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MOVEMENTS, SURVIVAL, AND SETTLEMENT OF RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) OFFSPRING[1]

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Abstract. Movement and settlement patterns of animal offspring, along with the costs of occupying familiar and unfamiliar habitats, have been inferred frequently, but rarely have they been documented directly. To obtain such information, we monitored the individual fates of 205 (94%) of the 219 offspring born over 3 yr in a population of the North American red squirrel (*Tamiasciurus hudsonicus*), at Fort Assiniboine, Alberta, Canada (54.20° N, 114.45° W). We located neonates by radio-tracking mother squirrels, and thereafter we documented the movements, survival, and settlement patterns of the offspring, using a combination of telemetry, live-trapping, and visual observations. Prior to settlement, offspring made forays of up to 900 m ($\bar{X}$ = 126 m) off the natal territory, but they did not abandon the natal territory until they had settled on their own territory. Foray distance was not related to the age or size of the offspring. We used the locations of offspring kills to show that the risk of predation significantly increased when the offspring were travelling off of their natal territories. Just under half of the 73 offspring that acquired territories did so on or immediately adjacent to their mother's; the farthest settlement distance was only 323 m from the natal territory, or about the distance of three territory widths. Movement data from adults in the population showed that all offspring settled within potential contact of their mother (and possibly their father). Offspring that settled relatively farther away from their natal territory were more likely to obtain larger territories, with traditional hoarding and overwintering sites (middens). These offspring also had higher overwinter survival, suggesting that the costs of making forays off the natal territory may be balanced by the advantages of locating a superior territory.

Key words: dispersal; exploration; mortality; philopatry; predation; Rodentia; Sciuridae; settlement; survival; Tamiasciurus; *telemetry; territory acquisition success.*

INTRODUCTION

All offspring must find a place to settle after becoming independent from their parents. Individuals have two options; remain where they were born (philopatry) or leave in an attempt to settle elsewhere (emigration). The choice made by an individual should depend on the costs and benefits of remaining philopatric vs. emigrating. Although researchers have identified a number of these costs and benefits, few have been measured directly (Johnson and Gaines 1990). Instead, inferences have been made by examining general patterns of settlement (Gaines and McClenaghan 1980, Waser and Jones 1983, Johnson and Gaines 1990). For example, in mammals, many offspring disappear near the time of weaning, whereas relatively few immigrate into established populations (reviewed by Anderson 1989). This had led to the conclusion that emigrants suffer higher mortality than those who remain philopatric with the result that most offspring settle close to where they were born. However, this may be incorrect because (1) many offspring that disappear may have died before emigrating, making survival of emigrants and non-emigrants more equal and (2) long-distance dispersal may be missed because emigrants move beyond the study area. To determine if this is the case requires that the settlement location and fates of all offspring in the population be known.

Another approach has been to compare observed settlement patterns with those produced by models based on competition for vacant home ranges (Waser 1985, Stamps and Krishnan 1990). Deviations from the simple competition model could provide clues to other factors that affect settlement patterns. However, one potential problem with many dispersal models is that emigration is modelled as a process whereby offspring leave their natal home range and never return. They either find a vacant spot or die. The actual pattern of movement employed by a juvenile during the period of settlement may be more complex and could be important in generating the pattern of settlement we would expect to see.

Detailed information on the movements and fate of offspring prior to settlement also is required if we are to understand the costs of settling in unfamiliar habitat. Movement through unfamiliar habitat is generally assumed to increase the risks associated with emigration (see reviews by Lidicker 1975, Gaines and McClenaghan 1980, Beaudette and Keppie 1992), and most theoretical models developed to explain the evolution of dispersal require a measure of the cost of dispersal

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(Johnson and Gaines 1990). However, the studies that have been cited as demonstrating these costs are anecdotal (Errington 1946, Carl 1971), have been conducted under laboratory conditions (Metzgar 1967, Ambrose 1972), have measured survival of animals that had already undergone part of the relocation process (Garrett and Franklin 1988), or have measured survival of individuals that have succeeded in settling (Johnson and Gaines 1985, Jones 1986, Krohne and Burgin 1987).

We studied the North American red squirrel (*Tamiasciurus hudsonicus*). In northern coniferous forests red squirrels are highly territorial, with each individual maintaining a separate territory that does not overlap with its neighbors' (Smith 1968). Given these conditions it is easy to determine whether individuals are on or off of their own territory, or if they are in the process of establishing a territory. The objective of our study was to determine the settlement patterns of offspring in this small-mammal population, and their fates. We determined the location of birth, patterns of movement during the settlement period, location of settlement, and the fate of nearly all of the individuals born in our study population over 3 yr. In this paper we examine the patterns found in light of some of the costs and benefits proposed to explain settlement patterns in birds and mammals.

NATURAL HISTORY OF THE POPULATION

This study was conducted in the Athabasca Sand Hills at Fort Assiniboine, Alberta (54.20° N, 114.45° W), from spring 1988 to spring 1991. The dominant habitat in this area is jack pine (*Pinus banksiana*) forest, with occasional, smaller stands of white spruce (*Picea glauca*). Interspersed in this forest are aspen (*Populus*) and birch (*Betula*) parks, and tamarack (*Larix*) and black spruce (*Picea mariana*) bogs. These patches of suboptimal habitat are devoid of resident red squirrels except during natal dispersal, when juveniles may occupy them. Population density was stable throughout the study, and annual adult survivorship ranged from 67 to 71%.

Red squirrels in the jack pine forest maintain individual, non-overlapping territories year-round. Territory boundaries are maintained by advertisement vocalizations (Lair 1990) and boundary patrols. Intrusions occur, but detected intruders quickly are expelled by the territory owner, by aggressive chases and vocalizations (Lair 1990). Mean territory size during the study was 0.65 ha (Larsen 1993). The activity center of each squirrel's territory is conspicuously marked by the presence of a midden (Gurnell 1984, Obbard 1987), where the winter hoard is stored. Midden sites are traditional, and when a territory owner is replaced, the new squirrel continues to utilize the established midden. Occasionally the construction of new middens is initiated, especially by young-of-the-year. To the best of our knowledge, possession of a territory and some form of midden is essential for overwinter survival. Without the resources of a territory and the security of the winter cache on the midden, it is probably impossible for a red squirrel to survive the winter (K. W. Larsen and S. Boutin, *personal observations*).

In central Canada, female red squirrels do not normally breed as yearlings (Wood 1967, Davis 1969, Rusch and Reeder 1978, Becker 1992), and during our study most females were ≥ 2 yr of age before bearing their first litters. Males develop scrotal testes in their first spring (Rusch and Reeder 1978; K. W. Larsen, *personal observation*) but it is not known if they breed. At Fort Assiniboine the ratio of adult males to reproducing females during the spring breeding periods of 1989 and 1990 was $\approx 2.2:1$. Adult females tolerate the presence of one or more males on their territory during the brief 1-d estrus (Lair 1985) that on the population level takes place over a 5-wk or longer period (Becker 1992). Mothers bear and raise their litters within their territories, and offspring have little direct contact with other conspecifics until they leave the mother's territory.

During our study females produced one litter per year, except in very rare cases ($\approx 4\%$ of all mothers) when an entire litter was lost early enough to permit a second successful mating. Data obtained from these late litters were not used in this study. Litter sizes ranged from 1 to 4 during the study. Sex ratio of offspring at birth did not differ significantly from a 1:1 ratio within each year, nor within the pooled sample (heterogeneity chi-square test following Zar 1984, all Ps $> .08$). Similarly, litter size and other measurements of female reproductive success did not differ significantly from year to year (Larsen 1993). Offspring emerged from the nest at ≈ 50 d of age (≈ 95–100 g), but nursing continued for up to an additional 3 wk. When offspring reached ≈ 110–115 g they began travelling off of the natal territory, presumably in search of vacant territory space. These movements continued until the offspring was either killed or was successful in acquiring a territory. This could occur as long as ≥ 60 d after emergence. There was no evidence of sex-biased settlement patterns in the population during the years of this study (Larsen 1993).

METHODS

General methods

A 30-m-interval grid was set up in ≈ 1.25 km^2 of forest. Each spring (25 April–15 May) and fall (23 August–1 September) we live-trapped all middens in the study area, at least once during each day, weather permitting (Larsen 1993). Squirrels trapped for the first time were marked with numbered metal eartags; females were equipped with small, colored tags threaded over the metal eartag, facilitating identification at a distance. Sex, weight, reproductive condition (Price et al. 1986), and behavior upon release were recorded for each trapped animal. Individuals trapped and released on their own territory often vocalize aggressively ("rattle," Lair 1990), whereas trespassers remain silent, or are immediately chased off by the resident squirrel. This information, along with recapture frequency and visual sightings, allowed us to identify each territory owner.

We identified postpartum females by a drop in body mass (≈10% over 1 or 2 d) and/or the presence of elongate nipples and matted fur. Postpartum females were equipped with radio collars and subsequently located in their nests. Offspring were removed temporarily from the nest, and their sex was noted. When possible, we revisited each litter ≈3 wk later, and the offspring were given metal and colored eartags.

We mapped the territories of mother squirrels by recording the locations of territorial vocalizations and other related behavior (Price et al. 1986). At least 15 perimeter observations were collected for mapping purposes. Often, females that had been held in traps for >30 min ran around the perimeter of their territory upon release, which simplified the mapping process.

Movement patterns

When possible, offspring were fitted with radio collars when they attained a body mass of ≥115 g (≈64 d old). Priority was given to those offspring living on or near the periphery of the study area. We searched for collared offspring, using hand-held antennas and receivers, at least once every 3 d, during the hours when the juveniles were most likely to be active (0800–1100, 1330–1700; compare with Wauters et al. 1992). Collared offspring were tracked at least until they obtained a territory, or until they were killed.

Offspring that could not be located at their scheduled time were extensively searched for, for at least three more days. Tower antennas set up on the highest points near the study area and/or in the bed of a truck provided effective monitoring of the area within a 2.25 km radius of the study area. Only 3 out of 90 collared offspring (3.3%) disappeared without us determining their fate. Six offspring temporarily disappeared for >3 d before being relocated in the study area. Locations of collared offspring were often recorded outside of the scheduled times, if the animals were unintentionally observed by anyone working in the study area. When possible, body mass was measured following each observation by live-trapping the collared offspring.

Mortality prior to settlement

We identified where offspring were killed by locating their radio collars and carcass remains. We believed these represented the approximate site of the kills because the remains of most (31/33) radio-collared territory holders killed during the study were found on the animals' respective territories. The main predators of juvenile squirrels in the study area are raptors, based on kill characteristics (K. W. Larsen, *unpublished data*). Goshawks (*Accipiter gentilis*) are probably responsible for most kills, because they are the only raptor species commonly observed in the forest at Fort Assiniboine. Three observations were made of goshawks taking red squirrels, and in each case the goshawk ate the squirrel within 5 m of the site of the kill.

Settlement

We could determine when offspring had acquired a territory because they displayed territorial behaviors (e.g., vocalizations or repelling intruders) and exhibited site fidelity (i.e., were constantly located in the same general area of the forest). Because radio-collared offspring were located and observed at least every 3 d, we were able to use the behavioral information to determine dates of territory acquisition within ±1 d. At the same time, we could determine that offspring were no longer residing on the natal territory by locating them late at night, very early in the morning, or during inclement weather. When possible, we mapped the territories of offspring following the same procedures used for the mothers (see *General methods,* above), but this was only accomplished for 17 out of 73 offspring because radio collars normally were removed from individuals that had acquired a territory. However, even when we failed to collect sufficient data for accurately mapping the territory, we still were able to determine the approximate location of the core of the territory in relationship to the mother's territory.

We classified all settled offspring according to the location of their acquired territories, relative to their mothers'. Class 1 offspring were those acquiring territories on or contiguous with their mother's territory. Class 2 offspring were those settling on territories completely disassociated from the mother's territory. Our reasoning was as follows: territories belonging to Class 1 settlers could be secured without leaving the familiar confines of the mother's territory (at least during the early stages of the territory acquisition), while a Class 2 settler was required to leave its mother's territory, and potentially interact with relatively unfamiliar squirrels along all sides of its chosen territory. Particular attention was paid to offspring that obtained the entire natal territory, along with its midden (see Boutin et al. 1993, Price and Boutin 1993). Unless the mother was outfitted with a radio collar at the time, we used repeated trapping of the study area to determine whether these transfers of ownership were accomplished through death or abdication by the mother.

Class 2 settlement distance was measured as the distance from the natal midden to the midden on the newly acquired territory. If an offspring's territory did not encompass a traditional midden (i.e., a site that had been previously used as a hoarding and overwintering site) then the arithmetic mean of the boundary coordinates was used as the center of the territory. Settlement distances were converted to "territory increments" by dividing the distance by 90 m, the di-

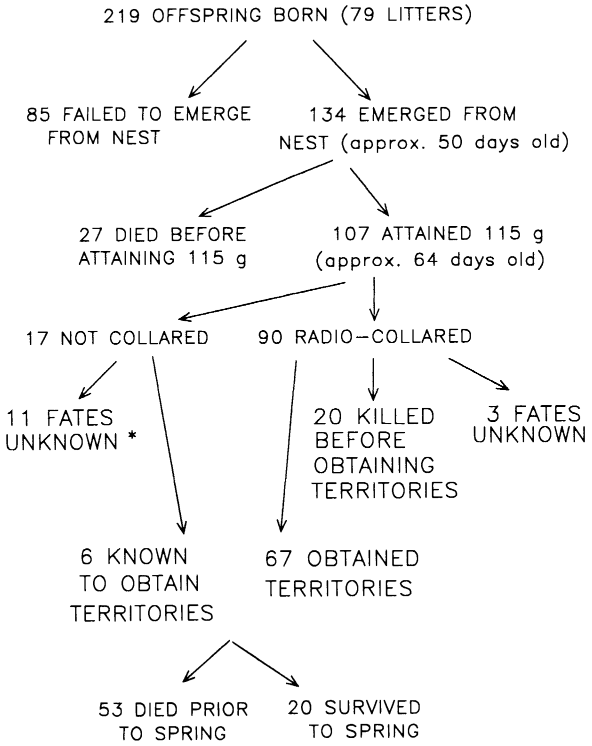

FIG. 1. Summary of results obtained from monitoring the 1988, 1989, and 1990 cohorts of red squirrel offspring, starting at birth, at Fort Assiniboine, Alberta, Canada. Out of 219 offspring, only 14 individuals had undetermined fates. *Eleven of these individuals were not collared, but it is likely that they were all killed prior to autumn (see *Results: Success at monitoring the cohort*).

ameter of a circle the size of the average territory (0.65 ha).

Survival of offspring before and after settlement

We could not calculate survival of offspring with or without territories using conventional methods because offspring acquired territories at different times, thereby eliminating them from the sample of offspring without territories. Therefore we used the methods presented by Heisey and Fuller (1985) to calculate survival based on data collected from radio-collared animals. This method uses total numbers of radio-days obtained per time period, as well as the number of deaths occuring during that time. Using the MICROMORT program (see Heisey and Fuller 1985) we calculated 10-d survival estimates for six time periods. For animals that had not acquired a territory, we calculated survival for 1–10, 11–20, and 21–30 d after collaring (all animals were collared at ≈64 d of age). We also calculated survival for animals that had obtained territories, during the periods 1–10, 11–20, and 21–30 d after territory acquisition. For both samples we were unable to calculate survival past 30 d because of dwindling sample size. MICROMORT survival estimates can be compared by a Z statistic.

Territory characteristics and overwinter survival of settlers

We compared the characteristics of the territories of offspring that survived or died prior to the ensuing spring. Comparisons were made based on settlement distance (from natal to acquired midden), territory area, and whether the acquired territory contained a "traditional" midden. We considered middens to be "traditional" if they had been continuously inhabited by other squirrels for at least the past year. Middens classified as "non-traditional" included those where the territory acquired by the offspring contained no discernible hoarding site. Traditional middens were visibly larger than non-traditional middens, due to the accumulation of cone rachii and bracts from previous territory holders.

Movements of adults

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

RESULTS

Success at monitoring the cohort

We were able to document the fates of 94% (205/219) of the offspring born in our study area (Fig. 1). In total, 219 offspring from 79 litters were monitored during the study. One hundred thirty-four of these offspring emerged from the nest, and 107 reached 115 g body mass (≈64 d of age). We are confident that we were able to monitor survival accurately during these time periods, for several reasons: (1) only two offspring that were not detected during the emergence were observed at a later date, (2) offspring are normally not weaned until 70–80 d of age, and (3) only 8/127 offspring weighing <115 g were observed >75 m from their natal middens.

Of the 107 individuals that reached 115 g, 90 received radio collars, leaving 17 uncollared emergent offspring. Twenty of the radio-collared offspring were killed before they had acquired a territory, providing data on the location of the kill relative to the natal territory. Three of the 90 radio-collared animals disappeared and could not be relocated. Their disappearances could have been due to extremely long-distance movements, transmitter failure, or destruction of the transmitter by a predator. The fates of 11 of the 17 uncollared emergent offspring were also undetermined; it is unlikely that most (or any) of these offspring moved or settled outside of the study area, because settlement in the radio-collared offspring was extremely philopatric (see *Where did offspring settle?,* below) and the natal middens of these uncollared offspring were located, by design, in the center of the study area.

Seventy-three of the offspring (67 collared and 6 uncollared) were followed until they had obtained a territory. Only three of the settled offspring were known to relocate later on in their lives. These three cases consisted of offspring that originally settled on a territory that overlapped their mother's territory, but upon the disappearance of their mother they assumed complete control of their natal territory.

Twenty of the 73 offspring that obtained territories survived to the following spring. During the first winter of the study the survival of offspring was monitored once a month, through a combination of telemetry, visual observation, and live-trapping. Winter mortality occurred at a constant rate. During the second and third winters of the study offspring mortality was not monitored.

What movements were made?

Movements by offspring.—Offspring did not abandon their natal territories until they had located a territory. Instead, they appeared to spend most of their time on the natal midden, making circling forays throughout neighboring areas. Out of 752 observations made of radio-collared offspring, 522 (69%) occurred on the squirrel's natal territory (Fig. 2A). The other observations ranged from just outside the natal territory to 922 m away ($\bar{X}$ = 126.1 m, 75th percentile = 159.8 m). Offspring undertaking the longest observed forays (≥500 m, n = 7) were always found in spruce/tamarack bogs or aspen/birch parkland.

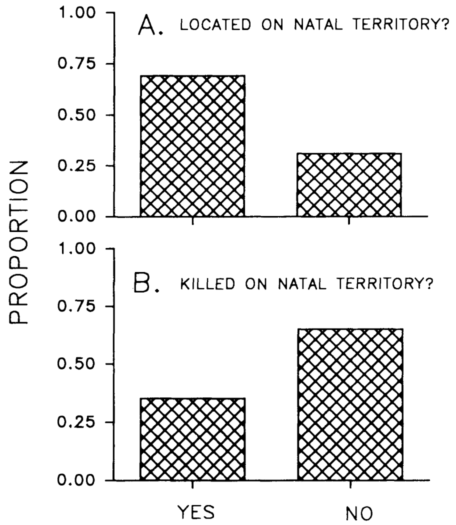

FIG. 2. (A) Total number of observations made on live, radio-collared red squirrel offspring that were not holding territories at the time of sighting. (B) Kill sites of collared offspring that had not yet acquired a territory. Both sets of observations are classified by whether they were made on or off the offsprings' natal territories. Using expected frequencies generated from the data in (A), the proportion of individuals killed off of their natal territories (B) was significantly greater than expected ($P < .005$). $N_A = 752$, $N_B = 20$.

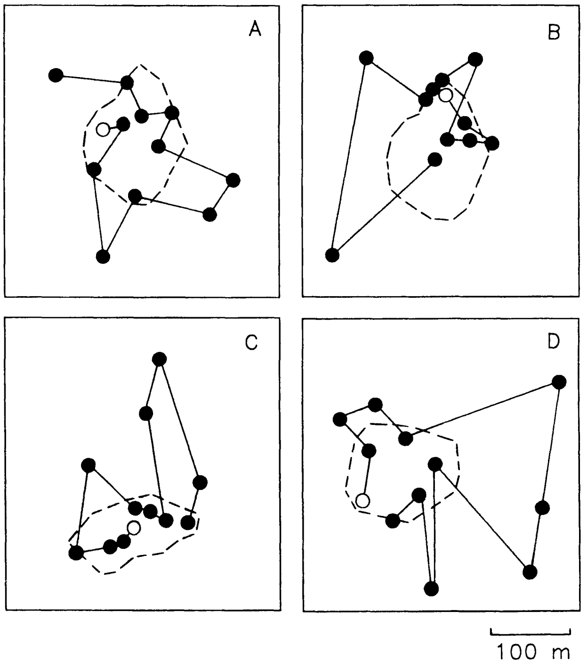

FIG. 3. Samples of the forays made by radio-collared red squirrel offspring. Each individual was located approximately every 45 min during a 9-h period, beginning at 0800. ○ = initial observation, ● = subsequent locations. Boundaries of the natal territories are indicated by – – –. Parts (A) and (B) depict the movements of a male offspring and his female sibling, respectively, that were both monitored on the same day (age 67 d). Parts (C) and (D) represent the movements of a male offspring (age 78 d) and an unrelated female offspring (age 92 d), respectively.

Nine different offspring were intensively followed throughout a 9-h period, and these offspring were observed to move off and on the natal territory (Fig. 3). Offspring located off their natal territory were normally silent, but when they did vocalize they usually were challenged by resident squirrels, which prompted them to relocate.

To test how widespread the foray behavior was in the population, we examined 93 instances (from 63 offspring) where collared offspring were located off their natal midden on one day and then relocated at least once within the next 24 h. In 78 (83%) of these cases the offspring were observed back on their natal territories. Within this sample, older individuals were not more likely to remain off of their natal territory (Fig. 4).

We also tested whether foray distance increased with age by using data obtained from collared offspring that were located repeatedly every 3rd d, for 24 d (8 observations/squirrel). Because all of these animals were

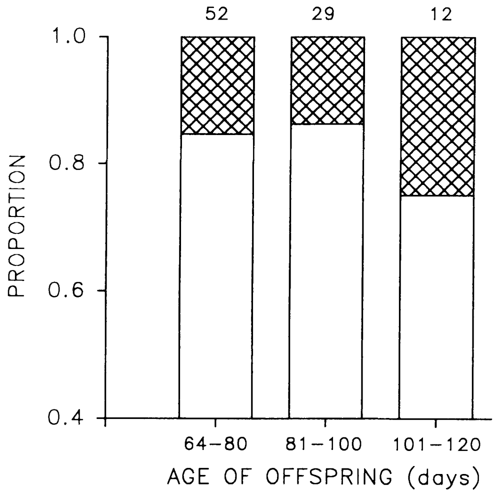

FIG. 4. Relative proportion of times (open bars) that different-aged red squirrel offspring were located back on their natal territory within 24 h after having been observed making a foray off the territory. Shaded bar section indicates proportion of times animals continued to be observed off of natal territory. No significant difference was seen among the three age groups ($G = 0.76$, df $= 2$, $P = .684$). Sample sizes appear above bars.

collared at approximately the same age, we could test whether the maximum distance recorded for each individual during the 24-d period was correlated to its age. There was no suggestion that the maximum distances recorded tended to occur when the offspring were older ($F = 0.27$, df $= 1, 28$, $P = .607$; Fig. 5).

To test if offspring moving relatively longer distances were less likely to return to their natal territories, we examined all cases from the above sample where collared offspring were located >250 m from their natal midden. Within the next 24 h 8/10 of these individuals were observed back on their natal territories. In the other two cases the offspring were killed off of the natal territory.

In general, the distance offspring were observed from their natal middens did not appear strongly related to age or body mass. A multiple regression of distance on body mass and age was significant for the first year of the study (1988: $F = 3.99$, df $= 3, 119$, $P = .009$) but not in the latter two years (1989: $F = 1.74$, df $= 3, 96$, $P = .164$; 1990: $F = 1.09$, df $= 3, 83$, $P = .357$). The percentage of variation in distance explained by the independent variables in any one year was very low ($R^2 = 0.09$, 0.05, and 0.04, respectively). In these samples the maximum number of observations used from one individual animal was 13, and the mode in each year was 1.

Movements by resident adults.—Fig. 6A shows the frequency distribution of the distances of all locations of adults found >45 m from their respective middens. It is clear that adults of either sex move considerable distances off of their home territories, and these movements equal or exceed the dispersal distances exhibited by offspring (Fig. 6B). Most observations of males off their home territories were made in early spring, when males spend considerable time searching for females in estrus (Rusch and Reeder 1975).

Where were offspring killed prior to settlement?

Twenty offspring were killed before they had acquired a territory. Seven of these animals were killed within the boundaries of their mother's territory. This was significantly less than that predicted by the proportion of time juveniles were found on their natal territories ($G = 9.63$, df $= 1$, $P < .005$; Fig. 2).

Where did offspring settle?

Seventy-three offspring obtained territories during the course of our study. Mean settlement distance was 88.6 m (range 0–323 m, 75th percentile = 123.2). Just under half of the individuals (20♂ + 16♀) settled on Class 1 territories (i.e., on or contiguous with their mother's territory) (Fig. 6B). Previous analyses have shown that there are no sex-biased trends in settlement patterns (Larsen 1993).

Only eight offspring assumed complete ownership of their natal midden and territory (5♂ + 3♀); in five instances the mother was known to be still alive during the transfer of ownership (in one of these cases, the offspring that first assumed control died, and was replaced by a sibling).

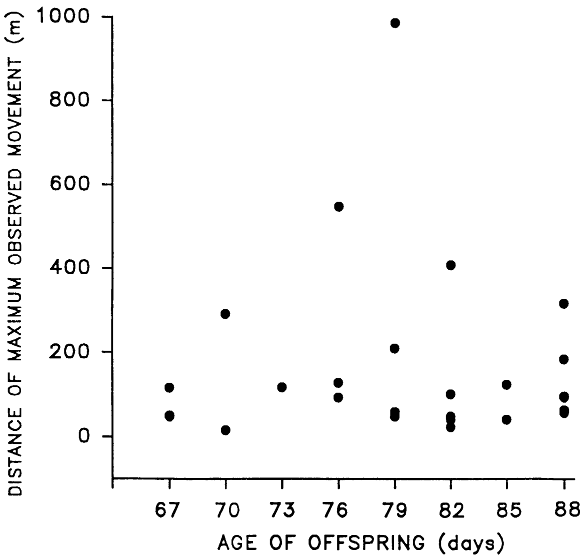

FIG. 5. Relationship of age and maximum observed foray distance observed in 30 radio-collared red squirrel offspring. Each offspring was collared at approximately the same age (64 d) and subsequently relocated every 3rd d over the following 24-d period (eight observations). Each point on the graph represents the maximum distance the offspring was observed from its natal midden. There was no relationship between these observations and the age of the animals.

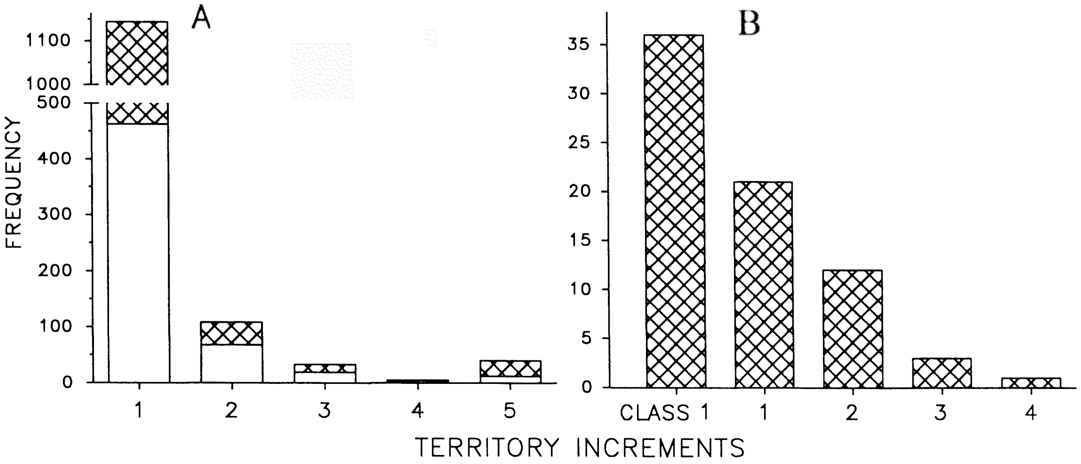

FIG. 6. (A) Histogram of distances for adult (shaded = ♀♀, open = ♂♂) territory-holding red squirrels located off of their home territories. (B) Distance from natal midden of territories acquired by 73 offspring. Distance is expressed in terms of 90-m territory increments (= diameter of mean territory size). In (A) the value of 1 includes all locations of adults that were >45–135 m from the home midden (45 m = radius of average territory). In (B) the Class 1 increment includes all territories acquired by offspring on or contiguous with the natal territory (roughly <135 m from the natal midden), whereas increments thereafter are 90-m intervals. Settlement distances fell within the range of movements observed by adults, implying all offspring settled within potential contact of their mother, and probably their father.

How did offspring survival compare before and after settlement?

Survival of offspring that did not possess territories was not significantly different among time periods (0–10, 11–20, and 21–30 d after collaring, all *P*s > .05), so data from all time periods were pooled to give a 10-d survival estimate of 0.902 for offspring without territories. Fig. 7 compares this value to the survival of territory holders at different time periods. Survival of offspring in the 10 d following territory acquisition was significantly lower than that of offspring not holding territories ($P = .006$), whereas survival of offspring 21–30 d after they had acquired a territory was significantly higher ($P < .001$).

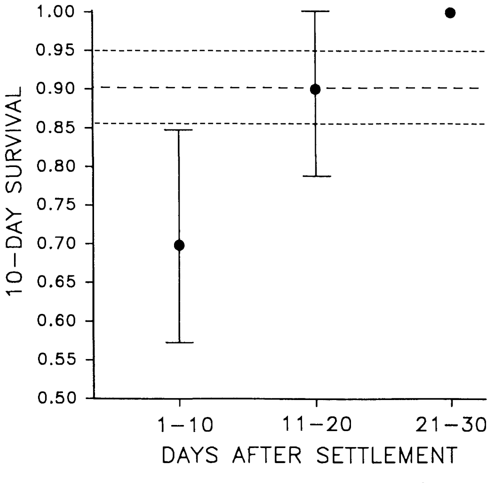

FIG. 7. Ten-day survival estimates (with 95% CL) of red squirrel offspring during three time periods after settling. ---- = the mean 10-d survival of offspring without territories; ----- = upper and lower 95% confidence limits. Offspring mortality was significantly higher during the 10 d following settlement, but decreased during the next two periods. Sample sizes—for number of individuals and number of radio-days—for the pre-settlement estimate are 76 and 1464, respectively. Sample sizes for the three estimates after settlement are 44 and 368, 20 and 192, and 12 and 120, respectively. All collared offspring with territories survived the 21–30 d period, hence the lack of 95% CL.

Did territory characteristics affect over-winter survival?

Offspring that acquired territories, but failed to survive the winter, settled on average a shorter distance away from their natal middens, but the difference was not significant (normal approximation to Mann-Whitney *U*, $Z = 1.76$, $P = .079$; Table 1). Offspring that survived the winter had significantly larger territories ($t = 2.89$, $P = .011$; Table 1), and their territories were more likely to encompass traditional middens ($G = 9.11$, df = 1, $P = .003$).

TABLE 1. Comparison of territories acquired by red squirrel offspring. Offspring that acquired territories, but did not survive over the winter, had a smaller mean settlement distance than offspring that survived over the same period ($P = .079$). Offspring that survived the winter had significantly larger territories ($P = .011$), and were more likely to possess traditional middens ($P = .003$).

Disperser survived over winter?	Mean dispersal distance (m)		Mean territory area (ha)			% with traditional midden	
	$\bar{X}$	*N*	$\bar{X}$	SE	*N*	%	Fraction
No	80.4	53	0.45	0.032	12	41	22 of 53
Yes	113.9	20	0.62	0.039	5	80	16 of 20

Discussion

Four important points emerge from our data. Firstly, red squirrel offspring attempting to disperse did not permanently abandon their natal territory when searching for a location to settle; instead they conducted forays, and continued to return to the natal territory until they succeeded in acquiring a territory. Secondly, offspring appeared to be more vulnerable to predation while off their mother's territory. Thirdly, dispersal distances were extremely limited in our population, with no offspring emigrating out of potential contact with their natal territory, their mother, and likely their father. Finally, survival of offspring appeared to be lower immediately after territory acquisition, than prior to acquisition or later on. However, offspring that survived their first winter tended to have settled relatively far away from their natal territory, and appeared to acquire larger territories with traditional middens.

Excursions have been reported in a variety of species (see review by Lidicker 1985; also Holekamp 1984). Lidicker and Stenseth (1992) outlined dispersal movement, or "quasi-dispersal," as taking three forms: (1) Nomadism, which occurs when a clearly defined home range does not exist, (2) Shifting, the gradual relocation of a home range through changes in boundaries, and (3) Excursions, or short-term explorations out of the home range. Red squirrel offspring definitely do not display nomadism; the mother's territory was maintained as a home base while an attempt was made to acquire a territory. The forays off the mother's territory could be classified as excursions, but in many cases settlement occurred on an area either in or overlapping the mother's territory. Hence, this could be viewed as "shifting." However, our data indicate that the red squirrel offspring acquiring Class 1 territories (i.e., on or contiguous with their mothers') did not exhibit less movement beforehand, suggesting these offspring are not inclined towards Class 1 settlement (Larsen 1993, this study). This, coupled with the fact that age and mass were poorly related to the distance offspring traveled, indicates that acquisition of Class 1 territories did not follow a true "shifting" sequence, such as that seen in Belding's ground squirrels (Holekamp 1984).

Our data indicate that offspring are more vulnerable to predation when off their natal territory. This provides empirical support for the underlying assumptions of many theoretical models of dispersal (but see Beaudette and Keppie 1992). Presumably this increased risk occurs because of unfamiliarity with the area being traversed, but this may result from being unfamiliar with escape routes, being preoccupied with avoiding resident territory holders (Metzgar 1967), or both. Regardless, the higher mortality faced by offspring while off of their natal territory affords at least some explanation for the circling foray movements. An individual that completely abandons its natal midden and begins an indefinite, long-distance movement will be continually at higher risk to predation, especially if the movement is through areas occupied by resident conspecifics. Conversely, offspring likely become very familiar with the natal area, both before and after they begin making forays.

Familiarity with their neighboring area may make offspring more aware of a sudden territory vacancy, or allow them to gradually appropriate a territory through increasing familiarity with neighboring adults (e.g., Stamps 1987). Waser (1985) presented two models designed to simulate settlement patterns. One model was based on Murray's (1967) assumption that animals attempting to relocate moved away in a straight line from their point of origin. Waser's second model considered that the would-be settler had "perfect information" concerning the availability of nearby sites. The observations we made in this study suggest that offspring are gaining familiarity with many territories surrounding the natal area, probably through their repeated forays. Models like Waser's that assume offspring have some working knowledge of their surrounding habitat may more accurately portray the settlement process.

We observed the longest movements off of the natal territory by offspring in suboptimal habitat, or in habitat unoccupied by resident adults. In some systems, such as pikas (Smith 1987), suboptimal habitat poses clear hazards for individuals attempting to disperse. At Fort Assiniboine, red squirrel offspring travelling or resting in bogs or muskeg are relatively free from potential harassment by resident adults. Hence, this habitat may be suboptimal in that it does not permit overwinter survival, but it may facilitate long-distance forays.

If any type of movement off of the natal territory incurs a higher risk to predation, why do offspring not simply remain on the natal territory indefinitely, until a nearby territory becomes vacant? Almost half of the offspring that acquired territories during our study did so at a location on or adjacent to their natal territory, yet there was no indication that these offspring were demonstrating reduced movement beforehand. There may be benefits associated with trying to locate a Class 2 territory (i.e., one completely disassociated from the mother's territory). During the 3 yr of our study, offspring aquiring Class 2 territories experienced higher overwinter survival. This may have been due to the larger traditional middens that accompanied these territories. Traditional middens may not only afford better protection from winter conditions, but they may also contain cones already hoarded by previous occupants. Class 1 territories frequently lacked traditional middens because the area was sectioned off of the mother's territory. Conducting forays off the natal territory should increase an offspring's chance of acquiring a territory with superior resources, which would counterbalance the costs of the forays.

Class 1 territories could include traditional middens, providing that one of the residents neighboring the natal territory dies at a time coincidental with the settlement period of the offspring. There is some evidence that breeding females may try to facilitate this process. Certainly, red squirrel offspring have been known to obtain part or all of the natal territory in more northern populations (Smith 1968, Zirul 1970, Price et al. 1986, Boutin et al. 1993, Price and Boutin 1993), and experimental manipulations at Fort Assiniboine indicate this may be a deliberate action on the part of the mother (Larsen 1993). The relatively high adult survival at Fort Assiniboine during this study may have reduced the incidence of this behavior. Higher adult mortality may increase the number of Class 1 settlers acquiring traditional, full-sized territories, because of nepotistic behavior on the part of the mothers. However, higher adult mortality also may enable offspring to locate vacant traditional territories more easily, without assistance from their mothers. Also, one would assume that mothers assist their offspring in obtaining territories only if it does not limit their own future reproductive success (see Clutton-Brock 1991). Monitoring settlement mechanisms and patterns through periods of high and low population density will be necessary to address this question.

What are the costs of settling? Our survival estimates indicate that mortality of offspring was highest immediately *after* settlement. Offspring that survived this time then had relatively high survival. Considerable energy and time probably is required to establish a territory, and predation risk probably remains high while the newly settled individual is establishing boundaries and familiarity with its neighbors. Therefore, it would not be too surprising if this was an especially costly time period for offspring. Whether these costs are different for offspring settling Class 1 or Class 2 territories is not clear at this time.

The major potential costs associated with limited settlement distances are deleterious inbreeding, and resource and mate competition with closely related individuals (Johnson and Gaines 1990). These costs, should they exist, must always be viewed in relation to the costs of emigrating (Anderson 1989). Waser et al. (1986), for example, presented models of dispersal that indicated that inbreeding depression would be less costly than mortality incurred during emigration. If inbreeding does exist in our study population, it is obviously less costly than attempted long-distance dispersal.

Residents might be expected to reduce resource competition by forcing offspring to emigrate (Anderson 1989). However, if long-distance movements are unlikely to result in the offspring surviving, then residents may increase their inclusive fitness by allowing related offspring to settle close by (or even facilitating it, in the case of the mothers). High adult survival during our study would suggest that mothers would face potential resource competition from Class 1 offspring, but this may be relatively unimportant. Waser and Jones (1983), for example, found that philopatric tendencies were relatively frequent even in species with high adult survivorship. Strong mate competition between closely related females is unlikely, given the promiscuous mating system and the short, asynchronous estrus periods. Male mate competition would be expected to be more intense, but without a knowledge of paternity we cannot determine how female mate choice and spatial and temporal overlap of sires and reproductively mature sons may affect mate competition.

If we had used indirect methods to monitor settlement, we might have produced very different interpretations of the processes and patterns occurring in the population. Without the use of radio collars, we would have failed to detect the round-trip forays of offspring. Creating a removal grid also results in considerably more immigrants into an area (Larsen 1993) than would normally be seen. Without radio collars we would not have been able to detect the acquisition of territories by many offspring, simply because they would have been killed before our fall census period. Also, the radio-collar data suggests that although risk to predation increases once offspring leave their natal territory, a very costly period may be immediately after territory acquisition. Direct methods, although often more difficult and costly, will likely prove the most successful means to obtain the empirical data necessary for theoretical investigations.

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