

A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model

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Abstract: The allegedly noncyclic dynamics of southern snowshoe hare (*Lepus americanus*) populations may be explained by a model invoking habitat fragmentation and facultative predation (the refugium model) under which animals dispersing from patches of preferred habitat fail to establish themselves because of predation by facultative carnivores. We compared the refugium model with a revised model invoking heavy on-site predation in preferred habitat as the proximal mechanism responsible for the stability of southern snowshoe hare populations. The survival and movements of hares in a fragmented habitat in central Idaho were monitored via radiotelemetry on 6 sites differing in habitat quality (indexed by understory cover) from 1998 to 2000. In support of the revised model, predation rates were high irrespective of cover availability or hare density, and predators did not kill dispersing animals disproportionately. Furthermore, predation was focused on small hares, suggesting that poor recruitment of juveniles may be the mechanism ultimately responsible for the damped dynamics of southern snowshoe hare populations. The low survival rates we measured suggest that the population under study was undergoing a marked decline. However, the observed decline, determined by comparing study-site population estimates, was less severe, implying that the persistence of local snowshoe hare populations in some areas of the species' southern range may be influenced by metapopulation dynamics. Specifically, southern snowshoe hare populations in small patches of usable habitat may be prevented from going extinct by the arrival of immigrants from similar nearby patches.

Résumé : La dynamique des populations australes de lièvres d'Amérique (*Lepus americanus*), que l'on présume n'être pas cyclique, peut s'expliquer à l'aide d'un modèle qui tient compte de la fragmentation de l'habitat et de la prédation facultative (le modèle du refuge), selon lequel les animaux qui quittent les parcelles de leur habitat préféré ne réussissent pas à s'établir à cause de la prédation par des carnivores facultatifs. Nous avons comparé le modèle du refuge à un modèle révisé selon lequel une prédation locale importante dans l'habitat préféré constitue le mécanisme responsable de la stabilité des populations australes de lièvres d'Amérique. La survie et les déplacements ont été étudiés, grâce à la radiotélémetrie, à 6 sites au sein d'un habitat fragmenté du centre de l'Idaho différents par la qualité de l'habitat (mesurée d'après la couverture de végétation du sous-bois), de 1998 à 2000. Les taux de prédation étaient élevés quelles qu'aient été la couverture végétale et la densité des lièvres, et les prédateurs ne s'attaquaient pas plus particulièrement aux animaux qui quittaient leur habitat, ce qui appuie le modèle révisé. De plus, les prédateurs sélectionnaient les petites proies, ce qui semble indiquer que le faible recrutement des jeunes lièvres est peut-être ultimement le mécanisme responsable de la dynamique amortie des populations australes de lièvres d'Amérique. Les faibles taux de survie enregistrés chez la population étudiée semblent signaler un déclin important. Cependant, la comparaison des estimations de densité des populations locales dans la zone d'étude permet de croire que le déclin observé n'est pas si important, probablement parce que certaines des populations de la zone de répartition australe persistent grâce à la dynamique de la métapopulation. Plus précisément, cela signifie que les populations australes de lièvres d'Amérique qui vivent dans de petites parcelles d'habitat approprié sont protégées de la disparition grâce à l'arrivée d'individus immigrants provenant de parcelles d'habitat semblables dans le voisinage.

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Introduction

Many organisms appear to belong to metapopulations, which consist of spatially discrete subpopulations connected through dispersal (Levins 1969; Hanski 1997, 1999). In theory, the majority of these local populations would not persist without the benefit of immigration, and those occurring along the margins of a given species' range should be especially prone to extinction because they tend to be located in regions where immigration rates may be curtailed by poor habitat or a high predation risk (Levins 1969; Hanski 1991; Holyoak and Lawler 1996; Villafuerte et al. 1997). The periphery of a given species' range should occur where immigration cannot prevent local extinction due to these or other factors (Carter and Prince 1981). Yet despite the potentially important influence of metapopulation dynamics on the viability of fringe populations and, consequently, on species distribution, few natural systems have been examined in this context (Harrison 1991; Gulve 1994; Hanski 1997).

Snowshoe hare (*Lepus americanus*) populations located along the southern fringes of the species' distribution exhibit dynamics that are attenuated relative to the cyclic fluctuations that characterize hare populations inhabiting the boreal forests of Canada and Alaska (Keith 1990; Hodges 2000b; Murray 2000). The mechanism responsible for the dynamics of northern snowshoe hare populations, putatively a time-delayed interaction between food shortage and predation (Keith et al. 1984; Krebs et al. 1995; Stenseth et al. 1997; King and Shaffer 2001), has been studied extensively over the last 50 years. In contrast, snowshoe hares in the south have received little attention, therefore information concerning their population biology is scant by comparison (Keith 1981, 1990).

Throughout the northern part of their range, snowshoe hares are found in continuous stretches of boreal forest; conversely, southern populations occur primarily in insular patches of suitable habitat set amidst less-preferred areas (Wolff 1980; Keith et al. 1993). This disparity has led a number of biologists to speculate that habitat fragmentation may be ultimately responsible for the anomalous dynamics manifested by southern snowshoe hare populations (Dolbeer and Clark 1975; Buehler and Keith 1982; Keith et al. 1993). Wolff (1980, 1981) described the mechanism by which a fragmented habitat might dampen or eliminate cyclic population fluctuations via the "refugium" model, which includes the following components: (i) a scarcity of refuge habitat offering protective cover, where survival is relatively high; (ii) the presence of an abundant and numerically stable guild of facultative predators that are largely absent farther north; and (iii) an inability of hares dispersing from patches of suitable habitat to establish themselves in less suitable habitat, owing to intense predation.

The few demographic analyses of snowshoe hare populations in the south have produced ample evidence that these populations are concentrated in isolated patches of suitable habitat and subject to predation by a suite of generalist predators (e.g., Litvaitis et al. 1985; Sievert and Keith 1985; Keith et al. 1993; Cox et al. 1997). However, Keith et al. (1993) found that extremely high on-site predation rates in cover-rich habitat, rather than predation on naturally dispersing individuals, seemed to be driving the changes in distribution and abundance manifested by a southern snowshoe hare

population in Wisconsin; indeed, predation pressure on populations occupying small (<7 ha) patches of preferred habitat was so severe that 3 of the 5 populations under investigation went extinct in the course of the 3-year study. These results suggest that hares in the south may not always enhance their likelihood of survival by occupying preferred habitat, especially in areas where the average patch size is small. Thus, at least in heavily fragmented landscapes, the refugium model could be modified so that low on-site survivorship of resident animals replaces mortality of individuals traveling through more perilous habitat as the mechanism that acts proximally to cause southern populations to remain depressed. Under this revised model, fragmentation of landscapes would exacerbate the effect of predation on prey population dynamics by allowing carnivores to concentrate their hunting efforts on islands of preferred prey habitat (especially small patches) instead of preying disproportionately on dispersing individuals.

We sought to compare the standard refugium model with our revised version by studying a snowshoe hare population located in the southern portion of the species' distribution. Under the hypothesis that the modified model provides a more realistic depiction of the mechanism by which predation and habitat fragmentation affect southern hare populations, we predicted that (i) habitat quality would influence hare abundance but not survival, and (ii) predation would not be higher on dispersing individuals.

Methods

Study area

This study was conducted in the Clearwater National Forest, Idaho (46°N, 114°W), between May 1998 and May 2000. Owing to local management practices such as timber harvest and fire suppression, the landscape in which we worked was characterized by a mosaic of small habitat patches (5–10 ha) surrounded by clearcuts and other areas not typically used by snowshoe hares (e.g., meadows, steep slopes) (K. Harvey, personal communication). Accordingly, six 10-ha study sites were established, and peripheral and internal grid lines were marked at 50-m intervals on each site. Four of these (sites 1–4) were lower elevation (1000 m above sea level) timber stands, whereas sites 5 and 6 were higher elevation (1600 m) stands. The study areas were selected originally to encompass a range of understory cover densities; with the exception of sites 5 and 6, which were surrounded by similar habitat, each site completely encompassed a patch of uniform habitat. Sites 1 and 2 were densely stocked early-seral stands featuring grand fir (*Abies grandis*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and white pine (*Pinus monticola*). Site 3 featured a mixture of early-seral, late-seral, and relatively mature portions and was characterized by an abundance of red-cedar (*Thuja plicata*), Engelmann spruce, and grand fir. Site 4 encompassed an open, mature stand dominated by red-cedar and grand fir; sites 5 and 6 also were relatively open, mature stands but were comprised primarily of lodgepole pine, Engelmann spruce, and subalpine fir (*Abies lasiocarpa*). With one exception the study sites were separated by >500 m, and hares were only rarely ($n = 2$ of 125 hares) found to move between them.

Field procedures

The amount of understory and canopy cover available on each study area was quantified during the summer in 1998 and 1999 at 30 randomly generated points per site. A density board, modified from that used previously (Nudds 1977), was used to assess visual obstruction resulting from understory vegetation; measurements were taken from three distances (2.5, 5, 10 m) in each cardinal direction. Because understory-cover densities were similar among areas at the 2.5-m ($F = 0.84$, $P = 0.53$) and 5-m ($F = 1.446$, $P = 0.22$) distances, we used the 10-m distance when relating understory-cover availability to hare population density. Canopy closure was assessed using point-quarter sampling (adapted from Brower and Zar 1977).

At each study site we livetrapped (30 traps per site; Tomahawk Live Trap Co., Tomahawk, Wis., U.S.A.) snowshoe hares for 7–10 consecutive days every 3 months (for a total of 9 trapping periods). Handling of hares was in accordance with standard guidelines (Canadian Council on Animal Care 1984) and was approved by the University of Idaho Animal Care and Use Committee (protocol No. 9029). At each capture, individuals were weighed, sexed, and affixed with numbered fingerling tags (National Band and Tag Co., Newport, Ky., U.S.A.) attached to the interdigital webbing of each hind foot. Hare structural size was indexed via hind-foot length (HFL) (Bailey 1968; Keith et al. 1968). Juveniles could be distinguished (based upon sexual characteristics; see Keith et al. 1968) until March 1 following their birth during the summer; after this date all animals were considered to be adults.

All hares weighing >500 g ($n = 125$) were equipped with a mortality-sensitive radio collar (Telemetry Solutions, Concord, Calif., U.S.A.). Dispersal status (i.e., on versus off the study site; determined using triangulation) and survival of radio-collared hares were monitored daily, and all live animals were located precisely once per 90-day trapping interval. Deceased animals ($n = 75$) were located promptly using a hand-held antenna and receiver (Advanced Telemetry Systems, Isanti, Minn., U.S.A.). Proximate cause of death was determined using evidence left at the kill site (Boutin et al. 1986; Keith et al. 1993; Murray et al. 1997) and, when possible, carcass necropsy. Kills made by particular predators or predator classes (i.e., bobcat, *Lynx rufus*; coyote, *Canis latrans*; mustelids; raptors) were categorized according to the location of carcass remains, tracks, and other distinguishing marks at the kill site, and carcass necropsy (Boutin et al. 1986; Cox et al. 1997; Murray et al. 1997). Hares that have perished because of starvation are readily identifiable (Boutin et al. 1986); thus, we differentiated between starvation- and other non-predator-caused fatalities. We assumed that carcasses were not scavenged because monitoring intensity was high (carcasses were retrieved <24 h after death), and because carcasses placed on study sites elsewhere (see Brand et al. 1976; Boutin et al. 1986; Murray et al. 1997) were rarely scavenged by predators.

Translocation program

We tested the effects of understory-cover availability on the dispersal behavior and survival of hares by translocating 32 individuals that were removed from areas >500 m from the study sites between July 1999 and May 2000. Seventeen

hares were released onto a low-cover study area (site 4), while the remainder were released onto a high-cover area (site 2); all translocated hares were equipped with mortality-sensitive radio collars. We monitored survival and proximate cause of death of these individuals daily. All translocated animals that dispersed (>300 m) from the release sites were located biweekly using a hand-held receiver and a global positioning system. Whenever possible, understory cover characterizing the locations from which these dispersing individuals were flushed was measured using the aforementioned protocol.

Analysis of data and model fitting

On each study site, hare numbers were estimated every 3 months using enhanced minimum-number-known-to-be-alive (MNA) counts that incorporated radiotelemetry information (number of animals trapped + number of radio-collared animals not trapped but known to reside in the study area). Given that not all hares are trappable, estimates based upon MNA counts may be conservative (Krebs et al. 1986). However, Krebs et al. (1986) showed that MNA estimates correspond well to those from more rigorous mark-recapture techniques where trapping success is high and hares are scarce. We felt confident about using this method, given that the study sites on which we worked were sparsely populated by snowshoe hares, and that during each trapping session we caught the majority ($80.0 \pm 0.1\%$, mean \pm SE) of known radio-collared residents. Furthermore, in comparing enhanced MNA counts for our relatively high-abundance study areas (sites 1–3; see Table 1) with estimates generated using a modified Chapman estimator incorporating radiotelemetry information (White and Garrott 1990; Murray 1999), we found that estimates furnished by the two methods were highly correlated ($r^2 = 0.96$; mean difference = 4%) and did not differ significantly (paired t test, $P = 0.27$; see Table 1), indicating that our modified method furnished relatively accurate population estimates. Herein we present our estimates as the number of hares known to occupy the 10-ha study site. To place our results in context with other studies, we also estimated density. For all density estimates, the effective trapping area was considered to include the study site proper plus a 200-m buffer strip (the approximate radius of the circular home range of a hare; see Boutin 1984).

Radio-collared hares that traveled >300 m from the perimeter of the study area where they were captured during a particular trapping interval (initial dates of departure during a given trapping interval were identified using triangulation data; movement distances were determined from seasonal locations) and did not return (i.e., were not captured) during subsequent trapping periods were deemed to have dispersed. Translocated hares were not considered to be natural dispersers (see Hodges 2000b). A 300-m dispersal threshold was selected because radio-collared hares that moved farther than this distance from their last place of capture were rarely recaptured on any of the study sites (4 of 86 hares; A. Wirsing, unpublished data); similarly low rates were observed in a companion study in northern Idaho (E. Ellsworth, unpublished data). Dispersal rates were calculated using the equation $1 - [(1 - \text{number of dispersals/number of radio-days})^t]$, where t is the time period being analyzed (90 days for the purposes of this analysis) and 1 radio-day is one 24-h period

Table 1. Estimates of snowshoe hare (*Lepus americanus*) abundance (number of hares occupying the 10-ha trapping site) in relation to understory cover (visual obstruction at 10 m; 60 sampling points per site) and canopy closure (measured using point-quarter sampling).

Site	Population estimate	Understory cover (%)	Canopy cover (%)
1	8.35 ± 1.86	63.2 ± 4.1	59.6 ± 3.36
2	9.69 ± 1.62	61.1 ± 4.06	59.0 ± 3.45
3	5.50 ± 0.85	57.4 ± 3.76	70.0 ± 4.53
4	0.12 ± 0.12	31.0 ± 3.04	70.0 ± 3.01
5	0.42 ± 0.42	34.0 ± 3.59	56.5 ± 2.93
6	0.85 ± 0.42	39.7 ± 3.59	54.0 ± 3.08

Note: Enhanced minimum-number-known-to-be-alive (see the text) estimates ($n = 9$) were generated seasonally between 1998 and 2000. Values are given as the mean ± SE.

over which a particular animal is known to be alive (Keith et al. 1984).

To evaluate the influence of selected parameters (see below) on predation rate rather than on mortality rate among our study animals, we selected predation rate as the dependent variable for our survival analysis. We likely incurred little bias in doing so, given that few (7%) mortalities were caused by factors other than predation. Seasonal and yearly hare predation rates were calculated using the equation $1 - [(1 - \text{number of predation deaths}/\text{number of radio-days})^n]$ (Trent and Rongstad 1974). Given that our study animals were recaptured every 3 months, we calculated 90-day predation rates. We used Poisson regression, a stepwise procedure in which the dependent variable (e.g., mortality or predation) is expressed as a rate and a Poisson distribution serves as the basis for statistical inference (Selvin 1995), to assess temporal, spatial, and cohort-specific trends with respect to predation.

Temporal variability in predation rate was examined among individual 90-day intervals (e.g., January–March 2000), as well as among intervals pooled across seasons (e.g., winter) and years (e.g., 2000). Spatial differences in predation rate were analyzed with respect to individual study area, study areas pooled according to habitat characteristics (i.e., high versus low cover), and dispersal status (on versus off the study site). The following individual attributes were also made available for inclusion in the survival model: age (juvenile versus adult), sex, hare density (during the current interval and time-delayed for 3, 6, 9, and 12 months), number of times trapped during 90-day interval, and reproductive status (pregnant, lactating, or non-reproductive for females; scrotal for males). In addition, we included several metrics of hare size and condition: values for body mass, HFL, and mass/HFL, a residual index of condition (see Green 2001), and the change in each of these parameters between successive live-capture periods.

In developing our regression model, we selected covariates in a forward stepwise manner (Hosmer and Lemeshow 1999), using the partial likelihood ratio test as a guide for retaining parameters. We set the level of significance for inclusion of main-effects parameters at $P = 0.05$ to insure model parsimony. All parameters retained in the model were subsequently evaluated using backwards selection, with the level

of significance for removal again set at $P = 0.05$. We tested the linearity of continuous variables by replacing them with three design variables (in a sense converting the continuous variable to a dummy coded categorical variable) and then plotting the estimated coefficient against the group midpoints (Hosmer and Lemeshow 1999). Seemingly nonlinear continuous variables were transformed if the transformation increased the fit of the model at $P = 0.05$. We tested all two-way interactions between variables retained in the main model. In addition, covariates that were not retained but were of interest (i.e., we wished to determine the magnitude of their effect) were added to the full model, and coefficient estimates were generated. Finally, whenever possible we described the influence of covariates on predation rates using rate ratios (rate ratio = $e^{\text{coefficient estimate}}$), which express the ratio of mortality rates as a function of different levels of the independent variable in question. We also used a Poisson regression to address the survival of our translocated hares. A survival model was constructed in a fashion similar to the one described above, except that we selected 15-day predation rates as the dependent variable, since the released hares were located every 2 weeks.

Results

Influence of cover on hare abundance

Study sites 1–3 afforded a greater amount of understory cover than did sites 4–6 as determined by density-board measurements ($t_{88} = 7.5$, $P < 0.001$; Table 1). Mean annual population estimates (enhanced MNA), which ranged from 0.1 to 9.7 hares/10 ha across the 6 study areas (Table 1), were correlated positively with understory-cover availability ($t_4 = 11.9$, $r^2 = 0.97$, $P < 0.001$). No relationship existed between hare abundance and estimated canopy closure ($t_4 = 0.1$, $r^2 = 0.004$, $P = 0.91$).

Predation characteristics

We equipped a total of 125 hares (64 postweaning juveniles, 61 adults) with radio collars. The average duration of monitoring per individual was 119 ± 10 days (mean ± SE). We recorded 75 natural mortalities, yielding an average 90-day survival rate of 63.4% and a mean annual survival rate of 15.8%. Predation was ruled to be the cause of 93% ($n = 70$) of these mortalities. Thus, we determined the mean 90-day predation rate to be 34.6% and the mean annual predation rate 82.2%. Among the known cases of predation, deaths were due to coyotes (44.3%), raptors (21.4%), mustelids (12.9%), bobcats (2.9%), and unknown predators (18.5%). Starvation was the cause of death for only one individual, while vehicles killed two. We were unable to ascertain the proximate cause of mortality for two animals.

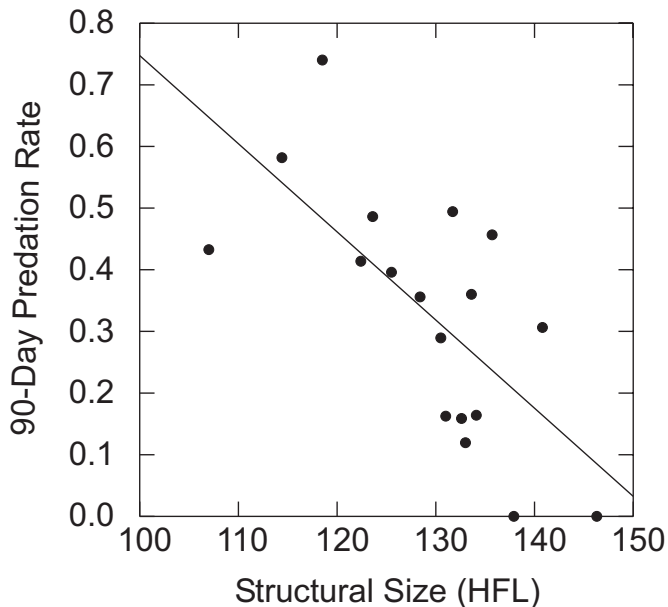
Factors influencing predation

The variable that best explained vulnerability to predation among snowshoe hares was structural size (i.e., HFL) (Table 2). The coefficient estimate for HFL in this model was -0.06 , implying that small hares were disproportionately vulnerable to predators. When converted to the rate ratio (0.94), this coefficient indicated that for every 1-mm decrease in HFL, a hare's vulnerability to predation increased by 6% ($1/0.94 = 1.06$). Therefore, given that HFL is a con-

Table 2. Results of a Poisson regression analysis of survival based on 125 radio-collared snowshoe hares monitored over 24 months in Idaho.

	Coefficient	95% CI	df	P-to-enter value
Constant	-5.34	(-5.57, -5.11)	1	
Hind-foot length (HFL)	-0.06	(-0.10, -0.03)	1	0.008
Trimonthly period	-0.21	(-0.43, 0.01)	1	0.006
Summer	-0.89	(-1.63, -0.14)	1	0.011

Note: Variables are presented in the order in which they were included in the model, and coefficient estimates represent those from the final model. The following parameters were not retained in the model: pooled site variable (P -to-enter ≥ 0.14); dispersal (P -to-enter ≥ 0.19); season (P -to-enter ≥ 0.27); year (P -to-enter ≥ 0.32).

Fig. 1. Relationship between structural size and 90-day predation rate for snowshoe hares (*Lepus americanus*). Each point represents the mean 90-day predation rate for 10 animals within a particular size class (range 98–153 mm hind-foot length (HFL); 3 mm per size class) ($y = 2.2 - 0.01x$; $t = -3.8$, $P = 0.002$, $r^2 = 0.47$).

tinuous measure of age (see Keith et al. 1968), juvenile hares were more vulnerable to predation than adults over the course of our analysis (indeed, the age variable was initially a significant predictor of vulnerability to predation with a P -to-enter value of 0.04, but was never retained after the inclusion of HFL), and moreover, within the juvenile and adult cohorts, small animals were apparently especially susceptible. The predation model indicated that the relationship between size and vulnerability to predation was approximately linear (see Fig. 1). The next variable to be retained was time. Thus, predation rates fluctuated significantly over the course of the study. Trimonthly time periods were more closely related to predation rate than were seasonal (all P -to-enter values ≥ 0.27) and annual (all P -to-enter values ≥ 0.32) periods, meaning that these fluctuations did not repeat themselves seasonally or annually. Summer was retained as the third variable in the model. The inclusion of summer indicates that after the influence of individual 90-day intervals was accounted for, hares were subject to a significantly different

predation rate during this season relative to the other seasons. The coefficient estimate for summer in our model was -0.89 , implying that hares were less vulnerable to predators during the summer relative to other seasons. When converted to the rate ratio (0.41), this coefficient indicated that after structural size was accounted for, an individual hare's vulnerability to predation decreased by 59% over the summer.

We recorded a total of 19 dispersal events, yielding an annual dispersal estimate of 37%. This dispersal rate did not differ according to age ($\chi^2_{[1]} = 1.01$, $P = 0.31$) or sex ($\chi^2_{[1]} = 0.8$, $P = 0.38$), but did differ according to understory-cover availability ($\chi^2_{[1]} = 7.9$, $P = 0.005$), with animals on low-cover sites more likely to disperse (annual dispersal estimate 88%) than those on high-cover sites (annual dispersal estimate 32%). The parameter identifying dispersing animals was never retained in the predation model (all P -to-enter values ≥ 0.19), implying that transient hares were at no greater risk of predation than were study-area residents, and thereby supported our second prediction. In fact, only 11 of the 70 (16%) instances of predation we recorded were on dispersing animals, and the mean annual predation rate on dispersers (76.8%) was qualitatively lower than that on residents (83.2%). Finally, when added to the full model, the dispersal variable was assigned a coefficient estimate of 0.03 (rate ratio = 1.04), indicating a mere 4% difference in predation rate between the 2 cohorts. In support of our first prediction, understory-cover availability also failed to affect vulnerability to predation. Hares ($n = 12$) occupying low-cover sites (4–6) were subject to an annual predation rate (82.3%) similar to that (82.2%) experienced by hares on the high-cover sites ($n = 113$). Furthermore, the pooled site variable, a parameter comparing hares on sites 1–3 (high cover) to those on sites 4–6 (low cover), was never retained in the predation model (all P -to-enter values ≥ 0.14). Finally, when added to the full model, the pooled site variable was assigned a coefficient estimate of -0.01 (rate ratio = 0.99), indicating only a 1% difference in predation rate between hares on high- and low-cover sites.

Translocated hares

Among the 32 individuals that were translocated, 24 (75%) were adults and 8 (25%) were juveniles. For these animals we recorded 23 natural deaths, yielding a 15-day survival rate of 80.8% and a mean annual survival rate of 0.6%; each of these mortalities resulted from predation. The variable that best explained vulnerability to predation among translocated hares was summer (Table 3), and the coefficient estimate for

Table 3. Results of a Poisson regression analysis of survival based on 32 translocated radio-collared snowshoe hares monitored over 14 months in Idaho.

	Coefficient	95% CI	df	<i>P</i> -to-enter value
Constant	-4.13	(-4.64, -3.63)	1	
Summer	-1.33	(-2.6, -0.12)	1	0.012

Note: Variables are presented in the order in which they were included in the model, and coefficient estimates represent those from the final model. The following parameters were not retained in the model: age (*P*-to-enter ≥ 0.54); study area (*P*-to-enter ≥ 0.82).

this variable (-1.33) implied that translocated animals were subject to a significantly lower predation rate during this season relative to other seasons. When converted to a rate ratio (0.264), this coefficient indicated that translocated hares experienced a 74% reduction in vulnerability to predation over the summer relative to the other seasons. Predation rate among the translocated hares may also have been a function of age. The age parameter was never retained in the main model, but the *P*-to-enter value with which it was associated was nearly significant (0.07). The coefficient describing the influence of age on predation rate was 0.93; when converted to a rate ratio this coefficient indicated that translocated juveniles were 2.54 times more susceptible to predation than their adult counterparts.

The study-site variable (site 2 versus site 4) was not retained in our survival model for translocated hares (all *P*-to-enter values ≥ 0.82), implying that the increased availability of cover on site 2 did not enhance the survival of hares released there relative to that of hares released onto site 4. However, the tendency to disperse among the translocated cohort was apparently influenced by cover availability: 71% (12/17) of the animals released onto the low-cover site dispersed, while only 20% (3/15) emigrated from the high-cover release site ($\chi^2_{[1]} = 8.2$, $P < 0.005$). Moreover, hares dispersing from the low-cover site (measurements were taken for five animals) established themselves in areas offering a significantly greater amount of understory cover (72.3%) than the mean amount that characterized their release site (31%) ($t_4 = 4.3$, $P = 0.008$). The number of days that elapsed prior to dispersal was 40 ± 29.1 (mean \pm SE) and 25.6 ± 23.7 for animals released onto the high- and low-cover sites (2 and 4), respectively, and did not differ significantly ($t_2 = 0.47$, $P = 0.68$).

Discussion

Evaluation of the refugium model

The outcomes of this analysis are consonant with the predictions of our modified model for explaining the dynamics of southern snowshoe hare populations in fragmented habitat. Like most of their southern counterparts, snowshoe hares in our study area died almost exclusively from predation, and the annual predation rate we calculated was high (82.2%). Although the mean annual dispersal rate characterizing hares in Idaho (37%) was relatively high (i.e., compared with the 8–21% calculated by Keith et al. 1993), the relative paucity of predation on dispersing animals, the failure of the dispersal parameter to be retained in the final predation model,

and the weak relationship between dispersal and vulnerability to predation all reveal that hares apparently did not increase their vulnerability to predation by leaving their native area. Therefore, like those in Wisconsin (Keith et al. 1993), hare populations in Idaho appear to be subject to heavy predation focused primarily on residents. A significant positive relationship between dispersal and predation rate is central to the refugium hypothesis.

Hare distribution throughout the study was correlated positively with the availability of understory cover. During our investigation, hares were invariably found in the greatest numbers where the habitat featured a dense understory; conversely, habitat patches without a dense understory were virtually devoid of hares. Understory cover availability appeared to affect hare movement patterns as well, given that (i) resident animals on low-cover sites dispersed less frequently than those on high-cover sites, (ii) individuals translocated onto a cover-poor site dispersed more frequently than did individuals released onto a cover-rich site, and (iii) translocated hares leaving the cover-poor site sought more protective environs. The behavioral response of hares to the absence of cover was apparently not accompanied by a reduction in susceptibility to predation, however, since all hares (resident and translocated) were equally vulnerable to predation regardless of the amount of cover surrounding them.

In sum, then, these results suggest that predation and cover availability both affect patterns of snowshoe hare distribution in the southwestern portion of the species' range, and that the abundance of hares in this region is influenced strongly by predation focused on resident as well as dispersing animals.

Hare size – predation relationship

Vulnerability to predation was apparently size-dependent in our study population. The observed negative relationship between size and predation may have been confounded if substantial changes in size occurred between final measurement and death. However, the number of days that elapsed between final measurement and death in our animals was 29.0 ± 3.0 (mean \pm SE), an interval that was likely too brief to allow notable changes to occur. Elsewhere, it has been shown that relatively small animals of a variety of species are selected by predators (e.g., Mesa et al. 1994; Koivunen et al. 1996), likely because they are typically inexperienced (Mykytowycz et al. 1959), prone to increased inovement, exploration, and risky feeding (Halle 1988; O'Donoghue and Bergman 1992), and less able to evade or repel predators (Mykytowycz et al. 1959; Curio 1993). The relationship between size and predation rate was linear in the present study, implying that very young animals were especially vulnerable to predation. Studies of cyclic populations have shown that newly weaned juveniles disperse at a high rate relative to older animals (Gillis and Krebs 1999), a tendency that may expose them to increased predation pressure (Sievert and Keith 1985); however, in the present analysis, young of the year were no more likely to disperse than adults, strengthening our contention that in the present study, predation rate cannot be explained in terms of costs associated with dispersal.

A period of enhanced susceptibility to predation among young juveniles has been implicated as an important factor limiting the rate of increase associated with cyclic hare

populations (Keith 1990; O'Donoghue 1994). A similar period of susceptibility among inexperienced weanlings in southern hare populations, if sustained, may be sufficient to prevent the recruitment necessary to generate the cyclic dynamics altogether. If the geographic disparity in hare population dynamics is due to variability in the mortality rates of recently weaned juveniles, we would expect increase-phase cyclic populations to manifest higher survival rates than in southern populations, particularly among small juveniles. Previous demographic studies involving increasing cyclic as well as southern snowshoe hare populations produced survival rates for juveniles over the interval between weaning and adulthood (early March) that apparently did not differ as a function of geography (Gillis 1998). Thus, until more information pertaining specifically to the survival of newly weaned juveniles in cyclic populations that are on the increase becomes available, this scenario must remain speculative.

Population status

Our annual population-density estimate (0.09 ± 0.09) (mean \pm 95% CI) fell below the range of densities typifying other southern populations (1.09 ± 0.52 ; see Murray 2000), as well as that of declining/stable cyclic populations (0.29 ± 0.13 ; see Hodges 2000a). The extremely low density characterizing our study population may mean that the observed heavy predation rate on young juveniles is atypical of southern populations in general. An evaluation of this possibility will require additional survival analyses targeting small juveniles in the south. Our density estimate may also be the result of a depression of reproductive rates caused by inadequate food quantity and quality (Batzli 1983) and (or) predator-induced stress (see Boonstra et al. 1998). In a companion analysis (A.J. Wirsing and D.L. Murray, unpublished data) we found that hare productivity rates were indeed reduced relative to those of northern populations, suggesting that limitation of hare populations along the southern extent of the species' range may be a function of several factors, including age-specific predation.

Hare abundance in each study area declined or remained near 0 over the course of our investigation. Wishing to explain this trend, we calculated predation and reproduction values using the study sites for which we had the best demographic information (1 and 2), and produced a simple population-projection model incorporating estimates of adult potential natality (see Cary and Keith 1979), as well as the annual juvenile and adult mortality rates reported herein. This exercise forecast a marked population decline ($\lambda = 0.58$), a startling result given that sites 1 and 2 featured relatively high amounts of understory cover and were therefore considered to be suitable hare habitat. However, the decline we observed in our population estimates was considerably less severe ($\lambda = 0.80$), implying that populations on sites 1 and 2 likely were components of a larger snowshoe hare metapopulation, and numbers were maintained via ingress. We approximated the immigration rate for these sites by calculating the percentage of unmarked (i.e., non-radio-collared and without a numbered fingerling tag) animals caught during each trapping interval (excluding the breeding season). We felt reasonably safe in making the assumption that unmarked hares were immigrants rather than residents that had escaped previous capture because capture rates among

known (radio-collared) residents was high (80%). The mean annual immigration rate was found to average 52%, higher than that reported elsewhere for most (see Hodges 2000a) but not all (e.g., Murray 1999) hare populations. When compared with the mean dispersal rate characterizing sites 1 and 2 (35%), this level of immigration yielded a positive net recruitment rate (17%) close to that necessary for our model to project the moderate population decline we observed (22%), suggesting that populations on sites 1 and 2 were in fact being bolstered by the arrival of immigrants from nearby areas.

In theory, collections of spatially discrete local populations may be connected via dispersal in two ways: (1) in an island-mainland or source-sink format, whereby a network of satellite populations with negative finite growth rates is sustained by individuals diffusing from a population manifesting positive growth (Slatkin 1977; Pulliam 1988); or (2) in a classical metapopulation format under which the persistence of all constituents depends upon immigration from neighboring units (Taylor 1990). The hypothesis that population networks can be organized under the latter format has received little empirical attention (Taylor 1990), even though simulation studies have shown that dispersal may sustain metapopulations comprised entirely of populations manifesting negative growth (Hanski 1985, 1999). Although this study was too brief to identify a long-term population trend, the system described herein seemed to consist entirely of isolated hare populations occupying apparently good habitat that were characterized by negative growth rates yet maintained by immigration. Our study area was in a heavily exploited, fragmented landscape where patches of good hare habitat are rare and exist as small islands set amidst clearcuts and mature, open stands. We strove to insure that our trapping sites encompassed the full range of habitats available to hares in the region, including these island patches. The 3 high-cover sites in this study featured dense and protective understories equaling or exceeding any we encountered during an extended survey of the region and, moreover, a fecal-pellet survey involving 100 transects placed throughout the Clearwater National Forest indicated that these sites housed relatively high numbers of hares as well (D. Murray, unpublished data). The possibility that patches of more suitable habitat located nearby acted as sources for these trapping sites is remote. Thus, we concluded that the hare populations residing on our study sites may have been sustained through exchange with other populations in similar patches (the classical metapopulation format) rather than by ingress from a source patch and, therefore, that our study area lacked refugia. We must note, however, that another study carried out in the south has shown a relationship between survival and cover where patch size is sufficiently large (49 ha; Litvaitis et al. 1985), suggesting that in areas where hare habitat is relatively continuous the traditional refugium model may still apply (i.e., dispersal-related mortality may take on added importance; refuge/source patches may exist).

Metapopulation dynamics have been invoked to explain the persistence of local New England cottontail (*Sylvilagus transitionalis*) populations in the fragmented landscape of the northeastern United States (Barbour and Litvaitis 1993). The possibility that southern snowshoe hares exist as classical metapopulations as well is intriguing and may help explain the alleged absence of population cycles in southern

Canada and the contiguous United States. If hare populations throughout much of the species' southern range do occur as extinction-prone islands buoyed by immigration, then we would not expect them to manifest the recruitment rates necessary to precipitate the dramatic population growth rates intrinsic to their northern counterparts. The first step in addressing this hypothesis should be the initiation of a study of sufficient length to verify the long-term consistency of the trends in dispersal and predation that we have noted. Such a design should enable biologists to assess whether snowshoe hare populations in the south are indeed perpetually threatened with extinction by predation focused on postweaning juveniles and, more importantly, whether the movement of hares between these populations is sufficient to produce regional stability.

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