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BREEDING DISPERSAL IN FEMALE NORTH AMERICAN RED SQUIRRELS

DOMINIQUE BERTEAUX[1] AND STAN BOUTIN

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract. Although natal dispersal has received considerable attention from animal ecologists, the causes and consequences of breeding dispersal have remained largely unexplored. We used telemetry, direct observation, and long-term mark–recapture (9 yr) to study breeding dispersal in the North American red squirrel (*Tamiasciurus hudsonicus*) at Kluane, Yukon, Canada. We recorded the postbreeding behavior (keep the territory, share it with juveniles, or bequeath it to juveniles) of mothers from 485 litters, and monitored the fates of eight cohorts of weaned juveniles (680 individuals). The proportion of mothers that bequeathed their territory to one of their offspring was roughly one-third of that keeping or sharing it. Breeding dispersal was a recurrent phenomenon that characterized a fraction of the population of reproductive females every year. Dispersing females did not improve the quality of their breeding environment. In contrast, by leaving their territory, mothers allowed some offspring to stay on the natal site, which increased juvenile survival. Breeding dispersal by female red squirrels was thus a form of parental investment. Dispersing females were older than others, had higher numbers of juveniles at weaning, and moved their breeding sites more frequently after reproducing when food availability was high. These patterns are consistent with the major predictions of parental investment theories. We detected no difference in survivorship or future reproduction between dispersing and resident mothers. Juvenile males dispersed more often than females, but not farther. The sex of offspring did not influence whether mothers dispersed or not. Although we showed that breeding dispersal can have major impacts on the dynamics of squirrel populations, the relative implications of natal and breeding dispersal for the genetic structure and demography of populations and the social evolution of species remain unknown.

Key words: bequeathal; breeding dispersal; Canada; juvenile survival; parental investment; philopatry; red squirrel, North America; Tamiasciurus hudsonicus; *territory.*

INTRODUCTION

Animal dispersal is an integrative phenomenon that bridges the disciplines of ecology, behavior, genetics, and evolution (Chepko-Sade and Halpin 1987, Lidicker and Stenseth 1992). Dispersal is often divided between natal dispersal (the movement of juveniles from the natal site to the site of first breeding or potential breeding), and breeding dispersal (the movement between breeding sites of individuals that have reproduced) (Howard 1960, Greenwood 1980, Shields 1987). Natal dispersal has important consequences for the genetic structure, demography, and social evolution of animal populations (Hamilton 1972, Lidicker 1975, Taylor and Taylor 1977). Accordingly, intensive debate has occurred during the last two decades regarding the evolutionary and proximate causes of natal dispersal (Greenwood 1980, Dobson 1982, Shields 1983, Moore and Ali 1984, Waser 1985, Johnson and Gaines 1990, Stenseth and Lidicker 1992*a,* Moore 1993, Wolff 1994). Models for the evolution of natal dispersal now fall broadly into three groups: competition for resources, competition for mates, and avoidance of inbreeding (Greenwood 1980, Dobson 1982, Greenwood and Harvey 1982, Moore and Ali 1984, Dobson and Jones 1985, Johnson and Gaines 1986, Ralls et al. 1986, Waser et al. 1986, Pusey 1987).

In sharp contrast, breeding dispersal has received only limited attention from ecologists, although it is known to exist in a large range of bird and mammal species (Myllymaki 1977, Greenwood et al. 1979, Greenwood and Harvey 1982, Harvey et al. 1984, Jones 1986, 1987, Peterson and Best 1987, Boyce and Boyce 1988, Wolff et al. 1988, Boutin et al. 1993, Price and Boutin 1993, Wauters et al. 1995; for other references see Cockburn [1988] and Lambin [1997]). As for natal dispersal, breeding dispersal may profoundly alter the genetic structure and demography of populations and could influence the social evolution of species. No general theory explaining breeding dispersal has yet been formalized, but two main hypotheses have emerged. First, breeding dispersal could result from reproductive individuals attempting to find higher quality mates or a better breeding environment (Greenwood and Harvey 1982, Boyce and Boyce 1988, Wauters et al. 1995, Haas 1998). Second, breeding dispersal could be a form of parental investment whereby parents would bequeath some resources (territory, food hoard, nest site) to juveniles, thus increasing offspring fitness (Myllymaki

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[1] Present address: Department of Natural Resource Sciences, McGill University, Macdonald Campus, 21,111 Lakeshore, Sainte-Anne-de-Bellevue, Québec, Canada H9X 3V9.

1977, Jones 1986, Cockburn 1988, Lambin 1997, Price and Boutin 1993, Price et al. 1993). The latter, "bequeathal", hypothesis seems to have been adopted by mammal ecologists more often. For example, Cockburn (1988) listed 12 rodent species in which "there is evidence that mothers abandon the brood nest as a form of parental investment in their offspring". Most published reports of territory bequeathal, however, were not based on rigorous tests of adaptive explanations (Lambin 1997).

A good understanding of the prevalence, causes, and consequences of breeding dispersal is critical for several reasons. First, the main hypotheses proposed to explain natal dispersal all assume that at least one parent remains on the natal site. If parents typically leave the natal site, this assumption may be violated and explanations of natal dispersal may need reexamination. Second, breeding dispersal can offer unique opportunities for key tests of both animal dispersal and parental investment theories. For example, the role of parents in sex-biased juvenile dispersal is unclear (Wolff 1993). Breeding dispersal of some mothers allows the comparison of situations where juveniles disperse while the mother is still on the natal territory to situations where juveniles disperse while the mother has left the natal area (e.g., Wolff et al. 1988). Such comparisons should clearly highlight, through "natural experiments", the role of mothers in sex-biased juvenile dispersal. Third, breeding dispersal can offer a new context to test predictions of parental investment theories. For example, older mothers should bequeath their territory more readily since a female with a low residual reproductive value is expected to invest more in her current litter (Fisher 1930, Williams 1966 *a, b,* Stearns 1976). Similarly, mothers with a large number of juveniles should disperse more often than other mothers (Lazarus and Inglis 1986, Winkler 1987).

We followed a population of the North American red squirrel (*Tamiasciurus hudsonicus*) for 9 yr, and here we use this long-term data set to provide a detailed analysis of the causes and consequences of breeding dispersal in a mammal species. Red squirrels are appropriate for this purpose because: (1) individuals occur at high densities and are easily observed in the field; (2) matrilineal relationships can be established reliably by marking pups in the nest; (3) individuals rely on semipermanent resources (burrows and food stores) that allow changes in territory ownership to be monitored in detail; (4) dispersal distances of juveniles are usually short, so that the fate of each offspring can be determined accurately (Larsen and Boutin 1994), and (5) unambiguous evidence indicates that breeding dispersal exists in this species (Price and Boutin 1993).

After weaning their juveniles, red squirrel mothers can either keep their territory and evict juveniles, share it with juveniles, or bequeath it to juveniles (Zirul 1970, Price and Boutin 1993). We addressed four general questions about breeding dispersal in red squirrels: (1) what are the factors that affect the postbreeding decisions of mothers; (2) what are the effects of each alternative on their survival and future reproduction; (3) which juveniles are most likely to stay on the natal territory when mothers share or bequeath their territory; and (4) what are the effects of the postbreeding decisions of mothers on the survival and future reproduction of their juveniles. Answering these questions allowed us to demonstrate clearly the parental investment function of breeding dispersal in red squirrels. We then used our detailed analysis of the context and consequences of breeding dispersal to test some of the key predictions of animal dispersal and parental investment theories.

METHODS

Study area

We studied red squirrels on three sites near Kluane Lake, Yukon, Canada (61° N, 138° W). Two sites (~40 ha each) were contiguous whereas the third (~60 ha) was located ~1 km away. None of the sites was isolated, and all squirrels belonged to a single population. The habitat was open boreal forest with white spruce (*Picea glauca*) as the dominant canopy tree. Studies began in 1987, and we report results for the years 1989 through 1997.

All squirrels were marked with numbered ear tags (n = 2835 individuals tagged), and a unique color combination of electrical wire was threaded through the tags for identification at a distance. The reproductive activity of each female was monitored by observations of body mass changes and nipple condition during repeated captures (Tomahawk traps) beginning in late March and ending in late August of each year. Shortly after parturition we located nests by visual inspection of trees located on the territory or by following radio-collared females. Once nests were located (n = 848 nests with offspring present), the young were counted, sexed, and weighed. Parturition date was estimated from the trapping records of the female and the size of the young when the nest was entered (Boutin and Larsen 1993). Most young were too small to ear tag at first nest entry, so the nest was found a second time when the young were 20–25 d old, at which time each was given an ear tag and colored wire in each ear (n = 1979 individuals tagged as pups). Juveniles emerged from the nest at ~45 d of age (n = 1481 individuals emerged), and remained on the territory for ~25 d before being weaned (n = 1109 weaned juveniles). We visited daily the territories of females with young expected to emerge, and conducted searches throughout the region for emerged juveniles. After young emerged, we followed their fates by live-trapping, visual observation, and radio telemetry (Boutin et al. 1993). Most identified young were followed longitudinally from birth through adulthood. We suspect that many losses after emergence were due to avian predators (O'Donoghue and Boutin 1995).

In the boreal forest, squirrels defend individual territories year round (Smith 1968, Kemp and Keith 1970, Zirul 1970, Rusch and Reeder 1978). At the end of summer, squirrels store unopened conifer cones on hoarding sites (called middens) located centrally on the territory. Middens are long lived and are used without interruption by successive occupants, which generates visible accumulations of cone debris (Larsen et al. 1997). Without a midden in its territory, it is virtually impossible for a red squirrel to survive the winter (Kemp and Keith 1970, Larsen and Boutin 1994). We located all middens to within 3 m on the study site using a 30-m-interval grid, and we determined the owner of each midden twice a year (~15 May and 15 August) by identifying the individual associated with or giving territorial calls on the midden (Smith 1978). Squirrels tend to own >1 midden. We assumed that the coordinates of the center of a squirrel's territory were the average coordinates of its middens. This allowed us to calculate distances moved by individuals from one midden census to the next. In most dispersal studies, there is a greater chance to observe short-distance than long-distance movements (König et al. 1996, Stenseth and Lidicker 1992*b*). However, radio-tracking data showed in another population of red squirrels that natal dispersal distances are short in this species (mean = 89 m [Larsen and Boutin 1994]), so we expect our bias to be small given the relatively large size of our study areas.

We determined the postbreeding behavior of mothers that had weaned ≥1 juvenile, using direct observation and trapping, and following the methods used by Price and Boutin (1993). Female behavior was classified as "keep the territory" if the mother remained on her territory without allowing a single juvenile to own one of her middens (i.e., mother resident and juveniles disperse), "share the territory" if the mother kept some of her middens while allowing ≥1 juvenile to own ≥1 of her middens (i.e., mother resident and ≥1 juvenile resident), and "bequeath the territory" if the mother abandoned her middens, thus allowing ≥1 juvenile to own her middens (i.e., mother disperse and ≥1 juvenile resident). This classification assumes that the difference between keeping and sharing is due to maternal, not offspring behavior. We considered a female to have bequeathed only if she was seen elsewhere subsequently, since sudden disappearance alone is consistent with predation (Price and Boutin 1993). We determined the dispersal status of juveniles from the August midden census. We classified juveniles as "resident" if they owned one of their mother's original middens, "successful disperser" if they owned a midden obtained independently, and "vagrant" if they were known to be alive through trapping or visual observation but did not own any midden on 15 August.

Exact age was known for mothers tagged as pups (n = 164), but only minimum age was known for those first trapped as adults (n = 138). We pooled all females in a single analysis, thus "age" should conservatively be understood as "minimum age". Parturition dates were expressed as the absolute value of the deviation from the annual mean parturition date to eliminate variation arising from between-year differences in environmental conditions. Spruce cone crops are variable at Kluane, and we assessed production by counting cones on the top 3 m of 296–315 trees every August (Boutin and Larsen 1993). We defined "body mass at parturition" of mothers as body mass (±1 g) measured ≤7 d following parturition, and "body mass at weaning" of mothers as body mass (±1 g) measured within 7 d of the date at which the last juvenile of the litter was weaned. "Body mass of juveniles at weaning" refers to body mass (±1 g) of juveniles measured within 7 d of the weaning date.

Statistical analyses

Factors influencing the postbreeding behavior of mothers.—We proceeded in two steps. In the first step, we used generalized additive regression models (Hastie and Tibshirani 1990, Hastie 1992) as an exploratory tool to examine the relationship between potential explanatory variables and the postbreeding behavior of females. The formal statement for a generalized additive regression model is

$$g(Y) = \alpha + f_1(X_1) + f_2(X_2) + \cdots + f_p(X_p)$$

where Y is the response variable, $g(i)$ is a link function such as a logit or logarithmic transform, α is a constant intercept term, χ_1, χ_2,. . . χ_p are the predictors, and $f_1(\cdot)$, $f_2(\cdot)$, . . . $f_p(\cdot)$ are parametric or nonparametric smooth functions to be estimated from the data (Hastie 1992, Hastie and Tibshirani 1990).

Model formulation depends primarily upon the nature of the response variable. Our response variable had three levels that were ranked according to the intensity of maternal care (keep = 1, share = 2, bequeath = 3). A preliminary examination of these categorical data showed that they were drawn from an underdispersed Poisson distribution. We thus used the quasi-likelihood family to estimate the dispersion parameter as part of the model fitting computations for Poisson families (MathSoft 1997*a*). Each term was fit using a smoothing spline with four degrees of freedom (MathSoft 1997*a*).

We selected the model that best fit the data using a forward stepwise procedure and the Akaike Information Criterion (AIC) (Sakamoto et al. 1986, Burnham and Anderson 1992). We also report results from F tests (MathSoft 1997*a*) comparing different models. We looked for the existence of interactions between variables by adding pairwise products to the model. We did not try to parameterize the smooth functions used in the final model since in this first step our goal was to screen for significant predictors rather than to pro-

TABLE 1. Explanatory variables used to model the postbreeding behavior of red squirrel mothers in a 9-yr data set from Kluane, Yukon, Canada.

Variable	Description	Data type	Range
Age	Minimum age of females (yr)	discrete	1–7
Breeding exp.	Minimum number of times females gave birth	discrete	0–7
Weaning exp.	Minimum number of times females raised ≥1 juvenile to weaning	discrete	0–5
Part. date	Deviance from the mean parturition date for each year	continuous	−54 to 56
Litter size	Number of juveniles at birth	discrete	1–7
Juv. wean	Number of juveniles at weaning	discrete	1–5
Dau. wean	Number of daughters at weaning	discrete	0–4
Prop. females	Proportion of juveniles females in the litter at weaning	ratio	0–1
Year	Year of study	category	1989–1997
Food (year $y-1$)	Index of cone abundance the year before female behavior was recorded	continuous	0–300.5
Food (year y)	Index of cone abundance the same year as female behavior was recorded	continuous	0–300.5
Middens	Minimum number of middens owned by the female in spring (15 May)	discrete	0–6
Vacancy	Number of vacant middens (15 May) located ≤150 m from the center of the female territory, divided by the total number of middens present in the same area	ratio	0–0.40

duce an analytical expression for the model. We used visual observation of residuals to test the statistical assumptions implicit in the fitted regression model (McCullagh and Nelder 1989).

Thirteen explanatory variables were used to model the behavior of females (Table 1). Given that breeding dispersal is related to both animal dispersal theories and parent–offspring conflict theories, we included all the available variables related to (1) the current or residual reproductive value of mothers, (2) the amount of resources available to mothers and juveniles, and (3) the expected costs and benefits of dispersal to mothers and juveniles. Because of reduced sample sizes, we analyzed separately (one-way ANOVAs) how body mass of mothers affected their behavior.

In a second step, we used logistic regressions as a post hoc analysis tool to identify the variables that were associated with breeding dispersal per se. The response variable was now binary (mothers did not disperse = 0, dispersed = 1). We constructed models using a forward stepwise selection procedure, adding terms one at a time and testing for significance using F tests (MathSoft 1997*a*). We looked for the existence of interactions between variables by adding pairwise products to the model.

Effects of the postbreeding behavior of mothers on their survival and future reproduction.—Mothers exhibiting each category of postbreeding behavior did not represent random samples of females (dispersers were, for example, older than residents; see *Results: Factors influencing . . . mothers*). As a consequence, we faced the problem of possible variation in individual potential (Lessels 1991) when comparing survivorship and future reproduction of females from the three groups. To circumvent this difficulty, we drew a subsample of females from each of the two categories that were better represented ("keep" and "share") and used these subsamples in our comparisons of females exhibiting each category of postbreeding behavior. This procedure enabled us to compare three groups of mothers that differed in their postbreeding behavior but had presumably similar individual potentials. The proportions of females surviving to spring and reproducing the next year were then compared using Pearson chi-square statistics, and we used Kruskal-Wallis one-way ANOVAs to compare parturition dates, litter sizes, and number of juveniles at weaning of females that reproduced the following year.

Which juveniles obtained a midden from their mother?—We assessed the effect of sex and body mass at weaning of juveniles on their likelihood of obtaining a midden from their mother using Pearson chi-square statistics and t tests, respectively.

Effects of the postbreeding behavior of mothers on the movements, survival, and future reproduction of juveniles.—We used Wilcoxon rank-sum tests to analyze how the behavior of mothers (share vs. bequeath) affected the number and proportion of resident juveniles. We compared the survivorship and future reproduction of residents, successful dispersers, and vagrants, using Pearson chi-square statistics for comparisons involving proportions and Wilcoxon rank-sum tests for comparisons involving characteristics of juveniles. We used Wilcoxon rank-sum tests to compare dispersal distances between groups of individuals.

All statistical analyses were performed in S-PLUS 4.0 (MathSoft 1997*a*, *b*, Venables and Ripley 1997). Probability values are two tailed and data are reported as means ±1 SD.

RESULTS

Squirrels produced 1013 litters during the 9 yr of the study, and 590 of these litters yielded ≥1 juvenile at weaning (Table 2). We recorded the postbreeding be-

TABLE 2. Sample sizes in a 9-yr data set used to study postbreeding behavior of female red squirrels at Kluane, Yukon, Canada.

	Year									
Variable	1989	1990	1991	1992	1993	1994	1995	1996	1997	$\bar{X} \pm 1$ SD
Individuals ≥1 yr	262	283	229	312	295	457	366	412	325	327 ± 73
Females ≥1 yr	127	127	116	161	141	226	163	191	147	157 ± 35
Litters produced	88	45	78	159	139	134	149	122	99	113 ± 38
Litters with data on the postbreeding behavior of the mother†	50	30	33	36	61	66	48	51	49	47 ± 12

† Data on the postbreeding behavior of mothers were unavailable when all juveniles died before weaning or when they were weaned after 15 August.

havior of mothers from 485 litters, for a total of 302 females (Table 2). The behavior of a mother for a given litter did not depend on the behavior of that mother for the previous litter (Table 3). We thus used litters (n = 485 cases) rather than females (n = 302 cases) as the unit of analysis. Second litters are rare at Kluane, and only six times did we record the postbreeding behavior of a female twice in a year. Data points were thus pooled in the analysis irrespective of litter number.

The proportions of litters in which mothers kept, shared, or bequeathed their territory were 43.9%, 41.2%, and 14.9%, respectively. These proportions varied greatly among years (Fig. 1). The distance moved by females between 15 May (before weaning of juveniles) and 15 August (after weaning of juveniles) averaged 4 ± 8 m (median = 0 m, n = 124 cases) for females of the "keep" category, 12 ± 14 m (median = 9 m, n = 134 cases) for "share", and 93 ± 51 m (median = 82 m, n = 29 cases) for "bequeath" (Kruskal-Wallis rank-sum test: $\chi^2 = 111.165$, df = 2, $P < 0.001$; Fig. 2).

Factors influencing the postbreeding behavior of mothers

Although we recorded the postbreeding behavior of mothers from 485 litters, there were missing cells for 61 litters and n = 424 cases (271 females) for the model selection process. Average values for explanatory variables are given in Fig. 3 for each category of behavior.

In the first, exploratory stage of our analysis, the stepwise procedure (Table 4) selected "age" as the factor explaining the largest amount of variation in female behavior (note in Table 4 the large difference in AIC value between the null model and the model including the age effect). Bequeathing females were on average ~1 yr older than keeping females, while sharing females were of intermediate age (Fig. 3). This age effect was remarkably consistent among years (Fig. 4). Cone production estimated the same year as female behavior was recorded (food [year y]) was the second factor to enter the model (Table 4). We assumed in our methods that keep, share, and bequeath represented increasing increments of maternal care. According to Fig. 3, postweaning maternal care was thus positively related to cone abundance. The number of middens owned by females in spring was selected in the third step of the modeling process (Table 4), and females who shared their territory owned on average 0.5 more middens than those from the two other categories (Fig. 3). The number of cones produced by spruce trees the year before the behavior of females was recorded (food [year $y - 1$]), entered the model in fourth position (Table 4), with postweaning maternal care being negatively related to cone abundance (Fig. 3). Year of study (Fig. 1) was the fifth factor retained in the model (Table 4), which may reflect some random fluctuations or the existence of unknown factors that influenced female behavior while varying in intensity from year to year. The number of juveniles at weaning was the last significant factor to enter the model (Table 4). The number of weaned juveniles was 13.3% higher for bequeathing females than for females who kept their territory (Fig. 3). Note that values for all significant factors (Table 4), except number of middens, were intermediate for

TABLE 3. Postbreeding behavior (keep, share, or bequeath the territory) of red squirrel mothers on successive litters at Kluane, Yukon, Canada. Sample size n = number of mothers.

	Year $y-1$					
	Keep		Share		Bequeath	
Year y	n	Percentage	n	Percentage	n	Percentage
Keep (n = 57)	19	33.3	30	52.6	8	14.0
Share (n = 63)	21	33.3	34	54.0	8	12.7
Bequeath (n = 19)	10	52.6	5	26.3	4	21.1
χ^2	2.652†		4.811		0.837	
P	0.266		0.090		0.658	

† Effect of female behavior in year y on female behavior in year y + 1, tested with Pearson's chi-square tests.

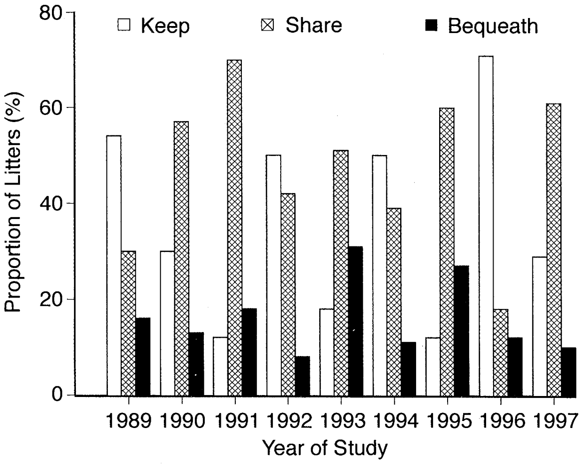

FIG. 1. Yearly variation in the proportion of litters in which the mother kept, shared, or bequeathed her territory in a population of red squirrels studied at Kluane, Yukon, Canada.

sharing females (Fig. 3). This confirms the validity of our initial assumption that keeping, sharing, and bequeathing the territory represented three successive increments along the same axis of behavioral strategies.

Sex of weaned juveniles was not useful in explaining variation in postbreeding maternal care (Table 5). This finding is illustrated by the following observation: there were 171 and 211 litters in which all weaned juveniles were males or females, respectively. The proportions of mothers exhibiting each behavior were remarkably similar in the two situations (all weaned juveniles were males: keep = 56.1%, share = 32.2%, bequeath = 11.7%; all weaned juveniles were females: keep = 54.0%, share = 34.6%, bequeath = 11.4%; $\chi^2 = 0.252$, df = 2, $P = 0.882$). Reproductive experience of mothers did not influence their behavior once the effect of age was removed (Table 5), nor did parturition date, litter size, and territory vacancy (Table 5).

We tried adding pairwise products to the model, but no significant interaction was found. One-way ANOVAs revealed no significant relationship between body mass of mothers at parturition or at weaning and their postbreeding behavior (Table 6).

In the second step of our analysis, we identified which factors were associated with breeding dispersal per se. Age and food (in year y) remained the two factors explaining the largest amount of variation in the probability of breeding dispersal (Table 7). The number of juveniles at weaning also remained a significant predictor of breeding dispersal (Table 7). However, the number of middens owned by females was no longer a significant predictor (Table 8), presumably because although sharing females owned on average more middens than females from the other two categories, there was virtually no difference in midden ownership between keeping and bequeathing mothers (Fig. 3). Year of study also lost its predictive power when the probability of dispersal became the dependent variable. Finally, the "best" logistic model predicting breeding dispersal included a significant interaction between food (in year $y - 1$) and food (in year y). Fig. 3 shows that mothers tended to disperse when food (year $y - 1$) was low while food (year y) was high. Parameter estimates for the final model are given in Table 9.

Effects of the postbreeding behavior of mothers on their survival and future reproduction

We subsampled females of the "keep" and "share" categories to compare three groups of females that differed in their postbreeding behavior while being similar in age, food resources, number of weaned juveniles, and year of study. We found no relation between postbreeding behavior and overwinter survivorship or the probability that survivors would reproduce the next year (Table 10). Among females that reproduced the next year (year $y + 1$), relative parturition date, litter size, and number of weaned juveniles in year $y + 1$

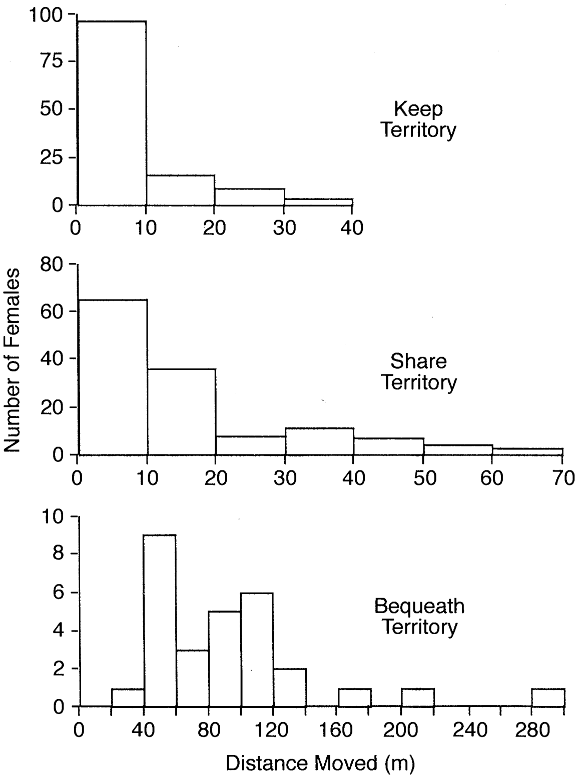

FIG. 2. Histograms of distances moved by reproductive female red squirrels from their spring territory to their fall territory. The coordinates of the spring territories were defined as the average coordinates of the middens owned by the females on 15 May, and the coordinates of the fall territories were defined as the average coordinates of the middens owned by the females on 15 August. At the study site, the average diameter of the territory is 42 m for an adult female red squirrel (after Price and Boutin [1993]).

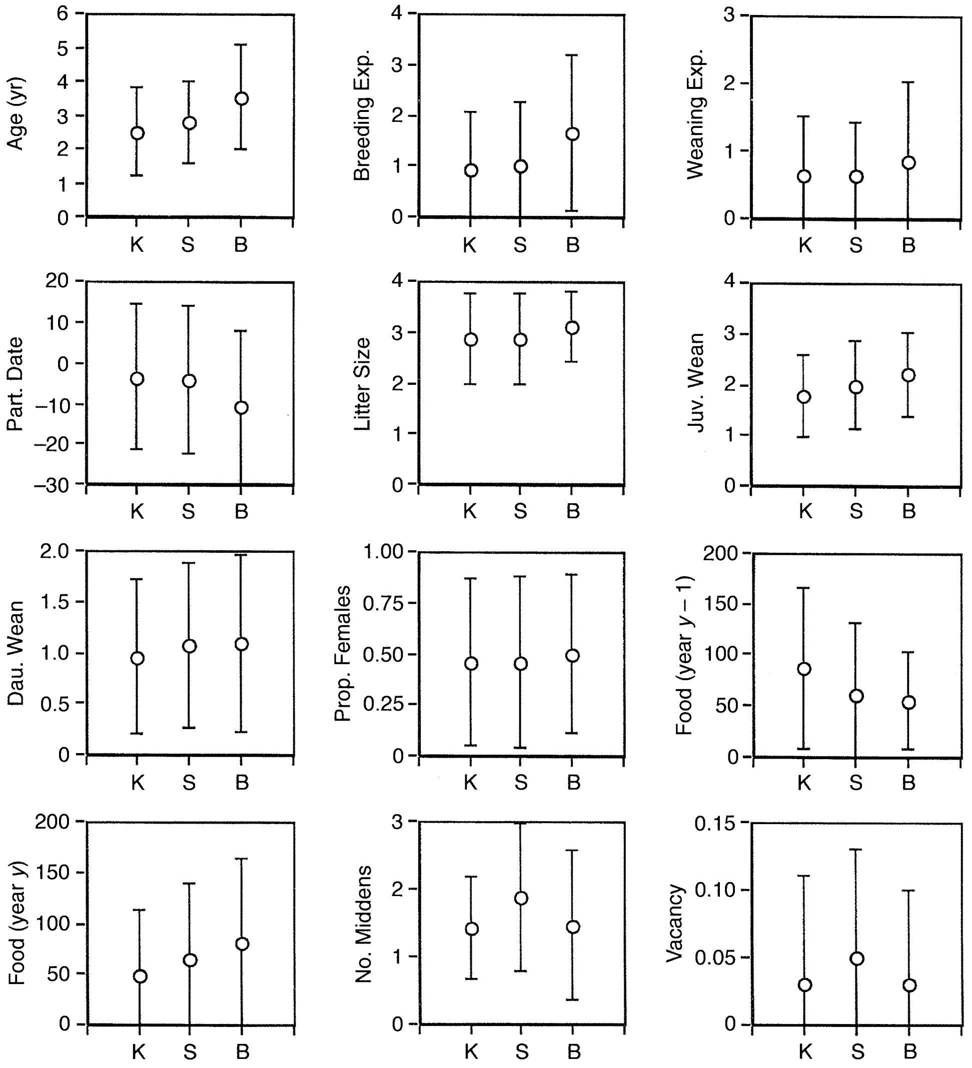

FIG. 3. Values (mean ± 1 SD) of explanatory variables for each category of postbreeding behavior exhibited by female red squirrels. Although female behavior was the dependent variable in our analyses, we represented the behavioral categories on the horizontal axis for ease of reading (K = keep, S = share, B = bequeath). See Table 1 for the definition of variables and the units of measurements.

TABLE 4. Modeling the postbreeding behavior of red squirrel females at Kluane, Yukon, Canada.

	Analysis of deviance			*F* test†		
Model	AIC	Res. dev.‡	df	*F*	df	*P*
Null model (m_0)	119.00	118.45	423.00			
m_0 + "Age" effect (m_1)	111.61	108.82	418.99	9.353	4.01	<0.001
m_1 + "Food (year $y-1$)" effect (m_2)	107.63	102.61	414.97	6.317	4.02	<0.001
m_2 + "Middens" effect (m_3)	105.69	98.45	410.98	4.360	3.99	0.002
m_3 + "Food (year y)" effect (m_4)	104.91	95.41	406.93	3.209	4.05	0.013
m_4 + "Year" effect (m_5)	102.97	91.27	402.93	4.583	4.01	0.001
m_5 + "Juv. wean" effect (m_6)	**102.49**	**88.62**	**399.04**	3.074	3.89	0.017
Full model (all variables)	105.79	82.47	371.11	0.999	27.93	0.470

Notes: The analysis of deviance tests the effect of explanatory variables in a generalized additive model. The model selected (lowest Akaike Information Criterion, AIC) is in boldface type.

† Results of *F* tests refer to a comparison of each row with the previous row.

‡ Residual deviance.

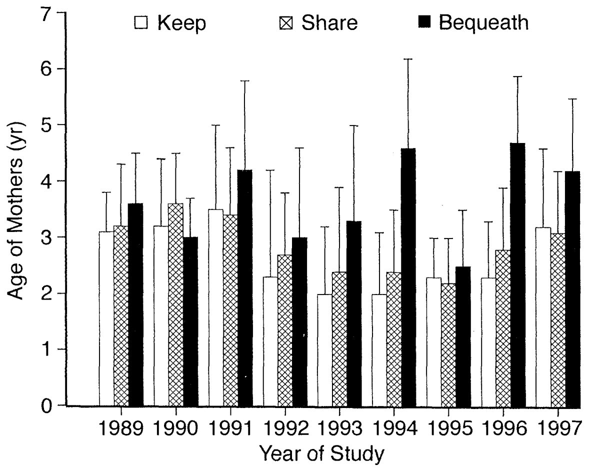

FIG. 4. Yearly variation in the average age (mean + 1 SD) of mothers that kept, shared, or bequeathed their territory in a population of red squirrels studied at Kluane, Yukon, Canada. Variable abbreviations are defined in Table 1.

TABLE 5. *F* values and probabilities for nonsignificant terms added alone to the "best" generalized additive model (Table 4) describing the postbreeding behavior of red squirrel females at Kluane, Yukon, Canada. Variable abbreviations are defined in Table 1.

Nonsignificant term	*F*	df	*P*
Breeding exp.	0.672	4.00	0.612
Weaning exp.	1.240	4.00	0.293
Part. date	1.231	4.01	0.297
Litter size	1.001	3.98	0.404
Dau. wean	1.158	3.90	0.329
Prop. females	1.092	4.05	0.360
Vacancy	1.535	4.010	0.191

did not vary according to postbreeding behavior in year *y* (Table 10). Therefore dispersing females did not increase or decrease their reproductive success relative to other females when they switched territory.

Which juveniles obtained a midden from their mother?

Using data from juveniles whose mother shared or bequeathed their territory, we found no difference in body mass at weaning between the juveniles that obtained a midden from their mother and those that did not (obtained a midden: body mass = 158.1 ± 20.7 g (n = 99 juveniles); did not obtain a midden: body mass = 158.1 ± 19.4 g (n = 140 juveniles); t = 0.024, df = 1, P = 0.981). Females who shared or bequeathed their territory weaned 548 juveniles (289 F and 259 M), of which 411 (228 F and 183 M) were still alive on 15 August. Among these 411 juveniles, a higher proportion of daughters (50.4%) than sons (37.2%) were residents (χ^2 = 6.721, df = 1, $P < 0.009$). A comparison of data from sharing females to data from bequeathing females showed that the presence of the mother on the natal area did not influence the proportion of daughters (share: 48.1%, n = 162 mothers, bequeath: 53.0%, n = 66 mothers, χ^2 = 0.273, df = 1, P = 0.601) and sons (share: 35.1%, n = 131 juveniles, bequeath: 42.3%, n = 52 juveniles, χ^2 = 0.546, df = 1, P = 0.460) that were resident on 15 August.

Effects of the postbreeding behavior of mothers on the movements, survival and future reproduction of their juveniles

The number of juveniles that owned one of their mother's middens on 15 August tended to be higher for bequeathing than for sharing females (bequeath: 0.80 ± 0.73 juveniles (n = 71 litters), share: 0.63 ± 0.67 juveniles (n = 200 litters), z = −1.793, P = 0.073). This was due to a higher number of juveniles being weaned by bequeathing females, rather than to a higher percentage of weaned juveniles obtaining a midden from these mothers (share: 36.0 ± 43.1% (n = 195 litters), bequeath: 39.1 ± 36.3% (n = 70 litters), z = −1.041, P = 0.298).

We excluded from the following analyses the juveniles born in 1997 because their future was unknown at the time of analysis. Of 680 juveniles that survived to 15 August (Fig. 5), 186 (27.4%) were residents, 206 (30.3%) were successful dispersers, and 288 (42.4%) were vagrants. Successful dispersers had moved on average 96 ± 94 m (median = 60 m, n = 189 juveniles, Fig. 6) from the natal site. This distance did not differ significantly by sex (males: 107 ± 111 m, n = 94 juveniles; females: 85 ± 72 m, n = 95 juveniles; z = −1.217, P = 0.224). Overwinter survivorship was higher for residents than for successful dispersers (75.3 vs. 57.8%, χ^2 = 12.587, df = 1, $P < 0.001$; Fig. 5), but did not differ significantly between successful dis-

TABLE 6. Effect of body mass (g) of red squirrel mothers at parturition and at weaning on their postbreeding behavior. Sample size n = number of mothers.

	Post-breeding behavior of females						
	Keep		Share		Bequeath		
Variable	$\bar{X}$ ± SD	n	$\bar{X}$ ± SD	n	$\bar{X}$ ± SD	n	One-way ANOVA
Body mass at parturition	258 ± 25	110	254 ± 20	129	256 ± 19	42	$F_{2,278}$ = 0.878, P = 0.417
Body mass at weaning	250 ± 18	163	253 ± 20	140	256 ± 18	46	$F_{2,346}$ = 2.060, P = 0.129
Body mass lost between parturition and weaning	8 ± 20	82	1 ± 17	87	0 ± 21	26	$F_{2,192}$ = 2.579, P = 0.08

TABLE 7. Modeling breeding dispersal of red squirrel mothers at Kluane, Yukon, Canada. The effect of explanatory variables is tested in a logistic model. The model selected is in boldface type.

Model	Residual deviance	df	F test†		
			F	df	P
Null model (m_0)	383.15	423			
m_0 + "Age" effect (m_1)	360.61	422	22.285	1	<0.0001
m_1 + "Food (year y)" effect (m_2)	350.45	421	10.436	1	0.0013
m_2 + "Juv. Wean" (m_3)	344.74	420	5.617	1	0.0182
m_3 + "Food (year $y-1$) × Food (year y)" effect (m_4)	**340.45**	**419**	4.332	1	0.038
Full model (all variables)	333.37	410	0.81	9	0.61

† Results of F tests refer to a comparison of each row with the previous row.

persers and vagrants (57.8 vs. 52.3%, $\chi^2 = 1.098$, df = 1, $P = 0.295$). The survivorship of successful dispersers did not differ significantly according to the distance moved from the natal site (survived: 99 ± 97 m, $n = 97$ juveniles; did not survive: 92 ± 86 m, $n = 79$ juveniles; $z = -0.732$, $P = 0.464$).

Among daughters that had survived to spring, probabilities of reproducing were similar for residents and successful dispersers (45.4 vs. 42.9%, $\chi^2 = 0.017$, df = 1, $P = 0.896$), but residents were more likely to reproduce than vagrants (45.4 vs. 28.4%, $\chi^2 = 5.205$, df = 1, $P = 0.022$) (see Fig. 5 for sample sizes). Kruskal-Wallis rank-sum tests revealed that relative parturition dates, litter sizes, and number of juveniles at weaning of daughters that reproduced as yearlings did not differ significantly between residents, successful dispersers, and vagrants (parturition date: $\chi^2 = 3.581$, df = 2, $P = 0.167$; litter size: $\chi^2 = 0.376$, df = 2, $P = 0.829$; number of juveniles at weaning: $\chi^2 = 2.106$, df = 2, $P = 0.349$; see Fig. 5 for mean values and sample sizes).

Among the juveniles that stayed on the natal territory, some were able to do so because the mother shared her territory, while others benefited from their mother's dispersal. Overwinter survivorship of resident juveniles did not differ significantly according to the behavior of the mother (mother shared: overwinter survival of resident juveniles = 58.1%, $n = 124$ juveniles; mother bequeathed: 71.9%, $n = 57$ juveniles; $\chi^2 = 2.637$, df = 1, $P = 0.104$).

TABLE 8. F values and probabilities for nonsignificant terms added alone to the "best" logistic model (Table 7) predicting the probability of breeding dispersal in red squirrel mothers. See Table 1 for definitions of variables.

Nonsignificant term	F	df	P
Breeding exp.	1.57	1	0.21
Weaning exp.	0.01	1	0.90
Part. date	1.63	1	0.20
Litter size	0.44	1	0.51
Dau. wean	0.05	1	0.82
Prop. females	0.13	1	0.72
Year	0.25	1	0.62
Food (year $y-1$)	0.37	1	0.54
No. middens	2.70	1	0.10
Vacancy	0.41	1	0.52

None of the successful dispersers or vagrants eventually came back to the natal territory and owned one of their mother's original middens the following spring. Among residents that were alive the next spring ($n = 140$ individuals), 79.3% remained on the natal territory. The average distance between the natal territory and the territory owned by yearlings in spring was not statistically different according to whether they were successful dispersers or vagrants on 15 August (successful dispersers: 111 ± 99 m, $n = 95$ yearlings; vagrants: 115 ± 98 m, $n = 90$ yearlings; $z = 0.408$, $P = 0.683$).

DISCUSSION

Four major patterns emerged from our long-term study of postbreeding behavior of red squirrel mothers at Kluane: (1) breeding dispersal was a recurrent phenomenon that characterized a fraction of the population of reproductive females every year; (2) dispersing females were not a random sample of mothers and we identified some of the predictors of breeding dispersal; (3) dispersing mothers did not have a lower than average reproductive success on their current territory, nor did they increase their reproductive success when switching to a new territory, which demonstrates that they were not seeking a better-quality breeding environment; and (4) breeding dispersal of the mother allowed some juveniles to increase their fitness by remaining on the natal territory, which demonstrates that breeding dispersal functioned as a form of parental investment. We now discuss the costs and benefits of natal and breeding dispersal, and consider our findings in light of the major predictions of animal dispersal and parental investment theories.

TABLE 9. Parameter estimates in the final model (Table 7) for the probability of breeding dispersal by red squirrel mothers at Kluane, Yukon, Canada.

Variable	Value	Standard error
Intercept	−4.544	0.561
Age	0.530	0.102
Food (year y)	0.012	0.003
Juv. wean	0.394	0.156
Food (year $y-1$) × Food (year y)	−0.00007	0.00003

TABLE 10. Effect of the postbreeding behavior of mothers in year *y* on their probability of overwinter survival, their probability of reproducing in year *y* + 1, and three measures of that reproduction.

Postbreeding behavior of mothers	Survival to spring?			Reproduced?			Paturition date			Litter size?			No. weaned juveniles?		
	yes	%	*n*	yes	%	*n*	Mean	1 SD	*n*	Mean	1 SD	*n*	Mean	1 SD	*n*
Keep territory	50	70.4	71	40	80.0	50	−1.3	26.5	39	2.73	1.07	40	0.98	1.04	40
	(140)	(65.7)	(213)	(109)	(77.9)	(140)	(−9.4)	(22.4)	(100)	(2.53)	(1.45)	(109)	(1.15)	(1.20)	(109)
Share territory	49	69.0	71	39	79.6	49	−6.7	21.8	38	2.87	1.30	39	1.54	1.19	39
	(128)	(64.0)	(200)	(107)	(83.6)	(128)	(−9.1)	(18.6)	(104)	(2.82)	(1.24)	(107)	(1.51)	(1.21)	(107)
Bequeath territory	41	57.7	71	33	80.5	41	−10.0	17.0	31	2.70	1.19	33	1.09	1.14	33
Statistical tests†															
χ^2	3.043			0.011			1.512			0.624			4.989		
df	2			2			2			2			2		
P	0.218			0.994			0.469			0.732			0.082		

Note: The results obtained before subsampling females from the categories "keep" and "share" to control for initial differences between females of the three categories (see *Methods: Effects of postbreeding behavior of mothers*. . .) are indicated in parentheses.

† Effect of female behavior on survival and reproduction was tested with Pearson's chi-square tests. Effect of female behavior on relative parturition date, litter size, and number of juveniles at weaning was tested with Kruskal-Wallis rank-sum tests.

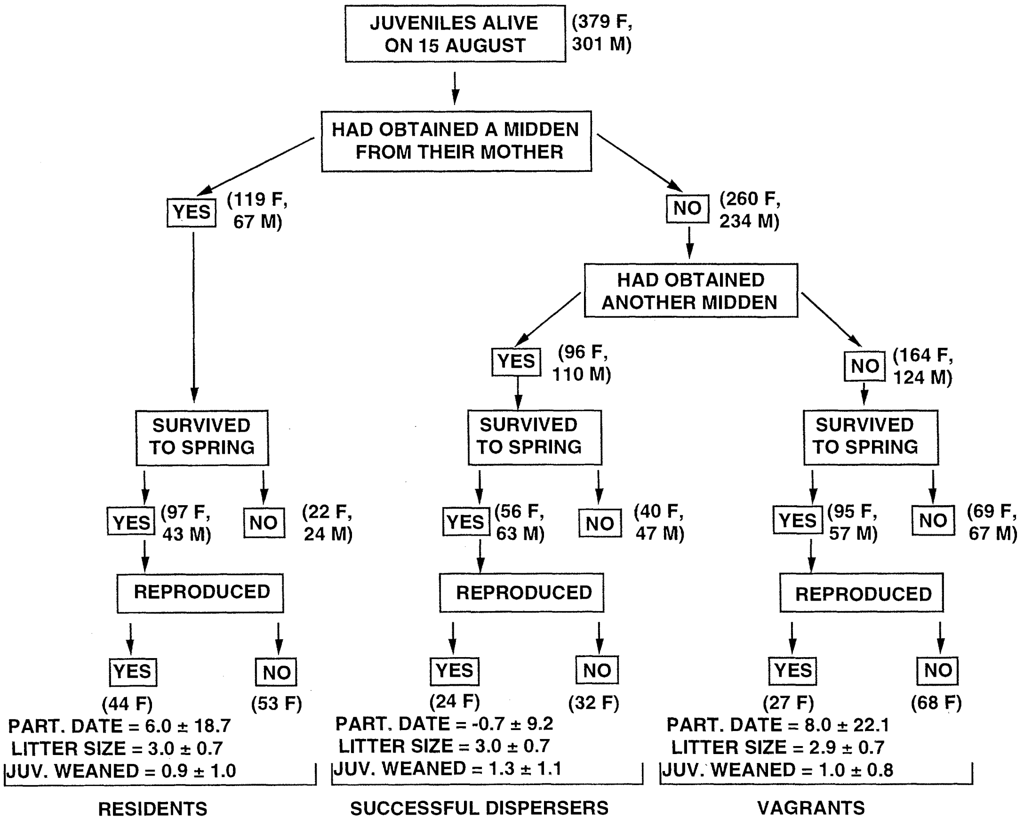

FIG. 5. Summary of results obtained from monitoring the 1989–1996 cohorts of red squirrel offspring, starting on 15 August of each year at Kluane, Yukon, Canada. Sample sizes are indicated for female (F) and male (M) individuals. "Part. date" and "Juv. weaned" refer to relative parturition date and number of juveniles at weaning, respectively.

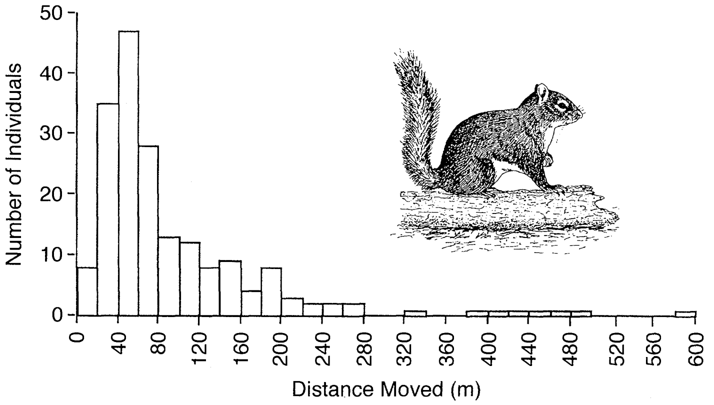

FIG. 6. Histogram of distances moved by juvenile red squirrels that dispersed from their natal site to their new territory before 15 August of each year at Kluane, Yukon, Canada. The coordinates of the natal sites were defined as the average coordinates of the middens owned by the mothers on 15 May, and the coordinates of the new territories of juvenile dispersers were defined as the average coordinates of the middens owned by the juveniles on 15 August. At the study site the average diameter of the territory is 42 m for an adult female (after Price and Boutin [1993]).

Costs to juvenile dispersal

There are two components to the cost of natal dispersal: (1) the cost of moving through unfamiliar habitat and establishing the boundaries of a new territory; and (2) the subsequent cost of living in a new environment without any resources from the parent (food hoard, burrows, etc.). We did not know if offspring dying before 15 August were residents or dispersers, so we could only measure the second component of the cost of dispersal. This was sufficient, however, to show clearly the costs associated with dispersal.

Possible advantages to philopatry include familiarity with the environment (Ambrose 1972, Greenwood and Harvey 1976), proximity to close relatives, which could imply greater tolerance from neighbors (Clutton-Brock and Harvey 1976, Waser and Jones 1983), and access to parental resources (Clark 1978, Jones 1984). In our case parental resources were middens and possibly food stores. We exclude proximity to close relatives and familiarity with the environment as major benefits of philopatry in our population. The distance at which juveniles settled from the natal site should indeed be inversely related to the probability of being close to relatives or to the familiarity with the environment, and this factor did not affect survival. Access to parental resources thus seems to be the more likely benefit of juvenile philopatry.

Costs and benefits to breeding dispersal

Relying on phenotypic correlations to measure behavioral costs is always problematic, because some confounding variables may obscure real costs (Linden and Moller 1989, Clutton-Brock 1991, Lessels 1991). We evaluated the effects of the postbreeding behavior of mothers while controlling for potential confounding variables (individual differences in age, food resources, number of weaned juveniles, and year of study), but failed to detect any survival or reproductive cost to territory sharing or breeding dispersal. Similarly, Waser and Jones (1991) found no cost or benefit to abdication of mounds by female kangaroo rats (*Dipodomys spectabilis*). It could be that costs were too subtle to be detected, that we did not control for the effect of all confounding variables in our statistical analysis, or that adult females were opportunistic and dispersed only when costs were minimal or absent.

When we analyzed the effects of explanatory variables on the behavior of mothers, we made the implicit assumption that it was increasingly costly to keep, share, or bequeath the territory. Although it remains uncertain whether this assumption is valid from a fitness perspective, there is little doubt that this is the case from an energy perspective, since considerable time and energy is required to establish the boundaries of a new territory (Larsen and Boutin 1994). More generally, analyses of parental investment are often impeded by fundamental difficulties in measuring costs of reproduction (Clutton-Brock 1984). The most important of these difficulties is that energy measures of reproductive effort may not reflect the consequences of parental effort on subsequent survival and breeding success (Clutton-Brock 1991). This should be kept in mind when interpreting our tests of parental investment theories.

Breeding dispersal of red squirrels and animal dispersal theories

Breeding dispersal and sex-biased natal dispersal.—How far individuals should move before settling, and which sex should leave the natal area, may be two independently determined phenomena (Jones 1986). We did not observe any sex bias in the distance moved by juveniles. Space to establish a territory and to harvest and store food is the most immediate and critical resource that both male and female red squirrel juveniles need before winter. There was thus no reason to expect that males should have dispersed farther than females. More generally, the sex-specific dispersal distances observed in many vertebrates may depend on what is being defended, mates or resources (Wolff 1994). Red squirrels of both sexes are highly territorial and clearly defend resources instead of mates.

We did, however, find that juvenile females were more likely to become residents on a bequeathed territory than were juvenile males. Did adults play a role in this sex-biased juvenile dispersal? Juveniles may ''voluntarily'' leave the natal site to avoid inbreeding (Wolff 1993) and thus disperse without any adult aggression, or juvenile dispersal may be forced by resident adults because of resource or mate competition (Dobson 1982, Anderson 1989). Boutin et al. (1993) observed that red squirrel mothers disperse when juveniles are still on the territory. Bequeathing mothers thus cannot influence the subsequent dispersal pattern of their juveniles. We found that the sex bias in juvenile dispersal was not different according to whether mothers had shared or bequeathed their territory. We thus conclude that the presence of the mother on the natal area was not a necessary cause for juvenile sex-biased dispersal.

Our results are in good agreement with the generally male-biased natal dispersal encountered in most mammals (Greenwood 1980, 1983). They contrast, however, with the specific pattern encountered in arboreal squirrels, where sex-biased dispersal had not been previously reported (Larsen 1993, Larsen and Boutin 1998). The occurrence of breeding dispersal in our study population may explain this contrast. As suggested earlier, which sex leaves the natal site and how far individuals move before settling may be two independently determined phenomena. In populations of red squirrels where breeding dispersal does not exist (e.g., Larsen 1993), all juveniles must leave the natal territory and no sex-biased dispersal can be observed, since males and females move the same distance before settling. In populations where breeding dispersal occurs, however, a fraction of the juveniles has the opportunity to remain on the natal territory and the tendency of females to be more philopatric can be observed, in good accordance with dispersal theory. Larsen and Boutin (1998) proposed that only the ''resource competition'' hypothesis predicts unbiased dispersal in red squirrels, a promiscuous, solitary species. Whereas the ''resource competition'' hypothesis may indeed predict juvenile dispersal trends in populations where breeding dispersal is absent, other hypotheses are necessary to account for sex-biased dispersal patterns observed when breeding dispersal occurs. This observation shows how the occurrence of breeding dispersal in a population affects our understanding of natal dispersal.

Effect of the number of middens owned by females on breeding dispersal.—Waser and Jones (1983) proposed that the extent of philopatry by young may be influenced by the level of the resource that females can share with juveniles, and Boutin and Schweiger (1988) showed that female red squirrels with large territories gave up part of their territory to their offspring. Our results are consistent with these patterns; mothers shared their territory more often when they had numerous middens. Breeding dispersal per se, however, was not influenced by midden ownership. Price and Boutin (1993) did not find that females with large territories shared their area more frequently. They suggested, however, that intruder pressure was high during their study, which maintained territory sizes very small. The small size of territories could have prevented females from sharing their territory.

Effect of territory vacancies on breeding dispersal.—In European and North American red squirrels, territory establishment by juveniles generally coincides with the availability of vacancies (Boutin et al. 1993, Wauters and Dhondt 1993, Larsen and Boutin 1994, Wauters et al. 1995). Boutin et al. (1993) showed experimentally that local vacancies increased breeding dispersal of females in North American red squirrels. In contrast with these results, we found no effect of territory vacancy on the postbreeding behavior of mothers. There may be a methodological explanation for our contrasting finding. We monitored the availability of vacant middens in May, whereas females disperse at the end of summer. Given that summer is a period of intense reorganization in the spatial structure of red squirrel populations, the index of vacancy that we used may have been too imprecise to detect the relationship between local vacancies and the probability of breeding dispersal.

Effect of food resources on breeding dispersal.—The postbreeding behavior of mothers was related to cone production in two ways. Female postweaning maternal care decreased with the previous year's cone production, but increased with the amount of cones produced the same year. At Kluane, squirrels harvest spruce cones in August. When cone production is high, squirrels do not completely deplete their stores during winter and spring, and middens still contain some cones the next summer, when females face the decision of keeping, sharing, or abandoning their territory. Our results suggest that females were more reluctant to share or abandon their middens when food stores were high than when they were low. Red squirrel mothers thus seemed to minimize costs with respect to food resources. They tended to keep their territory when their food stores were high and current cone production was low and, conversely, they dispersed more readily if they had few or no cones in their middens but current cone production was high. This contradicts Price and Boutin (1993), who had found no relation between the number of cones remaining in the middens and the postbreeding behavior of females. Their study, however, was conducted in a year with particularly low numbers of cones in the middens (possibly due to a cone failure the previous autumn), which hindered any trend detection.

Breeding dispersal of red squirrels and parental investment theories

Effect of maternal age on breeding dispersal.—According to evolutionary theory, parental investment should increase with age in iteroparous species in which survival or fecundity declines with parental age (Fisher 1930, Williams 1966*a*, *b*). Although this is one of the most important predictions of parental investment theories, few studies have demonstrated such a relationship. Cockburn (1988) applied parental investment theories to breeding dispersal and predicted that old females should be more likely to abandon their territory to offspring. We found that age of mothers was the factor explaining the largest amount of variance in postweaning maternal care, which is consistent with predictions. Note that this relationship was highly significant and consistent across years despite our inability to accurately assess the age of ~45% of mothers, which reduced the power of our test. Surprisingly, Jones (1986) did not find any relationship between breeding dispersal and age in female kangaroo rats.

Effect of the number of juveniles at weaning on breeding dispersal.—We found that maternal investment increased with the number of weaned juveniles. Winkler (1987) and Lazarus and Inglis (1986) predicted that total parental expenditure should increase with brood or litter size. Several studies have supported this prediction in birds (Biermann and Sealy 1982, Johnson and Best 1982) and mammals (Köning et al. 1988). It is often unclear, however, whether increased parental investment results from a parental strategy or from an increased demand from juveniles. Our results suggest that the effect of the number of juveniles at weaning on maternal investment resulted from a parental strategy alone, because juveniles were not able to force their mother to leave the territory. Mothers are indeed larger and clearly have higher competitive abilities than juveniles (Boutin et al. 1993, Price et al. 1986).

Effect of parturition date on breeding dispersal.—According to Winkler (1987), optimal parental effort should be lower in late breeding attempts. Although Winkler's model was developed for biparental monogamous species, it can serve as the foundation for applications to other mating systems, such as the promiscuous system of red squirrels (Winkler 1987). Three independent studies have related parental effort to breeding date in red squirrels. Price et al. (1990) showed experimentally that mothers defend early litters more strongly than late litters, suggesting that juveniles born early may be more valuable to their mother. In contrast, Price and Boutin (1993) found that mothers breeding early were less likely to bequeath their territory to their offspring than late-breeding mothers. Our results from the present long-term study show no relation between breeding dispersal and parturition date. Observation of maternal care in red squirrels thus yields conflicting evidence with respect to the relation between parental effort and breeding date, and is not conclusive regarding Winkler's predictions.

Effect of the availability of food resources on breeding dispersal.—Wittenberger (1979) and Carlisle (1982) predicted that parental investment should increase with resource availability, and some field studies have supported this prediction in mammals (e.g., Smith 1987). We found that the amount of cones produced in a given year was positively correlated with postbreeding maternal care, which offers more support for this prediction.

Effect of sex of offspring on breeding dispersal.—Parents are expected to invest more heavily in offspring of one sex if this sex bias in resource allocation provides a greater return in terms of parental fitness (Willson and Pianka 1963, Trivers and Willard 1973, Maynard-Smith 1980). In Columbian ground squirrels, mothers move their nest sites more often when a surviving yearling daughter is present (Harris and Murie 1984). In red squirrels, sexual dimorphism in body size is small, there are no major sex differences in juvenile growth, and there are no known differences in the reproductive costs of rearing sons and daughters (Boutin and Larsen 1993). Therefore, there is no suggestion that mothers should invest more in one sex than in the other. Our finding that there is no effect of the sex composition of the litter at weaning on the postbreeding behavior of mothers is thus in good agreement with predictions. It is often assumed that dispersing small mammal females should abandon their territory to daughters, not sons (e.g., Wolff 1994). Our results show that this assumption does not always hold and thus needs critical examination with any new species studied.

In conclusion, we showed that breeding dispersal in female red squirrels functioned as a form of parental investment, and that the decision to bequeath the territory to offspring was made by mothers in accordance with the major predictions of parental investment theories (Trivers 1972). We demonstrated that breeding dispersal can potentially have major impacts on the dynamics of populations, in our case through juvenile survival. Very little detailed information is currently available to compare our findings with those from other species, however, so that any generalization about the causes and consequences of breeding dispersal has to await more field data. The next step in our analysis of breeding dispersal by red squirrels should be to evaluate its effects on the demography and genetic structure of populations, and to contrast these effects with those of natal dispersal.

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