Dispersal of juvenile collared lemmings (*Dicrostonyx groenlandicus*) in a high-density population

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Abstract: We tested whether dispersal of juvenile lemmings occurs at high population densities and whether predation risk affects movements of juveniles. The study was conducted in July and August 1996 on the Kent Peninsula, Northwest Territories, during a peak in the lemming cycle. We fitted 43 juvenile collared lemmings (*Dicrostonyx groenlandicus*) of the summer generations on a control plot and a predator-exclosure plot with radio transmitters and examined their home ranges and movement patterns. We tested the following hypotheses: (*i*) extensive juvenile dispersal will occur at high population densities, (*ii*) male juveniles will move greater distances than females, and (*iii*) juveniles will move greater distances in the absence of predators. We rejected all these hypotheses. All juvenile collared lemmings remained in the vicinity of their original home ranges. Home-range sizes of all juveniles were similar, the mean size being 100 m^2. Mean and maximum distances moved were similar among all juveniles. However, juveniles moved less frequently on the control plot than on the exclosure plot. Juvenile collared lemmings do not disperse at high densities. The lack of dispersal may have been the result of avoidance of confrontations with other lemmings, and may also have been related to delayed breeding, since most juveniles and subadults did not mature in late summer. Differential predation risk or predation mortality may have had no effect on the distances moved by juveniles or may have been masked by strong density effects on both plots.

Résumé : Nous avons tenté de déterminer si les jeunes lemmings se dispersent lorsque la densité de la population est élevée et si les risques de prédation affectent leurs déplacements. Nous avons fait cette étude en juillet et août 1996, dans la péninsule de Kent, Territoires du Nord-Ouest, alors que la densité de la population de lemmings était très élevée. Nous avons muni d'émetteurs radio 43 Lemmings variables (*Dicrostonyx groenlandicus*) juvéniles des générations d'été dans une grille échantillon témoin et dans une enceinte sans prédateurs et avons évalué leurs domaines et suivi leurs déplacements. Nous avons éprouvé trois hypothèses: (*i*) il se fait une importante dispersion des lemmings juvéniles lorsque la densité de la population est élevée, (*ii*) les jeunes mâles parcourent de plus grandes distances que les femelles et (*iii*) les juvéniles parcourent de plus grandes distances en l'absence de prédateurs. Nous avons rejeté toutes ces hypothèses. Tous les lemmings juvéniles sont restés dans le voisinage de leur domaine d'origine. Les domaines de tous les jeunes étaient semblables, de 100 m² en moyenne. Les distances moyenne et maximale parcourues étaient à peu près les mêmes chez tous les juvéiles. Cependant, les juvéniles se sont déplacés moins fréquemment dans la grille témoin que dans l'enceinte. Les lemmings juvéniles ne se sont pas dispersés à densité élevée. Il est possible que les lemmings juvéniles ne se soient pas dispersés pour éviter les confrontations avec d'autres lemmings ou peut-être aussi à cause d'un retard dans la reproduction, puisque la plupart des juvéniles et des sub-adultes n'avaient pas atteint leur maturité à la fin de l'été. Les différences dans les risques de prédation ou la mortalité reliée à la prédation peuvent n'avoir eu aucun effet sur la distance parcourue par les juvéniles dans l'une ou l'autre grille ou alors leurs effets peuvent avoir été masqués par ceux de la densité élevée de la population.

[Traduit par la Rédaction]

Introduction

Dispersal is the permanent movement of an animal away from its birthplace (Lidicker 1975). Such movement can affect the dynamics of a population, not only through its effects on immigration and emigration rates, but also by altering the genetic composition of the population (Krebs et al. 1973; Tamarin 1977). Dispersing animals may experience differential mortality and reproductive success, and may influence individuals in the receiving population (Lidicker 1975). In cyclic populations of small mammals, the rate of dispersal may vary with the phase of the cycle (Myers and Krebs 1971). Changes in dispersal rate may in turn affect the rate of population change. Several researchers have proposed dispersal as a contributing cause of population cycles (Krebs et al. 1973; Lidicker 1975; Krebs 1978*a*; Stenseth 1983; reviewed by Krebs 1992).

A number of hypotheses have been proposed to explain the proximate causes of dispersal (Gaines and McClenaghan 1980). The decision to disperse may be based on the out-

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come of social interactions with siblings or others (Bekoff 1977), including aggressive socially superior animals (Christian 1970) and parents of the opposite sex (Wolff 1993). When the population is below carrying capacity, most dispersers may be animals in good condition responding to increasing population density or available habitat ("presaturation dispersal"; Lidicker 1975; Stenseth 1983; Stenseth and Lidicker 1992). When the population is at or near carrying capacity, the dispersing animals may instead be low-quality or subordinate animals that would die if they remained ("saturation dispersal"). Animals that disperse may be of a particular genetic (Howard 1960) or behaviour (Chitty 1967) type. Dispersal may become increasingly disadvantageous as the population grows, because the survival rate of dispersers is lowered by hostile interactions with animals they encounter (Krebs 1978*a*, 1978*b*).

In increasing populations, recruits can amplify crowding (Chitty 1960) or resource shortages (Pitelka 1957). Since juveniles may be poorly equipped to compete for space with established adults, they may be the primary dispersing age-class in high-density populations. Juvenile males are often the predominant class of dispersers in mammalian populations, and may be seeking better habitat or unrelated mates (Greenwood 1980). Krebs (1978*b*) proposed that most saturation dispersers should be pubertal juveniles.

There are also strong arguments against the likelihood of juvenile dispersal. First, at high population densities, declines in resources (Chitty 1960) and increased inbreeding (Charnov and Finerty 1980) may not be sufficient to affect individuals. Second, agonistic social interactions between unrelated individuals (Garrett and Franklin 1988) may deter juveniles from leaving their natal home ranges. Third, there may be no social pressure from within natal areas for juveniles to disperse (Holekamp 1984; Boyce and Boyce 1988; Wolff 1992). Finally, predation is a major cause of mortality of small mammals (Heske et al. 1993; Norrdahl and Korpimäki 1995; Reid et al. 1995; Steen 1995) and may be positively related to movement rates (Garrett and Franklin 1988; but see Boyce and Boyce 1988 and Brooks 1993). Predators may be abundant when prey densities are high. It is therefore possible that in some circumstances juvenile dispersal will be uncommon (Wolff 1994).

Lemming populations throughout most of the Arctic cycle (Elton 1942). Few studies have been made of the dispersal behaviour of lemmings, and the role of juvenile dispersal in the dynamics of lemming populations remains unclear (Rodgers 1990; Krebs 1993). We used radiotelemetry to measure the movements of juvenile collared lemmings (*Dicrostonyx groenlandicus*) during the peak phase of a 3-year population cycle on the Kent Peninsula in the Northwest Territories of Canada. We compared the movements of lemmings on a control site with those on a site that was protected from avian and mammalian predators, in order to test three hypotheses: (1) extensive juvenile dispersal will occur at high population densities, (2) male juveniles will move greater distances than females, and (3) juveniles will move greater distances in the absence of predators.

Materials and methods

Site description

Lemming numbers peaked every 3 years since 1984 near Walker Bay on the Kent Peninsula, Northwest Territories, Canada (68°21′N, 108°05′W), and in the surrounding region (Poole and Boag 1988; Cotter 1991; D.J. Wilson and R.G. Bromley[2]). This study took place between June and late August in 1996. The lemming population was at peak density throughout the study period, after a low phase in the summer of 1994 and an increase phase throughout the summer of 1995 (Wilson et al. 1999). The region is dominated by shallow tundra ponds and lakes separated by low-lying flat grassy areas, mud flats, sedge meadows, or moist broad hummocks (less than 20 m above sea level (asl)). Collared lemmings were most abundant in the hummocky habitats, which are dominated by low shrubs. Several ridges of higher land (less than 40 m asl) rise above the wet tundra; fox dens and owl and raptor nests are commonly situated on this high ground. Arctic foxes (*Alopex lagopus*) and pomarine jaegers (*Stercorarius pomarinus*) were the most commonly observed predators during the study period in 1996. Short-eared owls (*Asio flammeus*) and snowy owls (*Nyctea scandiaca*) were also frequently seen hunting in the study area. Arctic ground squirrels (*Spermophilus parryi*), rough-legged hawks (*Buteo lagopus*), parasitic jaegers (*Stercorarius parasiticus*), long-tailed jaegers (*Stercorarius longicaudus*), glaucous gulls (*Larus hyperboreus*), common ravens (*Corvus corax*), and short-tailed weasels (ermine or stoats) (*Mustela erminea*) were relatively uncommon. Brown lemmings (*Lemmus trimucronatus*) are potential competitors of collared lemmings and were abundant in 1996.

Field methods

We trapped juvenile lemmings on two 300 × 300 m (9 ha) plots in predominantly hummocky habitat. The two sites were 1.8 km apart and separated by ponds and mud flats. In 1995, one plot (predator exclosure) was surrounded by a chicken-wire fence and covered with parallel lines of taut monofilament fishing line to deter mammalian and avian predators. The fence was 1.5 m high; the monofilament lines were spaced approximately 45 cm apart, about 2 m above the ground. Reid et al. (1995) have described a similar construction. Lemmings and weasels could pass through the chicken wire (mesh size 2.5 cm), but there was no evidence of weasels in the exclosure until mid-August 1996, when two weasels were trapped and removed. Arctic ground squirrels could have burrowed under the fence but were never observed on either plot. The structure effectively excluded predators throughout most of the summer, but by mid-August at least one Arctic fox had learned to enter the exclosure and we then found evidence of fox predation (Wilson et al. 1999).

Juvenile lemmings were trapped in Longworth traps baited with apple and placed near active burrow entrances or runways. We tried to catch juveniles at their natal burrows by setting traps where we had trapped recently pregnant or lactating females, but we also caught juveniles during regular trapping sessions. We considered sexually immature lemmings (males with nonscrotal testes; nonlactating females with a nonperforate vagina and closed pubic symphysis) weighing up to 40 g to be juvenile. Each juvenile was ear-tagged and fitted with a radio transmitter when it was first captured. We used Biotrack radio collars (SS1 and SS2; weighing 2.7–3.2 g) and glue-on radios (SS2; weighing 0.9 g). No juvenile was given a radio weighing more than 10% of its mass. To apply each glue-on radio, we clipped a 10 × 10 mm square of fur between the shoulder blades of the lemming to a length of about 1 mm, then used Krazy Glue Gel to attach a radio to the skin and surrounding fur. These

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[2] D.J. Wilson and R.G. Bromley. Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests. Submitted for publication.

transmitters fell off within 3–7 days and the signal stopped, owing to battery failure, after about 10 days. Collars had a longer battery life and greater signal range than glue-on radios, so juveniles with collars could be tracked for several weeks. We observed no adverse reaction to collars or glue-on radios beyond the first few minutes after the radios were affixed to the lemmings. When glue-on radios were shed, they left an open patch of skin that filled in with fur within approximately 2 weeks. Animals were handled in accordance with the principles and guidelines of the Canadian Council on Animal Care.

The two plots were monitored in separate weekly episodes. Glue-on radios were used on one plot at a time, and the radios were retrieved and repaired before their next use. The position of each radio (“fix”) was recorded approximately every 4 h for the first 24 h after deployment and 1 or 2 times per day thereafter, between about 08:00–11:00 and 22:00–24:00. Elapsed time was roughly synchronous between fixes because animals on each plot were tracked consecutively. A straight antenna mounted on a 3-m pole was used to obtain fixes while minimizing disturbance to the lemmings. Our trapping grids were marked with wooden stakes every 30 m. Within the grids we marked the edges of 30 × 30 m squares with surveyors’ flags every 3 m and estimated the coordinates of each fix to a resolution of 0.3 m. Lemmings were usually underground when located. Telemetry for an individual animal continued until the radio fell off and was retrieved, the carcass was found, or the signal was lost. We searched extensively for lost animals and checked known dens and nests of predators. When possible, we recaptured lemmings after their glue-on transmitter had fallen off or when the signal was expected to fade, and replaced the radio, but often there was no opportunity to reexamine these juveniles. All radio-collared animals that were alive at the end of the study were recaptured and their collars removed. If an animal was recorded as stationary for more than two consecutive fixes, we scraped at the soil to prompt it to move and to establish whether the radio was still attached to it. Disturbance due to scraping and the discarding of dubious fixes may have resulted in under-representation of stationary behaviour for juveniles. Because both procedures were used to an approximately equal degree on each plot, the potential for error was assumed to be similar between the two plots.

Table 1. The fates of 43 juvenile collared lemmings fitted with glue-on radios or radio collars in control and predator-exclosure plots on the Kent Peninsula, N.W.T., during a population peak in summer 1996.

	Number of individuals	
	Control plot	Exclosure
Fate		
Radio removed or found discarded	11	15
Killed by weasel	1	0
Killed by pomarine jaeger	1	0
Suspected kill by fox	0	1
Unknown (lost)	11	3
Total no. of individuals	24	19

Analytical methods

Only animals for which 10 or more fixes had been obtained within 14 days were used for data analysis. The 14-day period was chosen to maximize the sample size and number of fixes available, while minimizing the age range over which data were collected from each animal. This restriction yielded a sample size of 24 animals (12 males and 12 females) on the control plot and 19 animals (9 males and 10 females) on the exclosure plot. The number of fixes per animal ranged from 10 to 55.

Home range describes the amount of space an animal occupies. The maximum distance between any two successive fixes and mean distance between fixes provided an indication of exploration and home-range use. The frequency of fixes for which a change in location was detected provided an indication of movement among burrows.

Home-range areas were estimated on the basis of 90% of the fixes for each animal by means of the adaptive kernel method (Worton 1987). A $\log_{10}$ transformation was applied to the data to normalize distributions before means and 95% confidence intervals (CI) were calculated. We did not adjust home-range estimates for the number of fixes taken because no significant relationship was found between home-range size and the number of fixes for either plot (Pearson’s correlation, control plot: $r = 0.37$, $n = 25$, $p > 0.06$; exclosure plot: $r = 0.13$, $n = 23$, $p > 0.5$; Jones 1983).

Positions recorded within too small a time span may not be independent of one another (Swihart and Slade 1985). In our study, juveniles could easily traverse their home ranges within a few minutes, and they often moved to opposite ends of their home ranges between consecutive fixes. We have assumed that all fixes were independent.

Results

Collared lemmings were abundant in May 1996 and continued to increase in numbers as a result of reproduction. In early June we caught juveniles that had been born under the snow in spring (April–May). Beginning in late June we caught summer-born animals that seemed to form two cohorts, those born in June and those born in July. All the juveniles that we radio-tagged were from the summer litters, except for one that was from a spring litter. At the end of July, the density of collared lemmings was approximately 11.7/ha on the control plot (95% CI = 9.0–16.3) and 28.1/ha (95% CI = 22.6–36.2) within the predator exclosure (mark–recapture estimates; Wilson et al. 1999).

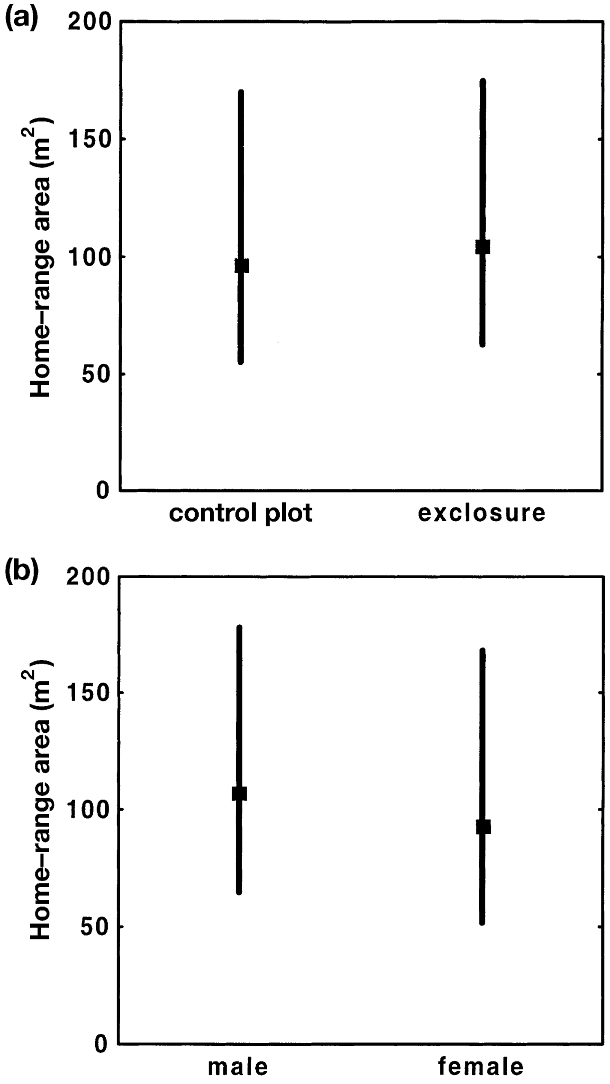
Fate of juveniles

The fates of the 43 lemmings we studied are shown in Table 1. Only two known mortalities occurred on the control plot and one within the exclosure (a suspected fox kill). Telemetered animals were lost from the control plot more than twice as often as from the exclosure (11 of 24 from the control plot and 3 of 19 from the exclosure). Of these, we suspect that 4 on the control plot and 2 in the exclosure were lost as a result of battery failure. The remaining losses could have been due to radio failure, predation, or long-distance dispersal. However, the fact that so many more radios were lost from the control than from the exclosure grid suggests that most losses were the result of predation. Of the 19 radio-tagged juveniles that we recaptured after 14 or more days of study, only 1 male and 1 female (both from summer litters) reached sexual maturity, even though 11 had grown heavier than 40 g.

Home ranges

No juvenile lemmings dispersed from the home ranges where they were first found; all juveniles had limited home ranges and none made repeated movements in any particular direction. The areas of home ranges did not differ signifi-

Fig. 1. Home-range areas estimated (on the basis of 90% of the fixes for each animal), using the adaptive kernel method, for juvenile collared lemmings grouped by plot (*a*) and sex (*b*). Values are shown as the means and 95% CI, calculated on the basis of log-transformed data (hence the means are geometric means).



cantly between plots or sexes (Fig. 1). The mean home-range size for juvenile lemmings of both sexes on both plots was 100 m^2 (95% CI = 69–145 m^2). We examined the data for trends in home-range area or pattern of movement with respect to mass, temperature, period of the season, location within the plot, and fate of the animal, but none were apparent. The home ranges of some juveniles overlapped; some juveniles used common burrows and locked-open traps.

The smallest lemming caught weighed 11.5 g and all others weighed at least 15 g. We caught 12 juveniles (7 weighing ≤25 g) for the first time at burrows where we knew of females that had given birth or were lactating. The smallest of these juveniles, at least, were probably on their natal home range. Twelve others first caught in regular trapping sessions weighed ≤25 g and the remainder weighed >25 g when first trapped. There is a chance that especially the larger juveniles caught in regular trapping sessions were born elsewhere, even though none of the small juveniles in our sample dispersed.

Patterns of movement

Mean distances between successive fixes for each animal ranged from 0.9 to 16.0 m and were similar between plots (control plot, 5.9 ± 0.7 m (mean ± SE); exclosure plot, 6.1 ± 0.7 m) and sexes (males, 6.2 ± 0.8 m; females, 5.7 ± 0.7 m). The maximum distances between successive fixes ranged from 1.9 to 102.7 m and were also similar between plots (control plot, 31.2 ± 5.4 m; exclosure plot, 20.9 ± 2.5 m; Mann–Whitney test, $U_{[19,24]} = 209$, $p > 0.2$) and sexes (males, 28.3 ± 5.5 m; females, 25.0 ± 3.4 m). The frequency of no movement between fixes (two consecutive fixes at the same place) was significantly higher for the control plot than for the exclosure plot (*t* test, $t_{41} = 2.9$, $p < 0.01$), but was similar between sexes (Fig. 2).

Discussion

Movements and home ranges of juvenile lemmings

The first and second hypotheses, which state that extensive juvenile dispersal will occur at high densities and that males will move farther than females, were not supported. All juveniles remained within the home ranges where they were originally caught and did not disperse. Juvenile collared lemmings in a low-density population (less than 1.0 lemming/ha) at Pearce Point, N.W.T., dispersed from their natal burrows at an average rate of 53 m/day within 10 days after weaning; one lemming travelled 600 m in a day (Reid et al. 1995). We cannot discount the possibility that some of the lemmings in our study whose fates were unknown were dispersers that quickly moved out of range of our transmitters. In spite of taking fixes every 4 or 12 h and making extensive searches for lost animals, we could have missed some movements of the greatest magnitude observed by Reid et al. (1995). However, since we found no instances of shorter dispersal distances, such extreme distances seem unlikely.

Density-dependent decreases in body mass (Myers and Krebs 1971), dispersal rate or distance (Rodgers 1990; Wolff 1992, 1994; Lambin 1994*a*), and home-range area (Brooks 1993) have been described for small rodents. Reduced movements have also been observed among snowshoe hares in a peak-phase population (O'Donoghue 1991). At our study site, between early June and late August, no individual of any age or size was recaptured more than 153 m (n = 252) from where it was initially trapped (Wilson et al. 1999). It is possible that all juveniles experienced social stress due to the high density of conspecifics. The limited home ranges and movement patterns among juveniles may reflect avoidance of confrontations with other animals (Hestbeck 1982). The few times we were able to observe lemmings directly, intraspecific and interspecific interactions between adults appeared to be negative and sometimes resulted in one chasing the other (G.S. Blackburn, personal observation), whereas some juveniles used common burrows and were observed foraging near one another. Juveniles may have minimized the number of encounters with unrelated and hostile adults by remaining near familiar burrows. Townsend's voles (*Microtus townsendii*) were less likely to disperse when a same-sex littermate was nearby (Lambin 1994*b*). However, of 264 collared lemmings with a mass of ≤40 g that we trapped during the summer, only 4 (none in the present study) had apparent injuries on their heads or bodies (D.J. Wilson, unpublished data) that might have been inflicted by adults. Heske et al. (1993) observed that encounters between adult and juvenile Norwegian lemmings (*Lemmus lemmus*) were usually amicable.

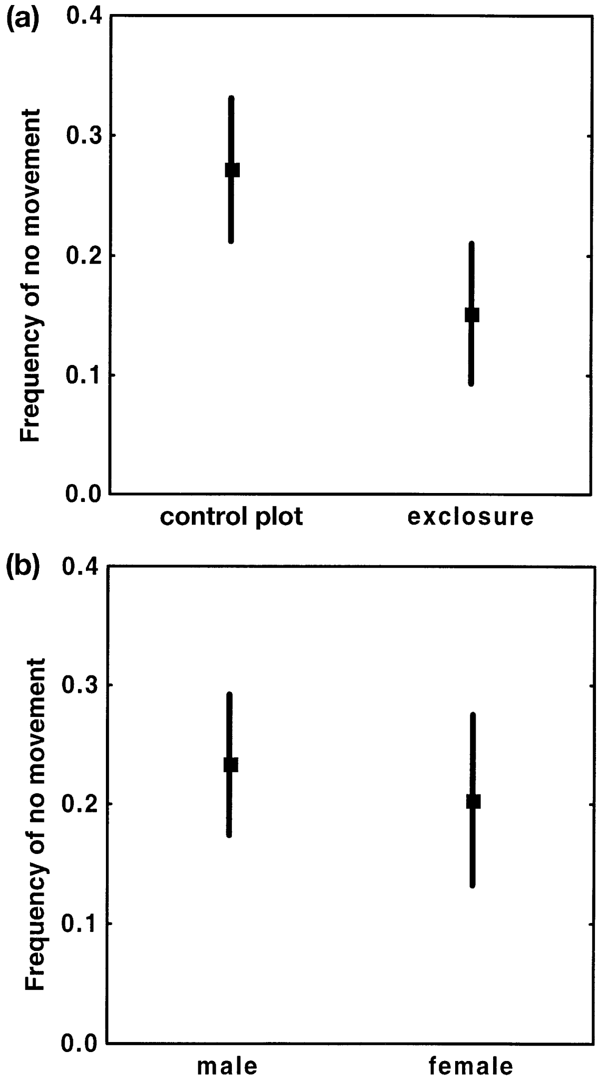
The dispersal of juveniles may instead have been postponed because of a delay in attaining sexual maturity (Gaines and McClenaghan 1980; Stenseth and Lidicker 1992). Among lemmings weighing 25–50 g that were outside the present sample, only 8 of 62 males and 7 of 52 females were in reproductive condition in late July (D.J. Wilson, unpublished data), even though collared lemmings can mature at less than 20 g. Sexual maturity might be delayed or prevented among juveniles when population densities are high (Boonstra and Boag 1987). Krebs (1964) found that summer-born male brown and collared lemmings did not mature in high-density populations. Gilbert et al. (1986) reported that the maturation of summer-born females was suppressed in high-density populations of the red-backed vole (*Clethrionomys rutilus*). Wolff (1992) reported suppression of reproduction among white-footed mice recruits due to the presence of opposite-sex parents. Delayed maturation might also have contributed to the lack of difference in movement patterns between male and female juveniles. Sexually mature male Richardson's collared lemmings (*Dicrostonyx richardsoni*) normally occupy large home ranges that overlap the ranges of several females (Brooks 1993), and Norwegian lemmings of both sexes shifted their home ranges when they matured (Heske and Jensen 1993). Boonstra and Boag (1987) found that male and female meadow voles (*Microtus pennsylvanicus*) travelled equal distances if they remained immature.

Differences in movement patterns between control and predator exclosure

The third hypothesis, which states that the distances moved will be greater in the absence of predators, was also not supported. The mean and maximum distances moved were similar between the two plots. The extent to which lemmings detect and respond to predators is unknown. Other small rodent species have been observed to react to the sounds, movements, and scents of predators (Merkens et al. 1991; Parsons 1992; Lagos et al. 1995). The perceived risk of predation may have been similar between plots, since predators flew over and scented around the predator-exclosure plot.

Although juveniles on the two plots moved similar distances, those on the control plot moved less frequently than those within the exclosure (Fig. 2*a*): they either returned to the same burrow or remained in a burrow between fixes. We know of no other studies that have measured frequency of movement in this way. There are several possible explanations for this result. Control-plot juveniles may have foraged closer to burrow entrances or ventured above ground less often in order to avoid predators. Alternatively, because of the high density of collared lemmings in the exclosure, individuals there may have been compelled to move among burrows more often because of frequent confrontations within occupied sites. Hence, the effect of predator reduction would be indirect. Lastly, control-plot juveniles may have moved less among burrows than did exclosure juveniles because of the greater chance of encounter with brown lemmings on the control plot. At the end of July, the estimated density of brown lemmings was 6.4/ha (95% CI = 5.1–8.8) on the control plot and 1.1/ha (95% CI = 0.8–2.3) in the exclosure (mark–recapture estimates; Wilson et al. 1999). The results of other studies have suggested that brown lemmings are more aggressive than collared lemmings (Pitelka 1973; Batzli and Jung 1980). Juvenile Norwegian lemmings often avoided or threatened (by squeaking) adults of other species (*Microtus* spp.; Heske et al. 1993). Brown lemmings may have had a greater effect on juvenile collared lemmings than did adult collared lemmings, and could have restricted the number of burrows available to juvenile collared lemmings on the control plot.

Fig. 2. Frequency of fixes for which juvenile collared lemmings did not change position from the previous location grouped by plot (*a*) and sex (*b*). Values were calculated as the number of fixes for which the position was the same as that in the previous fix, divided by the total number of fixes. Values are shown as the mean and 95% CI.



Implications for lemming population dynamics

If saturation dispersal (Lidicker 1975) of juveniles took place in this peak-density population, the rate was so low as to be undetectable without a larger sample size. Conversely, if many juveniles were programmed or stimulated to disperse voluntarily, we missed either the critical juvenile age or seasonal period of dispersal, or other factors negated the tendency to disperse. Smaller lemmings than those represented in our sample would not yet have been weaned. Captive collared lemmings in Alaska were 18 days old when fully weaned, when they weighed, on average, 19.5 g (range 12–28 g; Hansen 1957). We observed newly weaned juveniles weighing less than about 20 g, including 8 of the studied juveniles (4 from each plot), making short, hesitant movements, usually within 1 m of their burrows. The sole spring-born lemming we followed neither matured nor dispersed. Still, juveniles born in spring, when the population density was lower, may have dispersed at a higher rate than the summer-born ones. Lambin (1994*a*) found that male Townsend's voles born in spring were less likely to be recruited on their natal trapping grid than those born in other seasons. As well, both males and females born later in summer tended to mature in the following year (Lambin 1994*a*). The collared lemming population had not begun to decline significantly by the end of the study period and it is possible that large-scale juvenile dispersal occurred later in the autumn, despite reduced reproductive activity and deteriorating weather conditions. This possibility is not supported by the fact that movements were similar within the exclosure and on the control plot, nor by the lack of dispersal by any age-class in the population (Wilson et al. 1999).

The lack of juvenile dispersal may have been related to delayed sexual maturity and avoidance of confrontation with other lemmings. This "social fence" (Hestbeck 1982) might lead to a more rapid population growth rate, as occurred when voles were physically prevented from dispersing (Krebs et al. 1969). Changes in dispersal rate may therefore contribute to the shape of population cycles. A fall in the net emigration rate as the population approaches peak density might result in an earlier or a higher density peak. Under these conditions, any density-dependent effects, such as crowding or resource shortages, would be accelerated or exacerbated. Predators may moderate the processes leading to a social fence by lowering lemming population densities, resulting in less restricted movements, although at the high lemming densities we documented, this effect was not displayed among juveniles. Changes in factors such as reproductive output, frequency of encounters with other animals, and dispersal rate may be closely linked as both causes and effects of patterns of population dynamics in lemmings.

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