Natal dispersal of juvenile arctic ground squirrels in the boreal forest

Andrea E. Byrom and Charles J. Krebs

Abstract: Natal dispersal is assumed to be costly because of the risk of mortality, yet rarely are movement patterns and survival of dispersers observed directly. We determined the fates and dispersal distances of 150 radio-collared juvenile arctic ground squirrels from 1993 to 1995 at Kluane, Yukon Territory, Canada (61°N, 138°W). We tested the hypothesis that dispersal has a high mortality cost, and we also attempted to distinguish among three hypotheses to explain natal dispersal: competition for mates, competition for resources, and inbreeding avoidance. Juveniles were radio-collared at emergence from the natal burrow on five 9-ha grids nested within larger (1 km^2) experimental manipulations: two controls, a predator exclosure, a food-supplemented grid, and a predator exclosure + food grid. In all years and on all areas, dispersing juveniles were more likely to die than philopatric squirrels, and the risk of mortality increased with distance from the natal burrow for both sexes. Overall, survival of philopatric squirrels was 73%, whereas survival of dispersing squirrels ranged from a maximum of 40% to a minimum of 25%. Juvenile females were strongly philopatric independent of population density, except on the predator exclosure + food grid in 1995, where population density was extremely high and resources other than food were probably limiting. Resource competition may explain patterns of philopatry and dispersal in female arctic ground squirrels. Juvenile males moved farther from their natal site than females and more of them died. Males also had a strong tendency to disperse that was independent of food availability or population density, which suggests that male arctic ground squirrels ultimately may disperse to avoid either inbreeding with female relatives or intrasexual competition for mates.

Résumé : La dispersion à la naissance est considérée comme coûteuse à cause des risques de mortalité qui y sont reliés, et pourtant la survie et les déplacements des survivants ont rarement été observés directement. De 1993 à 1995, nous avons suivi 150 Spermophiles arctiques juvéniles porteurs d'un émetteur radio et déterminé leur distance de dispersion à Kluane, au Yukon, Canada (61°N, 138°O). Nous avons éprouvé l'hypothèse selon laquelle la dispersion et reliée à une mortalité élevée et nous avons également tenté d'établir laquelle, parmi trois hypothèses, peut le mieux expliquer la dispersion : la compétition pour les partenaires, la compétition pour les ressources et l'évitement de la consanguinité. Les spermophiles expérimentaux ont été munis d'un collier émetteur dès leur sortie du terrier natal dans cinq parcelles-échantillons de 9 ha situées dans des zones de manipulation expérimentale de plus grande envergure (1 km²) : deux parcelles témoins, un enclos à l'abri des prédateurs, une parcelle avec nourriture additionnelle, un enclos sans prédateurs avec nourriture additionnelle. Durant toutes les années de l'étude et à tous les endroits, les individus qui ont quitté le nid natal étaient plus susceptibles de mourir que les individus philopatriques et le risque de mortalité augmentait avec la distance parcourue depuis le nid chez les deux sexes. Globalement, la survie des juvéniles philopatriques a été évaluée à 73%, alors que celle des individus émigrants était de 40% au maximum, de 25% au minimum. Les femelles juvéniles étaient fortement philopatriques, indépendamment de la densité de la population, sauf dans la parcelle à l'abri des prédateurs avec nourriture additionnelle en 1995, alors que la densité de la population est devenue extrêmement élevée et les ressources autres que la nourriture ont probablement été limitantes. La compétition pour les ressources peut expliquer les patterns de philopatrie et de dispersion chez les femelles du Spermophile arctique. Les mâles juvéniles s'éloignaient plus de leur nid natal que les femelles et leur taux de mortalité était plus élevé. Les mâles avaient également une forte tendance à se disperser, en dépit de la disponibilité de la nourriture et de la densité de la population, ce qui semble indiquer que les Spermophiles arctiques mâles se dispersent probablement pour éviter la consanguinité ou pour éviter la compétition pour les partenaires sexuels.

[Traduit par la Rédaction]

Introduction

Natal dispersal is defined as the movement of pre-reproductive individuals from their place of birth to a new home range where they may attempt to breed (Howard 1960; Greenwood 1980; Stenseth and Lidicker 1992). It is a subject of intense interest to ecologists because it has been linked to a wide range of demographic and life-history traits (Arcese 1989; Stenseth and Lidicker 1992). The costs and benefits of dispersal may differ among age and sex classes in

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a population, depending on such factors as the evolution of mating systems and social behaviour (Greenwood 1980, 1983; Waser and Jones 1983; Wolfenden and Fitzpatrick 1984), optimal inbreeding (Shields 1982; Waser et al. 1986), habitat heterogeneity (Cockburn 1992; Gliwicz 1992), mate competition (Dobson 1982; Moore and Ali 1984), and population cyclicity (Lidicker 1975; Krebs 1992, 1996).

Processes such as dispersal and philopatry can be viewed as the behaviour of individual organisms that has demographic and genetic consequences for the population as a whole (Gaines and McLenaghan 1980; Armitage 1991). Ultimate (evolutionary) causes of animal dispersal historically have attracted considerable interest (Bengtsson 1978; Greenwood 1980, 1983; Dobson 1982; Waser 1985; Holekamp 1986; Waser et al. 1986; Shields 1987; Lidicker and Stenseth 1992). It has been proposed that individuals disperse to avoid competition for mates (Dobson 1982; Moore and Ali 1984) or to avoid inbreeding (Cockburn et al. 1985; Packer 1985; Waser et al. 1986; Halpin 1987). Food-resource limitation is also sometimes regarded as an ultimate cause of dispersal in mammals (Dobson and Jones 1985; Halpin 1987; Lidicker and Stenseth 1992). Quantifying the consequences of dispersal and philopatry can help in understanding the evolutionary costs and benefits of these processes.

To understand the ecological consequences of natal dispersal, we need to know the fate of dispersing individuals. Recent reviews of dispersal (e.g., Greenwood and Harvey 1982; Gaines and Johnson 1987; Shields 1987; Anderson 1989; Armitage 1991; Stenseth and Lidicker 1992) and field studies (e.g., Greenwood et al. 1979; Garrett and Franklin 1988; Arcese 1989; Wiggett and Boag 1989; Larsen and Boutin 1994; Van Vuren and Armitage 1994) have all emphasised the need to follow individual dispersers if we are to better understand the causes and consequences of natal dispersal. Dispersal is often associated with a high mortality rate (Gaines and McLenaghan 1980; Michener 1983; Stenseth 1983). Yet the fate of dispersing individuals is not often studied because of the inherent difficulties in identifying and tracking dispersers (Holekamp 1984*b*; McShea and Madison 1992; Waser et al. 1994). McShea and Madison (1992) highlighted some advantages of using radiotelemetry to identify dispersing individuals and determine their fate, and this technique has been used successfully to estimate sex bias, movement patterns, and survival of dispersers for a number of species (e.g., Holekamp 1984*b*; Hackett 1987; Wiggett et al. 1989; O'Donoghue and Bergman 1992; Larsen and Boutin 1994; Van Vuren and Armitage 1994).

Natal dispersal is common among ground-dwelling sciurids and is usually biased toward males (Michener and Michener 1977; Sherman 1977; Michener 1981, 1983; Holekamp 1984*a*, 1986; Wiggett et al. 1989; Armitage 1998). It has been suggested that poor survival of juvenile males during dispersal may contribute to the female-biased adult sex ratio observed in many ground squirrel species (Michener and Michener 1977; Schmutz et al. 1979; Wiggett and Boag 1992). Arctic ground squirrels (*Spermophilus parryii plesius*) are typical of this pattern, living in groups of related females and territorial males in a polygynous social structure (Armitage 1981; Michener 1983; McLean 1984). Squirrels emerge from a 7- to 8-month hibernation period in early to mid April; mating occurs when females emerge (typically 1–2 weeks after males emerge) (Carl 1971; Lacey 1991). Gestation lasts about 25 days (Lacey 1991). Both males and females are reproductively mature upon emergence as yearlings, and females normally reproduce every year during adult life, producing litters of four to seven offspring (Carl 1971; Green 1977; McLean 1985; Lacey 1991; Hubbs and Boonstra 1997). Juveniles emerge from natal burrows in mid to late June (approximately 28 days after birth). Weaning occurs within 1–2 weeks after juvenile emergence from the natal burrow, and juveniles disperse 2–3 weeks after emergence. By early to mid August, juveniles have usually settled in a permanent location (Green 1977).

Most of the geographic range of the arctic ground squirrel is in arctic and alpine tundra regions of North America and Siberia (Nadler et al. 1974; Nadler and Hoffmann 1977). Much of our understanding of the population ecology of arctic ground squirrels in North America comes from studies in arctic and alpine tundra habitats (Carl 1971; Green 1977; Batzli and Sobaski 1980) or in open meadows (McLean 1982, 1983, 1985; Lacey 1991). The population ecology of arctic ground squirrels living in boreal forest is less well known (Hubbs and Boonstra 1997). Our study is the first to investigate dispersal movements and survival of juvenile arctic ground squirrels in a boreal forest community. Potential predators of squirrels in this community include lynx (*Lynx canadensis*), coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), and great horned owls (*Bubo virginianus*).

Our objective was to investigate the consequences of dispersal and philopatry for individual juvenile arctic ground squirrels. Our first hypothesis addresses the survival cost of dispersal, whereas our second hypothesis attempts to distinguish among three evolutionary explanations for natal dispersal. We define *emigration* as the movement of a juvenile away from its natal area. Emigration may result in *dispersal* if the individual moves a distance greater than the mean diameter of an adult female's home range from its natal area and remains in the new location to breed (after Howard 1960; Greenwood 1980). Conversely, we consider *philopatry* to be minimal emigration resulting in a juvenile reaching reproductive age within an adult female's home range of average size or within contact of the maternal home range (after Anderson 1989; Greenwood 1980; Waser 1988; Smith 1993).

Hypothesis 1: Dispersing juvenile arctic ground squirrels have higher mortality rates than philopatric individuals

Predictions arising from this hypothesis are that (*i*) squirrels which move farther from their birthplace during their first active season will be more likely to die; (*ii*) if mortality during dispersal is due to predation, then juveniles protected from predators will have higher survival rates than juveniles on control sites; and (*iii*) males will have higher mortality rates than females (in this species, males are usually the dispersing sex; Carl 1971; Green 1977; Lacey 1991).

Three hypotheses have been proposed to explain natal dispersal in the context of mating systems: the competition for resources (CFR) hypothesis; the competition for mates (CFM) hypothesis; and the inbreeding avoidance (IA) hypothesis (Dobson 1982; Dobson and Jones 1985). We attempt to distinguish among these hypotheses using an existing experimental set-up designed to examine trophic linkages in the boreal forest (described below).

Hypothesis 2*a*: Juvenile arctic ground squirrels disperse in response to a shortage of limiting resources such as food (CFR hypothesis)

Predictions arising from this hypothesis are that (*i*) emigration distances will be shorter on food-supplemented areas because juveniles would be expected to move a shorter distance before finding an abundance of food; (*ii*) proportionally fewer juveniles will disperse from within food-supplemented areas; (*iii*) the proportion of juveniles dispersing will approximately equal annual survival of adults if juveniles are simply replacing residents that die; and (*iv*) emigration distances and the proportion of squirrels dispersing may increase with food supplementation if juveniles disperse in response to an increase in population density.

Hypothesis 2*b*: Juveniles disperse in response to intrasexual competition for mates (CFM hypothesis)

Because of the polygynous mating system in arctic ground squirrels (Carl 1971; Lacey 1991), it is unlikely that females disperse to avoid mate competition (Dobson 1982), so the following predictions apply only to juvenile males: (*i*) the proportion of males dispersing will be no greater than annual survival of adult males; and (*ii*) food addition will not affect emigration distances of males or the proportion of males dispersing. Alternatively, emigration distances and the proportion of males dispersing may decrease in response to food addition because males may more easily gain access to unrelated females as the population density increases.

Hypothesis 2*c*: Juveniles disperse to avoid inbreeding with close relatives (IA hypothesis)

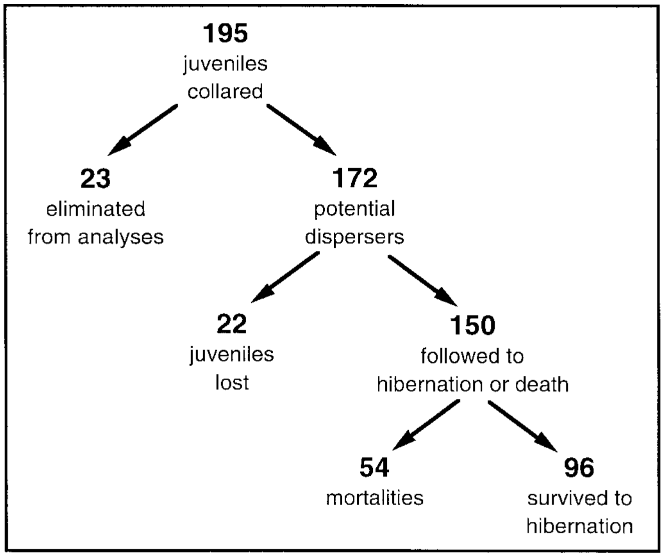
Predictions arising from this hypothesis are that (*i*) the rate at which juveniles disperse will be greater than the rate at which adults of the same sex disappear; (*ii*) juveniles of both sexes will disperse from their natal area for a distance equal to at least the diameter of one home range of an opposite-sex adult to avoid inbreeding with opposite-sex kin; and (*iii*) food addition will not affect dispersal distance or dispersal frequency of either sex. Alternatively, juveniles of both sexes may increase dispersal distances and proportion dispersing in response to supplemental food if it increases population density.

Methods

Study sites

Dispersal movements and survival of juvenile arctic ground squirrels were studied from 1993 to 1995 at Kluane in the southwestern Yukon Territory, Canada (61°N, 138°W). Squirrels of this region live in a patchy mosaic of boreal forest in which large stands of open and closed white spruce (*Picea glauca*) forest are interspersed with smaller areas of aspen (*Populus tremuloides*) stands and shrub-meadow consisting of gray willow (*Salix glauca*) and bog birch (*Betula glandulosa*). Herbaceous plants are found in meadows, open spruce, and shrub areas (Douglas 1974). All our study sites were situated in areas of approximately similar habitat (predominantly open spruce and shrub-meadow; Hubbs and Boonstra 1997).

Fig. 1. Fates of 195 juvenile arctic ground squirrels radio-collared at emergence from the natal burrow on two controls and three experimental grids from 1993 to 1995.



Squirrels were studied on five 9-ha grids nested within larger (1 km^2) manipulations. Each grid contained 100 grid points spaced 30 m apart in a 10 × 10 array: (*i*) two unmanipulated control grids; (*ii*) a food grid provisioned ad libitum with pelleted rabbit chow (minimum 16% crude protein) distributed by fertiliser spreader along four 600-m cut lines ("feeder rows"); (*iii*) a predator-exclosure grid 1 km^2 in area surrounded by an 8600-V electric fence to deter large terrestrial predators and partially covered by monofilament lines spaced approximately 30 cm apart to deter avian predators; and (*iv*) a predator exclosure + food grid 1 km^2 in area surrounded by an electric fence and provisioned with pelleted rabbit chow, but without monofilament lines. Our experimental and control grids were established in 1986 in order to examine trophic linkages in the boreal forest community as part of the Kluane Boreal Forest Ecosystem Project. The experimental set-up is described in Krebs et al. (1992, 1995), Boutin et al. (1995), and Hubbs and Boonstra (1997).

Field methods

Natal dispersal and survival of juveniles were monitored in 1993, 1994, and 1995. Juveniles emerged from the natal burrow in mid to late June each year. All juveniles were trapped in Tomahawk live traps, tagged with Monel No. 1005-1 tags (National Band and Tag Co.) in both ears, weighed to the nearest 2 g using a Pesola spring scale, sexed, and radio-collared with expandable collars (Byrom 1997). Radios were SM-1 transmitters (AVM, California) and SS-2 transmitters (Biotrack, England), both with Hg-675 batteries. The range of the radio transmitters varied from 300 to 500 m depending on topography, shrub cover, elevation of the observer, and whether individual squirrels were above or below ground. We collared at least 2 juveniles (where possible, 1 male and 1 female) per litter for a total of 8–18 juveniles on each treatment or control in each year. In total, 195 juvenile arctic ground squirrels were radio-collared (59 in 1993, 66 in 1994, and 70 in 1995); their fates are shown in Fig. 1. Not all squirrels could be used in our analyses because their radio collar fell off immediately or was chewed off by the mother (N = 22) or because they were killed on the Alaska Highway (N = 1). We located each squirrel once every 2 days with a hand-held antenna.

We measured the emigration distance of each juvenile as the straight-line distance between its place of birth (natal burrow or

Table 1. Home-range sizes for adult females and diameters of female home ranges on treatment and control grids from 1993 to 1995.

Grid	*N*	Home ranges of adult females (ha)*	Home-range diameter (m)
Controls			
1993	12	2.69±0.59	185
1994	12	3.05±0.68	197
1995	23	2.30±0.33	171
Predator exclosure			
1993	14	2.21±0.21	168
1994	15	2.37±0.56	174
1995	17	1.64±0.17	145
Food			
1993	18	0.42±0.08	73
1994	12	0.48±0.08	78
1995	16	0.38±0.13	70
Predator exclosure + food			
1993	12	0.46±0.11	77
1994	16	0.67±0.17	92
1995	20	0.37±0.09	69

Note: *N* is the number of adult females radio-collared for the entire active season. Home-range sizes on the food and predator exclosure + food treatment grids were significantly smaller than on the predator exclosure and control grids ($F = 47.47$, $p < 0.0001$).

*Mean ± SE.

mother's home burrow) and its sleeping burrow in autumn prior to hibernation. We focused on sleeping burrow locations because they provide precise end points (after Hackett 1987), and because we observed that young squirrels consistently used the same sleeping burrow post settlement. Sleeping burrows were located by radio-tracking sleeping individuals before sunrise (≈07:00) in late August. Emigration distances of squirrels that remained on the study grids were calculated using the grid coordinate system. Emigration distances of juveniles that moved beyond the study grids were determined using a Trimble Basic global positioning system (GPS). GPS coordinates obtained in the field were accurate to within approximately 20 m after being differentially corrected using a base station logging continuously at Kluane Lake Research Station.

We made four assumptions in this study. First, juveniles of both sexes were classified as dispersers if they moved a distance greater than the average diameter of an adult female's home range from the natal burrow (after Howard 1960; Greenwood 1980; Smith 1993). Home ranges of adult females were calculated using the 95% minimum convex polygon method (Jennrich and Turner 1969), and home-range sizes were estimated only for females that were present for the entire active season. Consequently, juveniles had to have moved different distances from their birthplace on different grids because females' home ranges were smaller on grids supplemented with food (Table 1). Second, we assumed that for every predated individual, the point of death (where the radio was found) was its emigration or dispersal distance. Some squirrels doubtless would have moved farther had they survived, but there was no way of knowing where they would have stopped. Third, 22 juveniles (1 female and 21 males) were lost during this study. Usually, the radio signal could no longer be picked up, and extensive searches were carried out on the treatment areas and for a radius of at least 1000 m around each area. We therefore calculated survival in one of two different ways, by censoring lost squirrels from the analyses or by assuming that all lost squirrels had died, to provide upper and lower bounds for survival estimates. We excluded squirrels that disappeared from analyses of emigration distance. Some radio collars may have failed; however, no squirrels with nonfunctional collars were caught during extensive trapping sessions on the grids in late summer each year. We therefore assumed that most of these lost individuals had dispersed beyond our study sites. Finally, we assumed that the location at which a squirrel was found dead was the location at which it was killed by a predator. Most predators of arctic ground squirrels were not breeding during our study because of low numbers of their primary prey, snowshoe hares (F. Doyle and M. O'Donoghue, personal communication). Hence, predators tended to kill prey and eat them immediately rather than carry them to another location. In addition, there was often other evidence that a squirrel had been killed where the collar was found, such as whitewash, pellets, feathers, or plucked fur (avian predators) or intestines or scats (mammalian predators).

Statistical analyses

Statistical analyses were carried out using JMP (SAS Institute 1994) following protocols in Sokal and Rohlf (1995). Data were checked for normality and homoscedasticity, and were log-transformed where appropriate. Nonparametric tests were carried out if the data did not satisfy these assumptions after transformation. Population densities on all grids were estimated using the program CAPTURE (Otis et al. 1978). We compared emigration distances of males and females using a Mann–Whitney *U* test. We used logistic regression to compare survival of dispersers and nondispersers, with distance as the continuous independent variable and survival (alive or dead) as a binomial dependent variable. Contingency-table analyses were performed to compare the proportions of individuals dispersing among treatments and controls. We used *G* tests to determine whether each sex was more or less likely to disperse than expected on the basis of home-range turnover in the adult population. Estimates of survival of philopatric and dispersing juveniles, and of juvenile survival on each treatment grid, were compared using a Kaplan–Meier estimate (Krebs 1989; Pollock et al. 1989).

Results

Population trends and survival, 1993–1995

Population densities of arctic ground squirrels on predator exclosure, food, and predator exclosure + food grids were 2–10 times higher than those on controls (Fig. 2). From 1990 to 1992, population densities declined on all grids, possibly as a result of increased predation after the decline in snowshoe hare numbers (Byrom 1997). From 1993 to 1995, densities of squirrels on most sites were relatively low but increasing. Densities on the predator exclosure + food treatment grid in 1995 were particularly high (45.6 adult and juvenile squirrels/ha by late summer 1995). We found no significant difference in juvenile survival among treatments and controls in any year (Table 2). Juvenile squirrels from the predator exclosure and predator exclosure + food treatments did not survive significantly better than squirrels from other study sites, perhaps because they occasionally dispersed beyond the relative safety of the fences or monofilament lines and were therefore exposed to the same predation intensity as squirrels from unfenced areas (Byrom 1997).

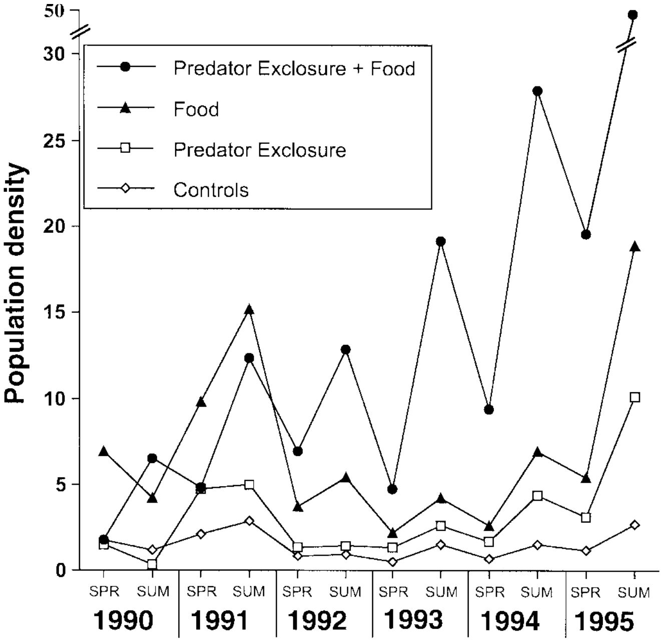
Sex-specific dispersal

Juvenile females moved a mean distance of 120.3 ± 27.9 (SE) m, with a median of 61 m, from their natal area. Juvenile males moved a mean distance of 515.0 ± 106.6 (SE) m, with a median of 241 m, from their natal area (Table 2). For juvenile males, median and mean dispersal distances are probably underestimated because we lost 21 males, many of which were long-distance dispersers. Over half (68%) of all juveniles classified as dispersers were male, and males moved significantly farther than females (Mann–Whitney U test, $U = 1302$, $N = 150$, $p < 0.0001$) when all treatments and all years were combined. Early in the dispersal process, males and females showed distinctly different patterns of emigration and dispersal. Most females remained close to their natal site and establishment of a new home range was the culmination of a gradual process involving increasingly ambitious exploratory forays. Conversely, males often appeared to make a one-time decision to leave the natal site and within 1–2 days were likely to be several hundred metres from their birthplace.

From livetrapping data, we calculated spring-to-spring annual mortality of adult females to be 0.47 from 1992 to 1995. Hence, if juvenile females were claiming spaces that became available, 47% would be expected to stay and 53% would be expected to disperse. However, most (88%) females were philopatric, and females were significantly more likely to remain philopatric than expected ($G = 25.76$, $\chi^2 = 10.83$, df = 1, $p < 0.001$). Similarly, we calculated adult male annual mortality to be 0.78. If juvenile males were filling available spaces left vacant by adult males, 78% of juvenile males would be expected to remain philopatric and 22% would be expected to disperse. Yet only 28% of juvenile males were philopatric and 72% dispersed. Hence, juvenile males were significantly more likely to disperse than expected on the basis of mortality or disappearance of adult males ($G = 55.8$, $\chi^2 = 10.83$, df = 1, $p < 0.001$).

None of our experimental manipulations had a consistent effect on emigration distance (Table 2). Emigration distances of males did not vary among years (Kruskal–Wallis test, $\chi^2 = 0.43$, df = 2, $N = 49$, $p > 0.81$), whereas females moved significantly farther in 1995 (Kruskal–Wallis test: $\chi^2 = 9.02$, df = 2, $N = 101$, $p < 0.01$), probably because females on the predator exclosure + food grid moved unusually long distances in 1995 (Table 2). There were no differences in emigration distance among sites for either sex in any year except on the predator exclosure + food grid in 1995, where both males and females moved significantly farther from their natal site. When all 3 years were combined, there were no significant differences among grid treatments in juvenile male and female dispersal distances (Kruskal–Wallis test, females: $\chi^2 = 2.11$, $N = 101$, df = 3, $p > 0.55$; males: $\chi^2 = 1.38$, $N = 49$, df = 3, $p > 0.71$). Neither sex dispersed shorter distances on treatment grids with supplemental food in any year.

Fig. 2. Population density (number of squirrels/ha) on two control and three experimental grids in spring (SPR) and summer (SUM) from 1990 to 1995.



Dispersal and survival

Juvenile squirrels that died moved a mean distance of 512.1 ± 125.5 (SE) m (median = 144 m) from their natal area, whereas squirrels that survived their first active season moved a mean of 143.8 ± 24.6 (SE) m (median = 62 m). Most (97%) juvenile squirrels died from predation (Table 3). In addition, the mortality rate of dispersers was significantly higher than that of philopatric squirrels (Fig. 3). This trend was consistent among treatments in all years. Overall, survival of dispersers ranged from a maximum of 40% (95% confidence limits (CL) = 23–57%) (calculated by censoring lost individuals from the analysis) to a minimum of 25% (95% CL = 13–36%) (calculated by assuming that all lost individuals had died). The survival rate of philopatric squirrels was 73% (95% CL = 62–83%) (Fig. 3).

We examined whether mortality increased with distance from the natal burrow by plotting the proportion of radio-collared squirrels that survived to any given distance from their natal site (Fig. 4). Squirrels of both sexes faced a low risk of mortality if they moved less than approximately 100 m from their natal site. Females were much more likely to perish if they moved farther than this, whereas male survival continued to decline more slowly until they were approximately 1000 m from the natal burrow (Fig. 4). While more juvenile males were classified as dispersers, and males were more likely to die, some juvenile females also dispersed long distances and died. Although mortality was usually male-biased, it was female-biased on the predator exclosure + food treatment grid in 1995. Overall, juveniles that moved farther from their natal site were more likely to die (logistic regression: $r^2 = 0.09$, $N = 150$, df = 1, $p < 0.002$).

Proportion of individuals dispersing from treatment grids

From 1993 to 1995, between 0 and 86% of radio-collared females and between 40 and 100% of radio-collared males dispersed from the treatment grids (Table 2). The proportions of dispersers of each sex were consistent among treatments in each year with the exception of the predator exclosure + food treatment grid in 1995, which had a significantly higher proportion of dispersers (Table 2). Plotting the rate of dispersal of both sexes from the treatment grids as a function of density of adults in spring (Fig. 5) revealed no trend for juvenile males and only weak density dependence

Table 2. Mean and median emigration distances, survival rates, and proportions of juveniles classified as dispersers on all grids for 150 juvenile arctic ground squirrels radio-collared during each active season from 1993 to 1995.

Year and grid	N	Emigration distance (m)		28-day survival rate (95% CL)	Proportion dispersing
		Mean ± SE	Median		
1993					
Controls	6 F	133.5±27.9	109	0.88 (0.62–1.00)	0.33
	2 M	—	—	—	1.00
Predator exclosure	9 F	122.4±35.4	91	0.84 (0.55–1.00)	0.33
	8 M	718.5±278.5	572	0.08 (0.00–0.17)	0.75
Food	9 F	122.4±49.4	99	0.85 (0.57–1.00)	0.56
	6 M	352.0±205.9	259	0.58 (0.00–0.86)	0.83
Predator exclosure	4 F	39.3±18.9	28	0.72 (0.00–1.00)	0.25
+ food	7 M	49.5±21.2	50	0.76 (0.40–1.00)	0.57
1994					
Controls	8 F	58.9±15.2	57	0.71 (0.46–0.87)	0
	4 M	502.5±208.1	529	0.68 (0.00–1.00)	0.75
Predator exclosure	10 F	47.0±8.5	51	0.92 (0.79–1.00)	0
	5 M	409.8±146.1	258	0.53 (0.00–0.80)	0.80
Food	13 F	42.5±7.0	43	0.97 (0.90–1.00)	0.08
	5 M	186.5±106.0	95	0.74 (0.00–1.00)	0.60
Predator exclosure	9 F	45.6±15.0	32	1.00	0.22
+ food	6 M	520.5±162.5	521	0.57 (0.00–0.78)	1.00
1995					
Controls	9 F	66.0±13.3	67	0.88 (0.62–1.00)	0
	7 M	256.5±214.1	65	0.57 (0.00–0.88)	0.57
Predator exclosure	9 F	53.7±18.2	49	1.00	0.11
	5 M	305.8±157.7	99	0.91 (0.36–1.00)	0.40
Food	9 F	252.8±197.4	47	0.87 (0.59–1.00)	0.33
	7 M	423.0±194.7	399	0.81 (0.00–1.00)	0.71
Predator exclosure	7 F	685.0±276.4	464	0.53 (0.00–0.78)	0.86
+ food	8 M	1693.4±792.0	1286	0.35 (0.00–0.61)	0.86
Total	102 F	120.3±27.9 (N = 101)	61 (N = 101)		
	70 M	515.0±106.6 (N = 49)	241 (N = 49)		

Note: Significantly more juveniles dispersed from the predator exclosure + food grid in 1995 (χ^2=16.82, df = 3, $p < 0.001$). Survival rates were calculated using a Kaplan–Meier estimate (Pollock et al. 1989). Numbers in parentheses are 95% CL.

Table 3. Proximate causes of mortality of radio-collared juvenile arctic ground squirrels during the active season, 1993–1995.

Predator	1993		1994		1995	
	N	%	N	%	N	%
Goshawk	7	33.3	3	17.0	1	6.7
Red-tailed hawk	2	9.5	1	5.5	—	—
Great horned owl	—	—	2	11.0	—	—
Suspected weasel	—	—	1	5.5	—	—
Unknown bird	6	28.6	3	17.0	3	20.0
Unknown mammal	2	9.5	—	—	—	—
Unknown predator	4	19.0	6	33.3	11	73.3
Unknown nonpredator	—	—	2	11.0	—	—
Total	21		18		15	

for females (males: $r^2 = 0.06$, $N = 12$, $F = 0.73$, $p > 0.41$; females: $r^2 = 0.51$, $N = 12$, $F = 10.20$, $p < 0.01$; females with predator exclosure + food treatment grid in 1995 excluded: $r^2 = 0.03$, $N = 11$, $F = 0.29$, $p > 0.60$). At artificially high densities (on the predator exclosure + food treatment grid in 1995), females showed strong density dependence in dis-

Fig. 3. Survivorship of dispersing and philopatric juvenile arctic ground squirrels in their first active season (from emergence from the natal burrow to hibernation) on all grids from 1993 to 1995. The lower curve shows minimum survivorship of dispersing squirrels, assuming that squirrels which were lost during the study ($N = 22$) had died. The middle curve shows maximum survivorship of dispersers; squirrels that were lost were censored for this analysis.

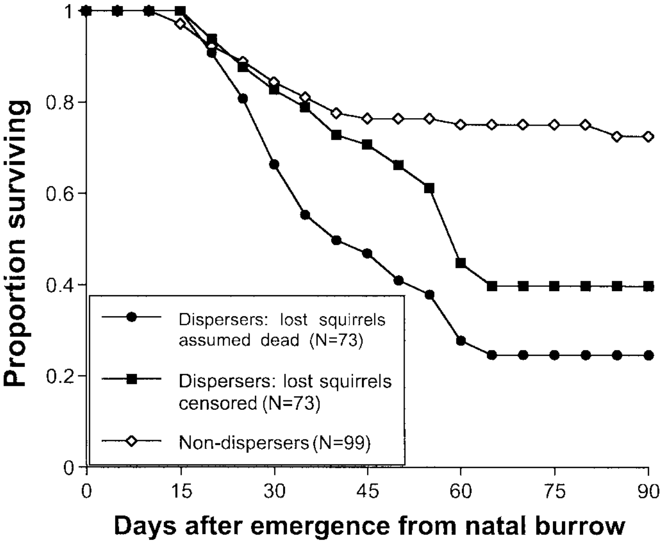


Fig. 4. Risk of mortality faced by juvenile arctic ground squirrels with increasing distance from the natal burrow. The curves show the proportion of squirrels moving a given distance and surviving until they reached that distance; points at which mortalities occurred are plotted. Note the logarithmic scale on the x axis.

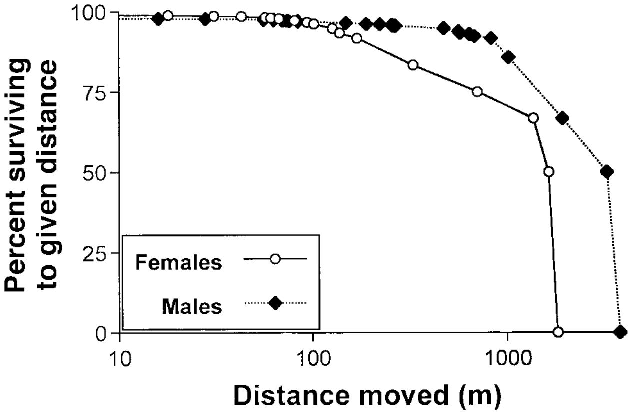
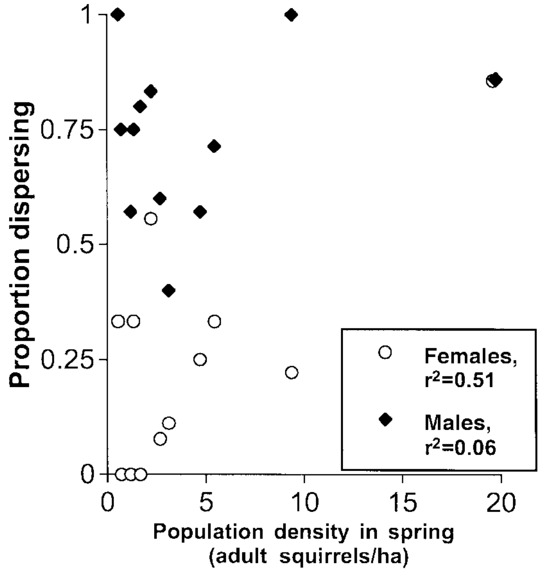


Fig. 5. Proportions of juvenile male and female arctic ground squirrels dispersing as a function of density of adults in spring from 1993 to 1995. Each point represents 3–13 radio-collared squirrels on a particular treatment in a particular year ($N =$ 12 treatment-years).



persal tendency. Male dispersal, however, was largely independent of density. We also correlated the proportion of each sex dispersing in each year with two other relevant demographic variables: adult survival during the active season and litter size. There was no relationship between litter size and dispersal rate (males: $r^2 = 0$, $N = 12$, $F = 0.005$, $p > 0.95$; females: $r^2 = 0.05$, $N = 12$, $F = 0.52$, $p > 0.49$) or between active-season survival rates for adults and dispersal rate (males: $r^2 = 0.11$, $N = 12$, $F = 1.34$, $p > 0.27$; females: $r^2 = 0$, $N = 12$, $F = 0.02$, $p > 0.89$).

Discussion

Patterns of mortality and dispersal in arctic ground squirrels

In this paper we describe the fate of 150 juvenile arctic ground squirrels from emergence to hibernation. We do not reject the hypothesis of no survival cost of natal dispersal for arctic ground squirrels. Juveniles that moved farther from their natal area were more likely to die, and the risk increased with distance from the natal site. Males also moved farther and had higher mortality rates than females. It is often assumed that dispersal is risky because dispersers may be more susceptible to predation while in transit (e.g., Metzgar 1967; Schmutz et al. 1979; Gaines and McClenaghan 1980; Greenwood and Harvey 1982; Stenseth 1983; Waser et al. 1994). Most of our radio-collared juveniles died from predation, and our study verifies these assumptions for a polygynous ground-dwelling squirrel.

Previously published evidence for higher mortality rates of dispersers is mixed. In some studies, dispersers are known or suspected to have lower survival rates than philopatric individuals. Schmutz et al. (1979) concluded that the disappearance of juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) during dispersal was probably due to predation mortality. Wiggett et al. (1989) followed eight radio-collared dispersers from a Columbian ground squirrel (*Spermophilus columbianus*) colony and estimated a minimum survival rate of 67% during dispersal, but they gave no estimate of survival of nondispersing squirrels. Van Vuren and Armitage (1994) radio-tracked 123 yearling yellow-bellied marmots (*Marmota flaviventris*) over an 8-year period; the survival rate of dispersers (73%) was lower than that of philopatric individuals (87%), but the authors concluded that the survival rate was high enough to make dispersal a viable option. Garrett and Franklin (1988) estimated a survival rate of 44% for intercolony natal dispersers from a black-tailed prairie dog (*Cynomys ludovicianus*) colony compared with 90% for residents and nondispersers. In other studies, reported survival costs of dispersal are negligible. Hackett (1987) found no evidence that yearling Columbian ground squirrels were more likely to die while making excursions or dispersing, and he concluded that dispersal was no more risky than philopatry. In his study, yearlings dispersed shorter distances than in our study (maximum 980 m, compared with at least 3815 m), and remained within a familiar open meadow habitat. Greenwood et al. (1979) could find no survival cost to natal dispersal in great tits (*Parus major*). Boyce and Boyce (1988) found the survival cost of dispersal in the field vole, *Microtus arvalis*, to be negligible (of 42 radio-collared juveniles, 1 young female disappeared). These figures compare with maximum survival rates in our study of 40% for dispersing arctic ground squirrels and 73% for philopatric individuals.

Patterns of dispersal and philopatry of radio-collared arctic ground squirrels differed markedly between the sexes. Holekamp (1984*a*) and Hackett (1987) have both suggested that exploratory movements in Belding's ground squirrels (*Spermophilus beldingi*) and Columbian ground squirrels, respectively, served to familiarise individuals with areas into which they might subsequently immigrate. In arctic ground squirrels, the risk of mortality was low for squirrels of either sex for approximately the first 100 m from the natal site (Fig. 4). Thereafter the risk increased substantially for juvenile females. Home-range diameters of adult females ranged from 69 to 197 m during our study and it is possible that if juvenile females left their mother's home range, their chances of survival declined. Conversely, the sudden increase in risk faced by a juvenile male at approximately 1000 m from the natal site was not coincident with the mean home-range diameter of adult squirrels of either sex. Males typically left their natal area quite suddenly and made long-distance dispersal movements, and we believe that such sudden moves into unfamiliar surroundings may expose young males to a higher risk of predation during dispersal. Interestingly, females on the predator exclosure + food grid in 1995 made uncharacteristically long and sudden movements and had correspondingly lower survival rates as a result (Table 2). We also found that squirrels from areas protected from predators did not have higher survival rates than control juveniles, because they often moved beyond the relative safety of the fences or monofilament lines (Byrom 1997).

The consistently high mortality rates of juvenile males in this study may explain the biased sex ratio among adult arctic ground squirrels. It also corroborates the results of other studies on ground-dwelling sciurids (e.g.,Waterman 1992; Wiggett and Boag 1992). Michener and Michener (1977) suggested that yearling male Richardson's ground squirrels had higher mortality rates because of lower over-winter survival and possibly predation in their first year of life. Schmutz et al. (1979) observed that mortality from predation fell disproportionately among male Richardson's ground squirrels, but found no disproportionate loss of males over winter. Armitage (1991) attributed the female-biased adult sex ratio in yellow-bellied marmots to differential mortality, specifically predation mortality on 2-year-old males. Our study provides support for the idea that active-season survival before an individual reaches reproductive age is probably a critical stage in the annual cycle of ground-dwelling sciurids (Michener and Michener 1977; Michener 1983; Armitage 1991).

Our observation that male arctic ground squirrels moved, on average, farther from their birthplace than females is consistent with observations by Carl (1971), Green (1977), Schmutz et al. (1979), Holekamp (1984*a*, 1984*b*), and Garrett and Franklin (1988) that young male sciurids disperse farther than females, as is commonly assumed for mammals. Not all studies support this assumption; dispersing yearling and adult female Columbian ground squirrels have been reported to move at least as far as adult males (Boag and Murie 1981; Hackett 1987). In our study, some females also made large movements, the longest (1820 m) being from the predator exclosure + food treatment grid in 1995. The high frequency of long-distance movements in males meant that we lost track of more males than females. We suspect that many of these young males died from predation in their first active season. If so, this strengthens our conclusion that differential mortality occurs during dispersal in this species. Likewise, estimates of mean and median emigration distances for males were probably underestimates, owing to the greater likelihood of locating squirrels whose emigration distances were shorter, so the differences we observed between males and females, and between squirrels that died and squirrels that survived their first active season, were probably conservative.

Hypotheses to explain the evolution of natal dispersal

We found little relationship between population density and dispersal of arctic ground squirrels of either sex over the range of population densities normally observed in boreal forest habitats. Female philopatry was largely independent of population density, although the high proportion of females dispersing from the predator exclosure + food grid in 1995 suggests that there may be a threshold at which some aspect of density (limited food availability, limited number of burrows, or high rates of social interactions) leads to a sharp increase in female dispersal. Hence, the relationship between population density and female dispersal is likely nonlinear in this species. We observed that natural food (herbaceous plants and willow leaves) was severely depleted on the predator exclosure + food grid in 1995, along with other resources such as suitable burrow sites. On all other grids, however, squirrel population densities were relatively low and increasing from 1993 to 1995 (Fig. 2), so available food resources, burrow sites, and moisture may not have been limiting at the densities normally observed during this study. Natal dispersal of males was density-independent, but no population density was so low that dispersal of males was unlikely to occur.

Juveniles from food-supplemented grids moved at least as far as juveniles from control grids, and food-supplemented grids had at least as many dispersers as control grids in all years. Juvenile male arctic ground squirrels showed little change in emigration distance or tendency to disperse in response to supplemental food, with the exception of the predator exclosure + food grid in 1995 (Table 2). Furthermore, males dispersed from their natal area more often than expected if juveniles were simply replacing residents that died and left home ranges vacant. We therefore rejected the hypothesis that resource competition explains natal dispersal for male arctic ground squirrels. The IA hypothesis is a better explanation for juvenile male dispersal in this species, although we cannot rule out the possibility that males also disperse to avoid intrasexual competition for mates. Conversely, juvenile females usually moved less than one adult female home range from their natal area, and were philopatric more often than expected on the basis of annual mortality of adult females. Dispersal of juvenile females occurred only at unusually high population densities, so the CFR hypothesis likely explains the movement patterns of juvenile female arctic ground squirrels. The process of dispersal involves not only emigration from the natal area and movement away from that area, but also settlement in a new location. In our study we were unable, for logistic reasons, to examine the ecological and environmental factors influencing settlement of dispersing squirrels. Had we been able to do so, we may have been able to examine settlement patterns in relation to the CFR, CFM, and IA hypotheses for both sexes. Factors such as conspecific density and habitat characteristics of areas travelled through, and settled in, remain largely unquantified in many dispersal studies.

Nevertheless, our results corroborate other available data which indicate that natal dispersal of male sciurids does not occur in response to resource limitation, whereas resource limitation may have a strong influence on philopatry and dispersal in females (Holekamp 1986; Nunes et al. 1997; Armitage 1998). Dobson (1979) gave a California ground squirrel (*Spermophilus beecheyi*) population supplemental food for 3 months to determine whether food availability influenced yearling dispersal, and monitored dispersal movements using peripheral trapping grids. Young males disappeared from their natal colonies regardless of food availability, whereas young females either moved onto the site with supplemental food or commuted regularly to it to obtain food. Dobson (1979) concluded that young males disperse to avoid inbreeding, whereas young females disperse only if population density is high relative to food availability. Dobson and Kjelgaard (1985) observed that supplemental food increased immigration of Columbian ground squirrels, particularly females, onto a food-supplemented site. Conversely, Nunes et al. (1997) supplied extra food to female Belding's ground squirrels during pregnancy and lactation and to their offspring for 6 weeks after weaning. Competition for food had no influence on dispersal of young males: they dispersed regardless of whether they and their mothers received extra food. However, young females on food-supplemented areas were more likely to emigrate from their natal area, which Nunes et al. (1997) attributed to higher rates of aggression and vigilance as a result of higher population densities in food-supplemented areas. It is possible that the dramatic increase we observed in female emigration distances and dispersal tendency on the predator exclosure + food grid in 1995 may be a similar response to high population density. By following radio-collared squirrels born on food-supplemented sites, we have confirmed in our study the patterns observed in other ground squirrel species, and have clarified the relationship between dispersal and resource availability for both sexes.

Several problems arise in attempts to explain dispersal patterns in the context of mating systems. First, Dobson (1982) and Dobson and Jones (1985) have pointed out that the three hypotheses commonly proposed to explain the evolution of natal dispersal (CFM, CFR, and IA) are not mutually exclusive. Consequently, juvenile males may be dispersing for the dual purpose of increasing access to unrelated mates and decreasing intrasexual competition (Dobson and Jones 1985), and this is also a plausible explanation for the dispersal patterns we observed in male arctic ground squirrels. Second, the conclusion that juveniles disperse to avoid inbreeding may be reached by combining a number of different proposed mechanisms. For example, Holekamp (1984*b*) concluded that Belding's ground squirrels were dispersing to optimise inbreeding (after Shields 1982) rather than completely avoid inbreeding. Clearly, the IA hypothesis needs further investigation at both the ecological and the genetic level, and requires some understanding not only of emigration patterns but also of the ecological, demographic, and environmental cues that animals use during settlement. Third, many authors have confused proximate and ultimate reasons for natal dispersal when explaining observed patterns of dispersal and philopatry. For example, Holekamp (1986) cautions that resource limitation can be regarded as either a proximate or an ultimate cue for natal dispersal. The reproductive success of dispersing individuals may be enhanced by improving access to food resources and breeding sites (Greenwood 1980), yet resource availability may also be the proximate mechanism causing animals to leave their natal area or to choose to settle in a new area (Holekamp 1984*b*, 1986). Finally, McCarthy (1997) presented several models of competition among dispersing individuals, and argued that dispersal distances can change in complex ways as population density increases. Our results are in accordance with these models; we found that an increase in population density did not necessarily lead to an increase in dispersal tendency for either sex, except at artificially high population densities (Fig. 5). Clearly, the relationship between dispersal and density bears further investigation, and future research could focus on whether and how individuals of a particular age or sex class use resource limitation as the cue for dispersal.

Two related factors cloud our interpretation of which of the three commonly proposed hypotheses, CFR, CFM, or IA, best explains the patterns of dispersal and philopatry we observed in arctic ground squirrels. First, increasing the amount supplemental food for small-mammal populations not only increases food availability per se, but also results in dramatic changes in a host of other demographic variables, including population density (Desy and Batzli 1989; Boutin 1990). Increases in density may lead to higher rates of agonistic interactions among conspecifics and a scarcity of resources other than food (e.g., burrows), causing females to emigrate from areas of high conspecific density, as was observed in Belding's ground squirrels by Nunes et al. (1997). In our study also, it appears that density on the predator exclosure + food grid reached some threshold at which many females dispersed. Likewise, although food addition had little influence on male emigration distance or tendency to disperse, the resultant changes in population density on food-supplemented grids may have complicated our interpretation concerning which of the hypotheses is the most appropriate to explain the dispersal tendency of males. For example, males may move shorter or longer distances on food-supplemented areas depending on relatedness among females in the population. Second, our study was carried out during a period in which population densities of arctic ground squirrels in the boreal forest were relatively low but increasing (Fig. 2). In particular, females on most grids tended to remain close to their natal site, and we observed that more than one female from each litter chose to do so, resulting in an increase in overlap of adult female home ranges and a buildup of matrilines from year to year (Byrom 1997). Strong philopatric tendencies in more than one female in each litter may explain the nonlinear relationship we observed between female dispersal and population density; if resources are not limiting, females may remain on or close to their mother's home range even when their sisters do also. We believe that the patterns of dispersal and philopatry we observed in juvenile male arctic ground squirrels may be the result of equally complex responses to changes in female density and home-range overlap.

Processes such as dispersal and philopatry are often regarded as the behaviour of individual organisms that has demographic and genetic consequences for the population as a whole (Gaines and McLenaghan 1980; Hackett 1987; Armitage 1998). Wolfenden and Fitzpatrick (1984) argued that cooperative breeding in Florida scrub jays (*Aphelocoma coerulescens*) evolved in response to limited opportunities for successful natal dispersal. Michener (1983) linked the evolution of sociality in ground-dwelling sciurids to the advantages of female philopatry and range sharing as well as the advantages of male dispersal and territoriality. Arctic ground squirrels fit this general pattern, and the fate of individual juvenile squirrels can be linked to the demography and social structure of the population as a whole. It would be fruitful to examine the fitness consequences of philopatry and dispersal to further clarify the ultimate reasons for these strategies. In a future publication we focus on the reproductive consequences of philopatry and dispersal for female arctic ground squirrels.

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