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Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die?

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We used radio-telemetry to monitor the survival of dispersing and philopatric juvenile snowshoe hares (*Lepus americanus*) in southwestern Yukon Territory, Canada, during a cyclic population increase. Neither 28-d survival nor the proportion of hares surviving to breed differed significantly between juvenile hares that dispersed and those that did not, nor was there a significant relationship between dispersal distance and fate (dead or alive). Our results indicate that the overall survival cost associated with natal dispersal is low for snowshoe hares during the early increase of the hare cycle.

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Many authors have discussed the potential effects of dispersal on population dynamics, demography, and genetics (Lidicker 1975, Gaines and McClenaghan 1980, Greenwood 1980, Dobson et al. 1997). The impact of dispersal on any of these parameters will be determined by the survival and reproductive fitness of dispersers. Although it is generally assumed that dispersers have a higher mortality rate than philopatric individuals (Errington 1946, Christian 1970), successful immigration is needed for the establishment or re-establishment of vacant habitats, as required for source-sink or metapopulation dynamics.

When the survival of dispersers has been compared directly to that of philopatrics, support for the assumption that dispersal is associated with a high mortality cost has been mixed. The assumption has been supported in studies of Columbian ground squirrels (*Spermophilus columbianus*, Hackett 1987), arctic ground squirrels (*Spermophilus parryii*, Byrom and Krebs 1999), black-tailed prairie dogs (*Cynomys ludovicianus*, Garrett and Franklin 1988) and root voles (*Microtus oeconomus*, Steen 1994, Aars et al. 1999). However, studies of red squirrels (*Sciuris vulgaris*, Wauters et al. 1994), Townsend's ground squirrels (*Spermophilus townsendii*, Olson and Van Horne 1998), yellow-bellied marmots (*Marmota flaviventris*, Van Vuren and Armitage 1994), kangaroo rats (*Dipodomys spectabilis*, Jones 1986) and meadow voles (*Microtus arvalis*, Boyce and Boyce 1988) have failed to find a significant decrease in survival associated with dispersal.

Our objective was to test the assumption that dispersing juvenile snowshoe hares (*Lepus americanus* Erxleben) have a higher mortality rate than philopatric juvenile hares. Snowshoe hares throughout North America undergo cyclic population changes, with peak hare densities occurring every 8–11 years (Keith 1990). Given that up to 50% of juveniles disperse (Gillis and Krebs 1999), the potential for dispersal to impact hare dynamics throughout the cycle will depend on the survival of the dispersers and whether or not their survival changes throughout the cycle. Any impact will be a function of the proportion of individuals that disperse, their survival, and the survival of philopatric individuals.

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Methods

Data were collected between June 1995 and April 1996 in conjunction with the Kluane Boreal Forest Ecosystem Project near Kluane Lake, Yukon Territory, Canada (60°57′ N, 138°12′ W). Details of the study area can be found in Boutin et al. (1995). The main hare predators resident in the area are coyotes (*Canis latrans*), lynx (*Lynx canadensis*), goshawks (*Accipiter gentilis*), and great horned owls (*Bubo virginianus*).

Hares were trapped on control areas (two 36-ha control grids and an off-grid control area) and food addition areas (two 36-ha food grids). Food addition areas had natural food supplemented with commercial rabbit chow (spread along four equally spaced cut-lines running the length of each grid) every 4 to 5 d. This treatment began in 1986 and continued year round until April 1996.

Throughout the summer and fall of 1995, juvenile hares were trapped and fitted with radio-collars (TW-3 transmitters with mortality switch, Biotrack Ltd., Dorest, UK). The sex, weight, and litter cohort (1–3) of each juvenile were recorded. Hares were monitored for mortality daily and when a mortality occurred, the cause of death was determined (Gillis 1999). For juveniles which survived until their first breeding season (March 1996), natal dispersal distance was defined as the linear distance from the juvenile's nest site to its location in February 1996 (after Howard 1960). For animals that died before March 1996, natal dispersal was defined as the linear distance from the hare's nest site to its mortality location. Details of nest site location determination and data collection can be found in Gillis and Krebs (1999).

A juvenile was defined as a disperser if its natal dispersal distance was > two adult home range diameters (males > 812 m, females > 554 m for the areas on and time over which this study occurred, K. E. Hodges unpubl.). This distance ensured an emigrant's home range did not overlap with its natal home range.

The proportions of dispersing and philopatric individuals dying before their first breeding season for each sex, litter, and treatment (food addition area and control areas) were compared using log-linear analysis. Twenty-eight-day survivals of dispersing and philopatric individuals were estimated using the Kaplan–Meier procedure (Pollock et al. 1989) and Cox's proportional hazard's survival analysis was used to determine if survival rates differed between dispersing and philopatric individuals. To eliminate any potential bias incurred by our definition of disperser, a logistic regression was used to determine if a correlation existed between natal dispersal distance and fate (dead or alive, Trexler and Travis 1993). Logistic regressions were done in JMP 3.1.6 and all other statistical analyses were done in SYSTAT 5.2.1. PASS 6.0 was used for power analyses.

Results

Of the 35 hares used in this study, 17 were classified as dispersers. There was no significant difference between treatments, sexes, or among litters in the proportion of dispersing or philopatric individuals surviving to their first breeding season (Table 1; Pearson $\chi^2 = 12.4$, d.f. = 19, $p = 0.87$). Therefore, data from all litters, sexes, and treatments were combined for further analyses. For details on dispersal rates and distances and overall survival of males and females on control and food addition grids, see Gillis and Krebs (1999) and Gillis (1999).

The proportion of juveniles surviving to breed did not differ significantly between dispersers and philopatrics (Pearson $\chi^2 = 0.85$, d.f. = 1, $p = 0.36$), and although survival rates were slightly lower for dispersers than for philopatric individuals (Table 1), this difference was not significant (Wald likelihood ratio $\chi^2 = 0.081$, d.f. = 1, $p = 0.78$). The apparent discrepancy between the magnitude of the difference between 28-d survival (2%) and the proportion of dispersers which survived (15%) arose because hares had to live several months before reaching sexual maturity. Logistic regression also failed to detect a significant relationship between dispersal distance and fate (Fig. 1; $r^2 = 0.01$, $\chi^2 = 0.52$, d.f. = 1, $p = 0.47$) even with an obvious outlier removed ($r^2 = 0.02$, $\chi^2 = 1.04$, d.f. = 1, $p = 0.31$).

Dispersing and philopatric hares experienced similar causes of death. Predation was the predominant cause of death for both (83% (10 of 12) of dispersers' deaths and 80% (8 of 10) of deaths of philopatric hares). Mammals accounted for 70% of deaths due to predation for dispersing hares (coyotes 1, lynx 3, and unknown mammals 3, deaths), while avian (goshawk 1, and unknown raptor 1, death) and undetermined

Table 1. Survival rates and the proportion of dispersing and philopatric juvenile hares surviving to their first breeding season. Sample sizes indicate the number of juveniles radio-collared within each category. 90% confidence limits associated with 28-d survival are provided in brackets (Pollock et al. 1989).

Category	N	28-d survival	Proportion surviving
Litter 1			
Dispersing hares	7	0.89 (0.60–0.95)	0.29
Philopatric hares	2	1.00[1]	1.00
Litter 2			
Dispersing hares	4	0.93 (0.77–0.99)	0.50
Philopatric hares	6	0.94 (0.85–1.00)	0.67
Litter 3			
Dispersing hares	6	0.65 (0.00–0.78)	0.17
Philopatric hares	10	0.62 (0.00–0.72)	0.20
All litters combined			
Dispersing hares	17	0.87 (0.77–0.92)	0.29
Philopatric hares	18	0.89 (0.80–0.93)	0.44

[1] Confidence limits were not estimated as there was 100% survival.

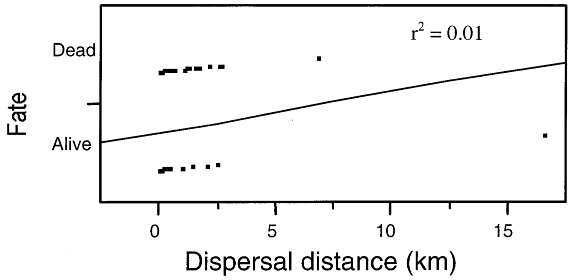

Fig. 1. Relationship, as determined by logistic regression, between natal dispersal distance and fate of hares (dead or alive) at the beginning of their first breeding season.

predators accounted for 20% and 10% of kills, respectively. Among philopatric depredated hares, mammals were responsible for 25% of kills (coyotes 2, and unknown mammal 1, deaths) and avian predators killed 38% (goshawk 3, and unknown raptor 1, deaths), with the remaining 25% killed by undetermined predators. The only death for which predation could be eliminated as a cause of death was for a philopatric individual. Cause of death could not be determined for 1 philopatric and 2 dispersing hares.

Discussion

Although dispersers appeared to survive less well than philopatric individuals, this difference is statistically and biologically insignificant. In other species where a survival difference between dispersers and non-dispersers has been established, the difference in the proportion of individuals surviving is typically greater than 30% (Garrett and Franklin 1988, Steen 1994, Byrom and Krebs 1999), a difference we had a power of 75% to detect with our sample size. However, given the high sensitivity of hare population growth rate (λ) to juvenile survival, if the true survival rate of juvenile dispersers is 0.87 and that of philopatrics is 0.89, λ in a population with no juvenile dispersal would be 2.0 while in a population in which 50% of juveniles dispersed (Gillis and Krebs 1999), λ would be reduced to 1.85 (Fig. 3 in Haydon et al. 1999).

In a study using a larger sample of hares, of which the hares used in this study are a subset, a significant difference between survival of third litter juveniles and first and second litter juveniles was found (Gillis 1999). Although this trend also appeared in both philopatric and dispersing hares in this analysis, the difference was not significant so data from all litter groups were pooled for further analysis. This decision did not bias our results as analyses conducted on survival estimates obtained with equal weighting by litter group did not alter our results.

For cyclic populations of snowshoe hares, there has been no indication of a survival cost to dispersal (Boutin 1984, Keith et al. 1984) and our results are consistent with this conclusion. Although the assumption that most dispersers die may hold true for some species, it cannot be applied universally. Species of small mammals have different life histories, social structures, and dispersal strategies, all of which may influence risks associated with dispersal.

We used only one measure and time period (hare survival from weaning to breeding) in examining the cost of dispersal. Other costs, including reduced reproductive success or long-term survival, have been documented in ground squirrels (Hackett 1987, Byrom 1997). Larsen and Boutin (1994) found that red squirrels had reduced survival during the actual dispersal process, but that this short-term survival cost was balanced by increased over winter survival of dispersers. Given the high proportion of juvenile hare dispersal during the early increase phase of the cycle (Gillis and Krebs 1999), any long-term costs of dispersal not captured by this study could impact the population.

Since dispersing hares did not have a lower survival rate than philopatric hares, the potential for dispersal to play a direct role in the regulation of hare numbers at the increase phase of the hare cycle is small. However, if refuges are used by hares during the cyclic low, the high survival of dispersing juveniles may facilitate the re-occupation of less optimal habitats left vacant during the low (Wolff 1980, 1981). A notable limitation of the current study is that it was conducted for only one year during the early increase phase of the hare cycle. The role of dispersal in regulation of hare numbers during other phases of the hare cycle is unknown, and cannot be inferred from the results of this single study.

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