favouring stable, cohesive relationships in small mammals.

Literature Cited

Adams, F., and Dams, R. 1970. Applied gamma-ray spectrometry. 2nd ed. Pergamon Press, Oxford.

Alexander, R. D. 1974. The evolution of social behavior. Ann. Rev. Ecol. Syst. 5: 325-383.

Altmann, J., Hausfater, G., and Altmann, S. A. 1988. Determinants of reproductive success in savannah baboons, *Papio cyanocephalus*. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 403-418.

Anderson, P. K. 1989. Dispersal in rodents: A resident fitness hypothesis. Amer. Soc. Mamm. Spec. Publ. No 9.

Armitage, K. B. 1981. Sociality as a life-history tactic of ground squirrels. Oecologia. 48: 36-49.

Armitage, K. B. 1984. Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. *In*: The biology of ground-dwelling squirrels. *Edited by* J. O. Murie and G. R. Michener. University of Nebraska Press, Lincoln and London. pp. 375-403.

Armitage, K. B. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. *In*: ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton. pp. 303-331.

Armitage, K. B. 1987. Do female yellow-bellied marmots adjust the sex ratios of their offspring? Am. Nat. 129: 501-519.

Armitage, K. B. 1988. Social organization of ground-dwelling squirrels. *In*: The ecology of social behavior. *Edited by* C. N. Slobodchikoff. Academic Press, San Diego. pp. 131-155.

Armitage, K. B., and Downhower, J. F. 1974. Demography of yellow-bellied marmot populations. Ecology. 55: 1233-1245.

Armitage, K. B., and Johns, D. W. 1982. Kinship, reproductive strategies and social dynamics of yellow-bullied marmots. Behav. Ecol. Sociol. 11: 55-63.

Barash, D. P. 1989. Marmots: social behavior and ecology. Stanford University Press, Stanford.

Begon, M. 1983. Density and individual fitness: asymmetric competition. *In*: Evolutionary ecology. *Edited by* Shorrocks, B. Blackwell Scientific Publications, Oxford. pp. 175-194.

Bleich, V. C., and Schwartz, O. A. 1975. Observations on the home range of the desert woodrat, *Neotoma lepida intermedia*. J. Mamm. 56: 518-519.

Boggs, J. R. 1974. Social ecology of the white-throated woodrat (*Neotoma albigula*) in Arizona. Ph.D. thesis. Arizona State University.

Bondrup-Nielson, S. 1986. Investigation of spacing behaviour of *Clethrionomys gapperi* by experimentation. J. Anim. Ecol. 55: 269-279.

Boonstra, R. 1984. Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) towards young. Oecologia. 62: 126-131.

Boonstra, R. 1977. Effect of conspecifics on survival during population declines in *Microtus townsendii*. J. Anim. Ecol. 46: 835-851.

Boonstra, R. 1978. Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. Ecology. 59: 242-248.

Boonstra, R., and Hogg, I. 1988. Friends and strangers: a test of the Charnov-Finerty hypothesis. Oecologia. 77: 95-100.

Boonstra, R., Krebs, C. J., Gaines, M. S., Johnson, M. L., and Craine, I. T. M. 1987. Natal philopatry and breeding systems in voles (*Microtus* spp.). J. Anim. Ecol. 56: 655-673.

Boutin, S. 1984. The effect of conspecifics on juvenile survival and recruitment of snowshoe hares. J. Anim. Ecol. 53: 623-637.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68: 203-220.

Boyce, C. C. K., and J. L. Boyce. 1988. Population biology of *Microtus arvalis*. I. Lifetime reproductive success of solitary and grouped females. J. Anim. Ecol. 57: 711-722.

Brody, A. K., and Armitage, K. B. 1985. The effects of adult removal on dispersal of yellow-bellied marmots. Can. J. Zool. 63: 2560-2564.

Bujalska, G. 1973. The role of spacing behaviour among females in the regulation of reproduction in the bank vole. J. Repro. Fert. Suppl. 19: 465-474.

Bujalska, G. 1985. Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. Annal. Zool. Fennica. 22: 331-342.

Burt, W. H., and Grossenheider, R. P. 1976. 3rd ed. A field guide to the mammals. Houghton Mifflin Company, Boston.

Cameron, G. N. 1971. Niche overlap and competition in woodrats. J. Mamm. 52: 288-296.

Charnov, E. L., and Finerty, J. P. 1980. Vole population cycles: a case for kin-selection? Oecologia. 45: 1-2.

Cheney, D. L., and Seyfarth, R. M. 1987. The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behav. Ecol. Sociobiol. 21: 375-386.

Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. Science. 201: 163-165.

Clutton-Brock, T. H. 1988a. Reproductive success. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 472-485.

Clutton-Brock, T. H. 1988b. Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, New Jersey.

Clutton-Brock, T. H., and Albon, S. D. 1985. Competition and population regulation in social mammals. *In*: Behavioural ecology: ecological consequences of adaptive behaviour. *Edited by* R. M. Sibly and R. H. Smith. Blackwell Scientific Publications, Oxford. pp. 557-575.

Clutton-Brock, T. H., and Iason, G. R. 1986. Sex ratio variation in mammals. Quart. Rev. Biol. 61: 339-374.

Clutton-Brock, T. H., Guiness, F. E., and Albon, S. D. 1982. Red Deer: Behavior and ecology of two sexes. University of Chicago Press, Chicago.

Clutton-Brock, T. H., Albon, S. D., and Guinness. F. E. 1988. Reproductive success in male and female red deer. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 325-343.

Cockburn, A. 1988. Social behaviour in fluctuating populations. Croom Helm, London.

Cowan, D. P., and Garson, P. J. 1985. Variations in the social structure of rabbit populations: causes and demographic consequences. *In*: Behavioural ecology. Ecological consequences of adaptive behaviour. *Edited by* Sibly, R. M., and Smith, R. H. Blackwell Scientific Publications, Oxford. pp. 537-555.

Creel, S. R., and N. M. Creel. 1991. Energetics, reproductive suppression and obligate communal breeding in carnivores. Behav. Ecol. Sociobiol. 28: 263-270.

Curry, R. L., and Grant, P. R. 1990. Galapagos mockingbirds: territorial cooperative breeding in a climatically variable environment. *In*: Cooperative breeding birds: long-term studies of ecology and behavior. *Edited by* P. B. Stacey and W. D. Koenig. Cambridge University Press, Cambridge. pp. 289-331.

Davis, L. S. 1984a. Behavioural interactions of Richardson's ground squirrels: asymmetries based on kinship. *In*: The biology of ground-dwelling squirrels. *Edited by* J. O. Murie and G. R. Michener. University of Nebraska Press, Lincoln and London. pp. 424-444.

Davis, L. S. 1984b. Kin selection and adult female Richardson's ground squirrels: a test. Can. J. Zool. 62: 2344-2348.

DeLong, K. T. 1978. The effect of manipulation of social structure on reproduction in house mice. Ecology. 59: 922-933.

Dial, K. P. 1988. Three sympatric species of *Neotoma*: dietary specialization and coexistence. Oecologia. 76: 531-537.

Dickman, C. R. 1988. Sex-ratio variation in response to interspecific competition. Amer. Nat. 132: 289-297.

Dittus, W. P. J. 1977. The social regulation of population density and age-sex distribution in the toque monkey. Behaviour. 63: 281-322.

Dobson, F. S., and Kjelgaard. 1985. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63: 2105-2109.

Dublin, H. T. 1983. Cooperation and reproductive competition among female African elephants. *In*: Social behavior of female vertebrates. *Edited by* S. K. Wasser. Academic Press, New York. pp. 291-313.

Dunbar, R. I. M. 1988. Primate social systems. Cornell University Press, New York.

Ebert, T. A. 1980. Estimating parameters in a flexible growth equation, the Richards function. Can. J. Fish. Aquat. Sci. 37: 687-692.

Egoscue, H. J. 1962. The bushy-tailed woodrat: a laboratory colony. J. Mamm. 43: 328-337.

Eisenberg, J. F. 1981. The mammalian radiations. An analysis of trends in evolution, adaptation, and behavior. University of Chicago Press, Chicago.

Emlen, S. T. 1991. Cooperative breeding. *In*: Behavioural ecology. An evolutionary approach. 3rd ed. *Edited by* J. R. Krebs, and N. B. Davies. Blackwell Scientific Publications, Oxfor' pp. 301-337.

Emlen, S. T., and Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. Science. 197: 215-223.

Environment Canada. 1983. Canadian Climate Normals. Temperature and precipitation 1951-1980. Prairie provinces. Environment Canada Atmospheric Service. Ottawa.

Escherich, P. C. 1981. The social biology of the bushy-tailed woodrat, *Neotoma cinerea*. Univ. Calif. Publ. Zool. 110: 1-132.

Ferkin, M. H. 1988. The effect of familiarity on social interactions in meadow voles, *Microtus pennsylvanicus*: a laboratory and field study. Anim. Behav. 36: 1816-1822.

Festa-Bianchet, M., and King, W. J. 1984. Behavior and dispersal of yearling Columbian ground squirrels. Can. J. Zool. 62: 161-167.

Finley, R. B. 1958. The wood rats of Colorado: distribution and ecology. Univ. Kan. Publ. Mus. Nat. Hist. 10: 213-552.

Fitch, H. S., and D. C. Rainey. 1956. Ecological observations on the wood rat, *Neotoma floridana*. Univ. Kan. Publ. Mus. Natl. Hist. 8: 499-533.

Fleming, A. S. 1979. Maternal nest defense in the desert woodrat *Neotoma lepida lepida*. Behav. Neur. Biol. 26: 41-63.

Galindo, C., and Krebs, C. J. 1987. Population regulation in deer mice: the role of females. J. Anim. Ecol. 56: 11-23.

Gibson, A. R., Baker, A. J., and Moeed, A. 1984. Morphometric variation in introduced populations of the common myna (*Acridotheris tristis*): Principal component analysis. Syst. Zool. 33: 408-421.

Gilbert, B. S., Krebs, C. J., Talarico, D., and Chichowski, D. B. 1986. Do *Clethrionomys rutilus* females suppress maturation of juvenile females? J. Anim. Ecol. 55: 543-552.

Gipps, J. H. W., Flynn, M. P., Gurnell, J., and Healing, T. D. 1985. The spring decline in populations of the bank vole, *Clethrionomys glareolus*, and the role of female density. J. Anim. Ecol. 54: 351-358.

Gittleman, J. L. 1989. Carnivore group living: comparative trends. *In*: Carnivore behavior, ecology, and evolution. *Edited by* J. L. Gittleman. Cornell University Press, New York. pp. 183-207.

Goertz, J. W. 1970. An ecological study of *Neotoma floridana* in Oklahoma. J. Mamm. 51: 94-104.

Gomendio, M., Clutton-Brock, T. H., Albon, S. D., Guinness, F. E., and Simpson, M. J. 1990. Mammalian sex ratios and variation in costs of rearing sons and daughters. Nature. 343: 261-263.

Gosling, L. M. 1986. The evolution of the mating strategies in male antelopes. *In*: Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton. pp. 244-281.

Goundie, T. R., and Vessey, S. H. 1996. Survival and dispersal of young white-footed mice born in nest boxes. J. Mamm. 67: 53-60.

Gross, M. R., and Sargent, R. C. 1985. The evolution of male and female parental care in fishes. Amer. Zool. 25: 807-822.

Haigh, G. R. 1987. Reproductive inhibition of female *Peromyscus leucopus*: female competition and behavioral regulation. Amer. Zool. 27: 867-878.

Hall, E. R. 1981. The mammals of North America. 2nd ed. Wiley Press, New York.

Halpin, Z. T. 1981. Adult-young interactions in island and mainland populations of the dearmouse *Peromyscus maniculatus*. Oecologia. 51: 419-425.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I. and II. J. Theor. Biol. 7: 1-52.

Hannon, S. J., Mumme, R. L., Koenig, W. D., and Pitelka, F. A. 1985. Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. Behav. Ecol. Sociobiol. 17: 303-312.

Harris, M. A., and Murie, J. O. 1984. Inheritance of nest sites in female Columbian ground squirrels. Behav. Ecol. Sociobiol. 15: 97-102.

Harvey, P. H., Stenning, M. J., and Campbell, B. 1988. Factors influencing reproductive success in the pied flycatcher. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 189-200.

Hausfater, G., and Hrdy, S. B (Eds). 1984. Infanticide: Comparative and evolutionary perspectives. Aldine Press, Chicago.

Hickling, G. J. 1987. Seasonal reproduction and group dynamics of bushy-tailed woodrats, *Neotoma cinerea*. Ph.D. thesis, University of Western Ontario, London, Ontario.

Hickling, G. J., Millar, J. S., and Moses. R. A. 1991. Reproduction and nutrient reserves of bushy-tailed woodrats (*Neotoma cinerea*). Can. J. Zool. 69: 3088-3092.

Holekamp, K. E. 1984. Dispersal in ground-dwelling squirrels. *In*: The biology of ground-dwelling squirrels. *Edited by* J. O. Murie and G. R. Michener. University of Nebraska Press, Lincoln and London. pp. 295-320.

Honacki, J. H., Kinman, K. E., and Koeppl, J. W. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Kansas.

Hoogland, J. L. 1981a. Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *In*: Natural selection and social behaviour. *Edited by* R. D. Alexander., W. D. Tinkle. Chiron Press, New York. pp. 283-310.

Hoogland, J. L. 1981b. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucerus* and *Cynomys ludovicianus*). Ecology. 62: 252-272.

Hoogland, J. L. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. Science. 230: 1037-1040.

Hoogland, J. L. 1986. Nepotism in prairie dogs (*Cynomys ludovicianus*) varies with competition but not with kinship. Anim. Behav. 34: 263-270.

Howard, R. D. 1988. Reproductive success in two species of anurans. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 99-117.

Hrdy, S. B. 1981. The Woman that never evolved. Harvard University Press. Cambridge.

Hrdy, S. B., and Williams, G. C. 1983. Behavioral biology and the double standard. *In*: Social behavior of female vertebrates. *Edited by* S. K. Wasser. Academic Press, New York. pp. 3-17.

Ims, R. A. 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. Ecology. 70: 607-616.

Jones, W. T. 1984. Natal philopatry in banner-tailed kangaroo rats. Behav. Ecol. Sociobiol. 15: 151-155.

Jones, W. T. 1986. Survivorship in philopatric and dispersing kangaroo rats (*Dipodomys spectabilis*). Ecology. 67: 202-207.

Justice, K. E., and Smith, F. A. 1992. dietary fiber utilization by small mammalian herbivores: a model and test with three species of woodrat (*Neotoma*). Am. Nat. 139: 398-416.

Kawata, M. 1987. The effect of kinship on spacing among female red-backed voles, *Clethrionomys rufocanus bedfordiae*. Oecologia. 72: 115-122.

Kawata, M. 1990. Fluctuating populations and kin interactions in mammals. Trends in Ecology and Evolution. 5: 17-20.

Keith, L. B., and Windberg, L. A. 1978. A demographic analysis of the snowshoe hare cycle. Wildl. Monogr. 58.

Kelly, P. A. 1989. Population ecology and social organization of dusky-footed woodrats, *Neotoma fuscipes*. Ph.D. thesis, University of California, Berkeley.

King, J. A. 1973. The ecology of aggressive behaviour. Ann. Rev. Ecol. Syst. 4: 117-138.

Kinsey, K. P. 1976. Social behavior in confined populations of the Allegheny woodrat, *Neotoma floridana magister*. Anim. Behav. 24: 181-187.

Kinsey, K. P. 1977. Agonistic behavior and social organization in a reproductive population of Allegheny woodrats, *Neotoma floridana magister*. J. Mamm. 58: 417-419.

Krebs, C. J. 1985. Do changes in spacing behaviour drive population cycles in small mammals? *In*: Behavioural ecology. Ecological consequences of adaptive behaviour. *Edited by* Sibly, R. M., and Smith, R. H. Blackwell Scientific Publications, Oxford. pp. 295-312.

Krebs, C. J., Redfield, J. A., and Taitt, M. J. 1978. A pulsed-removal experiment on the vole *Microtus townsendii*. Can. J. Zool. 56: 2253-2262.

Labov, J. B., Huck, U. W., Vaswani, P., and Lisk, R. D. 1986. Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters (*Mesocricetus auratus*). Behav. Ecol. Sociol. 18: 241-249.

Lambin, X., and Krebs, C. J. 1991a. Spatial organization and mating system of *Microtus townsendii*. Behav. Ecol. Sociobiol. 28: 353-363.

Lambin, X., and Krebs, C. J. 1991b. Can changes in female relatedness influence microtine population dynamics? Oikos. 61: 126-132.

Le Boeuf, B. J., and Reiter, J. 1988. Lifetime reproductive success in northern elephant seals. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 344-362.

Linsdale, J. M., and Tevis, L. P. 1951. The dusky-footed woodrat. University of California Press, Berkeley.

Lusk, S. J. G., and Millar, J. S. 1989. Reproductive inhibition in a short-season population of *Peromyscus maniculatus*. J. Anim. Ecol. 58: 329-341.

Madison, D. M., Fitzgerald, R. W., and McShea, W. J. 1984. Dynamics of social nesting in overwintering meadow voles (*Microtus pennsylvanicus*): possible consequences for population cycling. Behav. Ecol. Sociobiol. 15: 9-17.

Mares, M. A., and Lacher, M. R. 1986. Ecological, morphological and behavioral convergence in rock-dwelling mammals. *In*: Current Mammalogy. Volume 1. *Edited by* H. H. Genoways. Plenum Press, New York. pp. 307-348.

Martin, R. J. 1973. Growth curves for bushy-tailed woodrats based on animals raised in the wild. J. Mamm. 54: 517-518.

McClure, P. A. 1981. Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*). Science. 211: 1058-1060.

McQuaig, J. M., and Green, R. H. 1983. Unionid growth curves derived from annual rings: a baseline model for Long Point Bay, Lake Erie. Can. J. Fish. Aquat. Sci. 40: 436-442.

McShea, W. J., and Madison, D. M. 1984. Communal nesting between reproductively active females in a spring population of *Microtus pennsylvanicus*. Can. J. Zool. 62: 344-346.

Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. *In*: Advances in the study of mammalian behavior. *Edited by* J. F. Eisenberg and D. G. Kleiman. Amer. Soc. Mamm. Spec. Publ. No. 7. pp. 528-572.

Michener, G. R. 1989. Reproductive effort during gestation and lactation by Richardson's ground squirrels. Oecologia. 78: 77-86.

Millar, J. S., Innes, D. G. L., and Loewen, V. A. 1985. Habitat use by non-hibernating small mammals in the Kananaskis Valley, Alberta. Can. Field-Nat. 99: 196-204.

Moehlman, P. D. 1989. Intraspecific variation in canid social systems. *In*: Carnivore behavior, ecology, and evolution. *Edited by* J. L. Gittleman. Cornell University Press, New York. pp. 143-163.

Montgomery, W. I. 1981. A removal experiment with sympatric populations of *Apodemus sylvaticus* (L.) and *A. flavicollis* (Melchior) (Rodentia: Muridae). Oecologia. 51: 123-132.

Mori, U. 1979. Reproductive behaviour. *In*: Ecological and sociological studies of gelada baboons. *Edited by* M. Kawai. Karger, Basel. pp. 183-197.

Murie, J. O., and Boag, D. A. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. J. Mamm. 65: 688-690.

Murie, J. O., and Dobson, F. S. 1987. The costs of reproduction in female columbian ground squirrels. Oecologia. 73: 1-6.

Murie, J. O., Boag, D. A., and Kivett, K. 1980. Litter size in Columbian ground squirrels. J. Mamm. 61: 237-244.

Myers, P., and Master, L. L. 1983. Reproduction by *Peromyscus maniculatus*: size and compromise. J. Mamm. 64: 1-18.

Newton, M. A. 1990. The ecology, behavior and evolutionary dynamics of the white-throated woodrat (*Neotoma albigula*). Ph.D. Thesis, Arizona State University, Arizona.

Ogilvie, R. T. 1969. The mountain forest and alpine forest zones of Alberta. *In*: Vegetation, soils and wildlife. *Edited by* J. C. Nelson and M. J. Chambers. Methuen Press, Toronto. pp. 24-44.

Ollason, J. C., and Dunnet, G. M. 1988. Variation in breeding success in fulmars. *In* Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 263-278.

Ostfeld, R. S. 1985. Experimental analysis of aggression and spacing behaviour in

California voles. Can. J. Zool. 63: 2277-2282.

Ostfeld, R. S., Pugh, S. R., Seamon, J. O., and Tamarin, R. H. 1988. Space use and reproductive success in a population of meadow voles. J. Anim. Ecol. 57: 385-394.

Packer, C. 1986. The Ecology of sociality in felids. *In*: Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton. pp. 429-451.

Packer, C., Herbst, L., Pusey, A., Bygott, J. D., Manby, J. P., Cairns, S. J., and Borgerhoff Mulder, M. 1988. *In*: Reproductive success. *Edited by* T. H. Clutton-Brock. University of Chicago Press, Chicago. pp. 363-383.

Porter, J. H., and Dueser, R. D. 1986. A test for suppression of body growth and sexual maturity in small male meadow voles (*Microtus pennsylvanicus*) in field enclosures. Amer. Midl. Nat. 115: 181-190.

Price, K., Broughton, K., Boutin, S., and Sinclair, A. R. E. 1986. Territory size and ownership in red squirrels: response to removal. Can. J. Zool. 64: 1144-1147.

Pulliam, H. R., and Caraco, T. 1984. Living in groups: is there an optimal group size? *In*: Behavioural Ecology. An evolutionary approach. 2nd ed. *Edited by* J. R. Krebs, and N. B. Davies. Sinauer Associates Inc., Sunderland, Mass.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. Am. Nat. 111: 917-938.

Raun, G. G. 1966. A population of woodrats (*Neotoma micropus*) in southern Texas. Tex. Mem. Mus. Bull. 11: 1-62.

Redfield, J. A., Taitt, M. J., and Krebs, C. J. 1978. Experimental alteration of sex ratios in populations of *Microtus townsendii*, a field vole. Can. J. Zool. 56: 17-27.

Reeve, H. K., and Sherman, P. W. 1990. Intracolonial aggression and nepotism by the breeding female naked mole-rat. *In*: The biology of the naked mole-rat. *Edited by* P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander. Princeton University Press, Princeton. pp. 337-357.

Reiter, J., Panken, K. J., and LeBoeuf, B. J. 1981. Female competition and reproductive success in northern elephant seals. Anim. Behav. 29: 670-687.

Ribble, D. O. 1992. Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. J. Anim. Ecol. in press.

Rodd, H. F., and Boonstra, R. 1988. Effects of adult meadow voles, *Microtus pennsylvanicus*, on young conspecifics in field populations. J. Anim. Ecol. 57: 755-770.

Rood. J. P. 1986. Ecology and evolution in the mongooses. *In*: Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton. pp. 131-152.

Rood. J. P. 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. Anim. Behav. 39: 566-572.

Rowe, J. S. 1972. Forest Regions of Canada. Department of Fisheries and the Environment. Can. Forest. Serv. Publ. 1300.

Rubenstein, D. I. 1986. Ecology and sociality in horses and zebras. *In*: Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton. pp. 282-302.

Rubenstein, D. I., and Wrangham, R. W. 1980. Why is altruism toward kin so rare? Zeit. fur Tierpsychol. 54: 381-387.

Rubenstein, D. I., and Wrangham, R. W. 1986. Socioecology: origins and trends. *In*: Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W.

Wrangham. Princeton University Press, Princeton. pp. 3-17.

Saitoh, T. 1981. Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. J. Anim. Ecol. 50: 79-87.

SAS Institute Inc. 1990. SAS user's guide. Version 6 Edition. SAS Institute Inc., Carey, North Carolina.

Sauer, J. R., and Slade, N. R. 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? Ecology. 68: 642-650.

Seger, J. 1991. Cooperation and conflict in social insects. *In*: Behavioural ecology. An evolutionary approach. 3rd ed. *Edited by* J. R. Krebs, and N. B. Davies. Blackwell Scientific Publications, Oxford. pp. 338-373.

Sherman, P. W. 1980. The limits of ground squirrel nepotism. *In*: Sociobiology: beyond nature/nurture? *Edited by* G. W. Barlow and J. Silverberg. Westview Press, Boulder. pp. 505-544.

Sherman, P. W. 1981. Kinship, demography, and Belding's ground squirrel nepotism. Behav. Ecol. Sociol. 8: 251-259.

Sherman, P. W., and Morton, M. M. 1984. Demography of Belding's ground squirrels. Ecology. 65: 1617-1628.

Sheridan, M., and Tamarin, R. H. 1988. Space use, longevity, and reproductive success in meadow voles. Behav. Ecol. Sociobiol. 22: 85-90.

Silk, J. B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. Amer. Nat. 121: 56-66.

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

Smith, A. T. 1988. Patterns of pika (Genus *Ochotona*) life history variation. *In*: Evolution of life histories of mammals. *Edited by* M. S. Boyce. Yale University

Press, New Haven.

Smith, A. T., and Ivins, B. L. 1983. Colonization in a pika population: dispersal vs philopatry. Behav. Ecol. Sociol. 13: 37-47.

Smith, J. N. M. 1990. Summary. *In*: Cooperative breeding in birds: long-term studies of ecology and behavior. *Edited by* P. B. Stacey, and W. D. Koenig. Cambridge University Press, Cambridge. pp. 593-611.

Smith, R. H., and Sibly, R. 1985. Behavioural ecology and population dynamics: towards a synthesis. *In*: Behavioural ecology. Ecological consequences of adaptive behaviour. *Edited by* Sibly, R. M., and Smith, R. H. Blackwell Scientific Publications, Oxford. pp. 577-591.

Snyder, R. L., and Christian, J. J. 1960. Reproductive cycle and litter size of the woodchuck. Ecology. 41: 647-656.

Sokal, R. R., and Rohlf, F. J. 1981. Biometry. W. H. Freeman and Company, New York.

Solomon, N. G. 1991. Current indirect fitness benefits associated with philopatry in juvenile prairie voles. Behav. Ecol. Sociobiol. 29: 277-282.

Stockrahm, D. M. B., and Seabloom, R. W. 1988. Comparative reproductive performance of black-tailed prairie dog populations in North Dakota. J. Mamm. 69: 160-164.

Tamarin, R. H., Sheridan, M., and Levy, C. K. 1983. Determining matrilineal kinship in natural populations of rodents using radionuclides. Can. J. Zool. 61: 271-274.

Tamarin, R. H., Ostfeld, R. S., Pugh, S. R., and Bujalska, G. 1990. (Eds). Social systems and population cycles in voles. Birkhäuser Verlag, Basel.

Trivers, R. L. 1972. Parental investment and sexual selection. *In*: Sexual selection and the descent of man. *Edited by* B. Campbell. Aldine Press, Chicago. pp. 136-179.

Trivers, R. L. 1974. Parent-offspring conflict. Amer. Zool. 11: 249-264.

Trivers, R. L., and Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science. 179: 90-92.

Vandenbergh, J. G. 1987. Regulation of puberty and its consequences on population dynamics of mice. Amer. Zool. 27: 891-898.

Vaughan, T. A., and Czaplewski. 1985. Reproduction in Stephen's woodrat: the wages of folivory. J. Mamm. 66: 429-443.

Vehrencamp, S. L. 1979. The roles of individual, kin, and group selection in the evolution of sociality. *In*: Handbook of behavioral neurobiology. Vol. 3. *Edited by* P. Marler and G. H. Vandenbergh. Plenum Press, New York. pp. 351-394.

Wallen, K. 1982. Social organization in the dusky-footed woodrat (*Neotoma fuscipes*): a field and laboratory study. Anim. Behav. 30: 1171-1182.

Waser, P. M. 1988. Resources, philopatry, and social interactions among mammals. *In*: The ecology of social behavior. *Edited by* C. N. Slobodchikoff. Academic Press, San Diego. pp. 109-130.

Waser, P. M., and Jones, W. T. 1983. Natal philopatry among solitary mammals. Quart. Rev. Biol 58: 355-390.

Wasser, S. K. 1983. Reproductive competition and cooperation among female yellow baboons. *In*: Social behavior of female vertebrates. *Edited by* S. K. Wasser. Academic Press, New York. pp. 349-390.

Wasser, S. K., and Barash, D. P. 1983. Reproductive suppression among female mammals: Implications for biomedical and sexual selection theory. Q. Rev. Biol. 58: 513-538.

Wauters, L., and Dhondt, A. A. 1989. Body weight, longevity and reproductive success in red squirrels (*Sciurus valgaris*). J. Anim. Ecol. 58: 637-651.

Williams, B. K., and Titus, K. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. Ecology. 69: 1275-1285.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton.

Wilson, E. O. 1975. Sociobiology. Harvard University Press, Boston.

Wittenberger, J. F. 1981. Animal social behavior. Duxbury Press, Boston.

Wolff, J. O. 1989. Social Behavior. *In*: Advances in the study of *Peromyscus* (Rodentia). *Edited by* G. L. Kirkland and J. N. Layne. Texas Tech University Press, Texas. pp. 271-291.

Wrangham, R. W., and Rubenstein, D. I. 1986. Social evolution in birds and mammals. *In*: Ecological aspects of social evolution. *Edited by* D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton. pp. 452-470.

Ylönen, H. 1990. Phenotypic flexibility in the social organization of *Clethrionomys*. *In*: Social systems and population cycles in voles. *Edited by* R. H. Tamarin, R. S. Ostfeld, S. R. Pugh, and G. Bujalska. 1990. Birkhäuser Verlag, Basel. pp. 203-212.

Ylönen, H., Mappes, T., and Viitala, J. 1990. Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*. Oecologia. 83: 333-337.

Zar, J. H. 1984. Biostatistical Analysis. 2nd Ed. Prentice-Hall Inc., New Jersey.

Zullinger, E. M., Ricklefs, R. E., Redford, K. H., and Mace, G. M. 1984. Fitting sigmoidal equations to mammalian growth curves. J. Mamm. 65: 607-636.

APPENDIX 1. Estimation of Age in Juveniles

In order to investigate patterns of growth and initiation of reproduction, I needed to estimate dates of birth for all juveniles born to resident females. I estimated dates of birth (parturition) in two ways. Some females were removed from the field (i.e., for removal experiment) when pregnant, and subsequently gave birth in captivity. Those that were captured in mid-pregnancy (see Chapter 2) gave birth, on average, 10 days after capture (mean=9.6, range=8-13, N=7), while those captured in late pregnancy (see Chapter 2) gave birth, on average, 2 days after capture (mean=1.8, range=1-5, N=12). Hence, I estimated the parturition dates for field-born litters by adding 10 days or 2 days to the date of capture for juveniles associated with mothers caught in mid-pregnancy or late pregnancy, respectively. Dates of parturition for 115 of 188 litters (258 of 424 juveniles, [61%]) were estimated in this way.

To estimate birthdates of the remaining 165 juveniles (i.e., associated with mothers caught in early pregnancy or post parturition), I generated a regression model to predict age from weight at first capture. Because male bushy-tailed woodrats exhibit faster post-weaning growth than females (Egoscue 1962; Martin 1973; Hickling 1987), I developed separate models for each sex. I assumed that the birthdates estimated by the first method outlined above were reliable enough to consider the 258 juveniles as "known age". I used the weights and dates of all captures for these juveniles to generate predictive models, and to test their adequacy by calculating the mean (absolute) difference between known age, and the age predicted by the models. I developed and tested 2 models for each sex; a non-linear, asymptotic regression of weight on age, and a linear regression of age on weight.

Mammalian growth may be described by various asymptotic growth curves that differ in their point of inflection, or the age at which the rate of growth is maximal (Zullinger et al. 1984). To determine which asymptotic growth curve was most appropriate, I tested the fit of data from the known-aged juveniles using Walford plots (i.e., regressions of weight at time [T+1] on weight at time [T]) corresponding to monomolecular, Gompertz, and logistic growth curves (Ebert 1980).

All time intervals between time T and time T+1 must be equal in Walford plots (Ebert 1980). As intervals between trap sessions varied, I only included measures of weight that were recorded at least 17, but no more that 25, days apart. Following Hickling (1987), I standardized all remaining intervals to 21 days, assuming that growth was linear within any interval. I insured independence of data points for the Walford plots by randomly picking only 1 interval (2 weight measures) for any known-aged juvenile that was captured more than 2 times in its' year of birth.

The coefficient of determination was highest for both sexes (females: $r^2=0.86$, $N=75$; males: $r^2=0.78$, $N=66$) for the untransformed regression of weight at time [T+21] days on weight at time [T] days, indicating that the data were best described by monomolecular, or Von Bertalanffy's, growth (Ebert 1980; McCuaig and Green 1983).

The general equation for the linear form of a monomolecular growth curve is:

$$\log(1 - Y \div K) = a - bX \qquad \text{(eqn. 1)}$$

where: Y = weight (g)

X = age (days)

a = weight at X=0 (birth)

b = growth rate

K = asymptotic weight,

and K can be estimated from the parameters (intercept, a_w, and slope, b_w) of the Walford plot as: $a_w \div (1 - b_w)$. I regressed log (1 - weight÷K) on age (where K=345 [females], 450 [males]) for all data collected for the known-aged juveniles during their year of birth. Estimates of K from the Walford plots extended beyond the range of most of the weight data, and hence may have been unstable parameter estimates. The final predictive monomolecular models were developed by varying K, in increments of 5, from 300 to 400 for females, and from 400 to 500 for males, such that r^2 was maximized, and realistic estimates of weight at birth were generated. The final model for females was:

$$\log(1 - \text{weight} \div 345) = -0.057 - 0.011(\text{age}),$$
$$(r^2 = 0.82,\ p = 0.0001).$$

The final model describing growth in juvenile males was:

$$\log(1 - \text{weight} \div 450) = -0.045 - 0.009(\text{age}),$$
$$(r^2 = 0.84,\ p = 0.0001).$$

I regressed age on weight-50 (minimum weight at first capture of unknown-aged juveniles was 50g) for known-aged juveniles to generate predictive linear models. Examination of residual variation did not reveal any obvious heteroscedasticity, and log-transforming the variables did not increase the coefficient of determination. Simple linear regression models of age on weight described the relationship between age and weught of the known-aged juveniles for both sexes as well as the non-linear models did. The linear model for juvenile females was:

$$\text{age} = 7.71 + 0.417(\text{weight-50}),$$
$$(r^2=0.83,\ p=0.0001),$$

and for juvenile males:

$$\text{age} = 9.21 + 0.336(\text{weight-50})$$
$$(r^2=0.85,\ p=0.0001).$$

Ages predicted by the two models were simply calculated by solving for X in the non-linear models, and Y in the linear models. The two models were then evaluated by examining the mean deviation of predicted age from the known age. The linear models predicted ages, on average, more accurately than did the non-linear models (Table I), and were therefore used to predict ages of all juveniles of unknown age from their weight at first capture. If estimated birth dates of littermates differed, the parturition date of that litter was calculated as the mean of their estimated birthdates.

Analysis of growth in juveniles revealed differences in post-weaning growth rates in juvenile females with respect to age of mother and removal class (see Chapter 3, section 3.2.3). These differences could cause bias in the general (mother age and removal classes pooled) predictive age on weight model. Hence, I developed separate predictive models for juvenile females from each mother age/removal class, and tested their accuracy as I did for the general model. However, none of these models predicted age more accurately than the general model, and I retained the use of the general model to predict ages of all juvenile females.

Table I. Non-linear and linear regression for predicting age from weight of known-aged juveniles. Non-linear regression is monomolecular growth equation of weight regressed on age. Linear model is age regressed on weight. *N* is the number of all captures for known-aged juveniles. Accuracy of models measured as the mean absolute value of (predicted age - known age).

				| Predicted age - Known age |	
	r^2	*N*	*p*	Mean ±SE	Range
FEMALES					
Non-linear	0.82	320	0.0001	7.4 ± 0.32	0.01 - 25.0
Linear	0.83	320	0.0001	6.9 ± 0.28	0.00 - 19.1
MALES					
Non-linear	0.84	245	0.0001	7.6 ± 0.34	0.03 - 22.8
Linear	0.85	252	0.0001	6.4 ± 0.31	0.05 - 19.2

APPENDIX 2. Description of behaviour of bushy-tailed woodrats recorded during dyadic trials in a neutral arena

Behaviour	Description
Allogroom	One animal grooms another
Avoid	One animal maintains > one body length, and is oriented away from the other
Box	Both animals wrestling with forelimbs while standing on hindlimbs
Face	One animal maintains orientation toward the other
Fight	Both animals tumbling, often with biting and/or kicking
Flee	One animal runs/leaps away from the other
Follow	One animal follows closely behind other
Foot Drum	Rapid drumming of hindlimb
Groom	One animal grooms itself
Huddle	Both animals at rest, in contact, usually side by side
Investigate	Walking/climbing around arena, not oriented toward other animal
Lunge	One animal runs/leaps toward the other and usually strikes hard with forelimbs
Move Away	One animal walks away from the other
Move Toward	One animal walks toward the other
Nose-Abdomen	One animal extends nose toward, and establishes contact with flank/abdomen of other
Nose-Genital	One animal extends nose toward, and sniffs and/or establishes contact with genital/anal region of other
Nose-Neck	One animal extends nose toward, and establishes contact with, neck region of other
Nose-Nose	Close approach and/or contact nose to nose
Stand	One animal standing on hindlimbs, not in contact with other
Tooth Chatter	Rapid chewing with audible tooth contact
Vocalize	Any vocalization made by one animal