Research

Sinks without borders: snowshoe hare dynamics in a complex landscape

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A full understanding of population dynamics of wide-ranging animals should account for the effects that movement and habitat use have on individual contributions to population growth or decline. Quantifying the per-capita, habitat-specific contribution to population growth can clarify the value of different patch types, and help to differentiate population sources from population sinks. Snowshoe hares, *Lepus americanus*, routinely use various habitat types in the landscapes they inhabit in the contiguous US, where managing forests for high snowshoe hare density is a priority for conservation of Canada lynx, *Lynx canadensis*. We estimated density and demographic rates via mark–recapture live trapping and radio-telemetry within four forest stand structure (FSS) types at three study areas within heterogeneous managed forests in western Montana. We found support for known fate survival models with time-varying individual covariates representing the proportion of locations in each of the FSS types, with survival rates decreasing as use of open young and open mature FSS types increased. The per-capita contribution to overall population growth increased with use of the dense mature or dense young FSS types and decreased with use of the open young or open mature FSS types, and relatively high levels of immigration appear to be necessary to sustain hares in the open FSS types. Our results support a conceptual model for snowshoe hares in the southern range in which sink habitats (open areas) prevent the buildup of high hare densities. More broadly, we use this system to develop a novel approach to quantify demographic sources and sinks for animals making routine movements through complex fragmented landscapes.

Movement connects the fate of individual animals to the landscapes they inhabit. For species with narrow habitat requirements, the matrix of intervening habitats is an obstacle to dispersal between habitable patches, but for species that occupy a wide range of habitat types in a landscape, the matrix itself and its patches of varied quality define the area on which population dynamic studies should focus. Whereas many published metapopulation studies focus on species with habitat requirements so narrow that they are confined to 'islands' of habitable patches surrounded by a hostile 'matrix' (Noon and McKelvey 1996, Hanski 1997, Bjørnstad et al. 1998), many more species live in so-called 'patchy metapopulations' (Harrison 1994), in which individuals move regularly through a landscape composed of many nearby habitat types. Animal movement through the matrix of varying habitats influences ecological interactions with conspecifics, predators, and forage (or prey). Routine movement in such a landscape may expose individuals to risks and benefits that vary across space, with survival or reproductive rates influenced by the amount of time spent in each habitat type used.

If individual survival, emigration, and reproductive rates are partially functions of the habitual use of multiple habitat types, then demographic models should incorporate those effects (Conroy et al. 1996). Estimating habitat-specific rates in a varied landscape is difficult, though, and empirical studies that synthesize the effects of multiple patch use on individual fitness, patch-level density, and overall population dynamics have been rare (Wiens 1997).

A dominant paradigm for quantifying dynamics of individual populations in a multi-population context centers on source–sink dynamics (Lidicker 1975, Holt 1985, Pulliam 1988), where a source is a kernel for population increase and a sink is a nexus of decline. A crucial step for applied ecology – to operationally classify subpopulations in fragmented landscapes as sources or sinks – has been stymied by both the lack of a definition that links to field-based parameter estimates and by the challenges in estimating the necessary among-population and within-population vital rates. These challenges have largely limited diagnosis of sources and sinks to small species for which experimental manipulation is tractable or for species with narrow habitat requirements (Diffendorfer 1998).

Recently, Runge et al. (2006) developed an approach to delineate sources and sinks from field data on within- and among-population vital rates; this approach is both theoretically sound and operational with modern field data. First,

they define self-recruitment of subpopulation r (R^r), using data on the apparent survival of adults that remain in subpopulation r, ($\varnothing_A^{rr}$), the apparent survival of juveniles that are born and remain in subpopulation r, ($\varnothing_J^{rr}$), and the habitat-specific reproductive rate, B^r:

$$R^r = \varnothing_A^{rr} + B^r \varnothing_J^{rr}$$

Runge et al. (2006) note that R^r has been used to define sources ($R^r > 1$) and sinks ($R^r < 1$), but the lack of an emigration term is problematic; for example a subpopulation that provides emigrants to other subpopulations, thereby acting as a source for overall population growth, could have $R^r < 1$. Likewise, immigration (I) versus emigration (E) rates alone cannot operationally distinguish sources and sinks because they do not account for mortality of emigrants or for birth and survival processes that can cause non-equilibrium conditions (when local subpopulation $\lambda \neq 1.0$).

As a metric based on field data for operationally defining source and sink populations, Runge et al. (2006) propose the "contribution metric", C^r, which includes emigration rate, E, in accounting for the contribution of a subpopulation. A source has a $C^r > 1$ and a sink $C^r < 1$. The general equation, $C^r = R^r + E$, can be connected to apparent survival by including the apparent survival of animals that move from subpopulation r to other subpopulations, s:

$$C^r = \varphi_A^{rr} + \sum_{s \neq r} \varphi_A^{rs} + \beta^r \left(\varphi_J^{rr} + \sum_{s \neq r} \varphi_J^{rs} \right)$$

The contribution metric can also be calculated based on estimates of true survival, assuming survival is the same for emigrants and non-emigrants:

$$C^r = S_A^r + S_J^r \beta^r$$

Importantly, recent advances in survival rate analyses allow parameterization of the contribution metric, expanding the possible diagnosis of source and sink habitat types in complex fragmented landscapes, and for species that range among habitats. For example, the inclusion of time-varying individual covariates (Catchpole et al. 2000, King et al. 2008) in known fate survival rate analyses (e.g. from radio-marked animals) allows for the estimation of habitat-type specific survival rates, even for studies in which animals move among habitat types. The proportion of time that an animal spends in various habitat types can be represented by covariates that potentially influence survival rate estimates (Schwartz et al. 2006).

These advances in survival rate analysis are especially important because source–sink analyses to date have been restricted to assuming that animals are restricted to particular patches (as in the subpopulation r designation in Runge et al. 2006). However, many animals move through multiple habitat types, so the question becomes how the patch types affect population dynamics for animals that regularly use multiple patch types.

In this study we assess the role that habitat type plays on survival rates for a species that regularly moves through a range of habitat types within a heterogeneous landscape. The regular 9–11 year snowshoe hare population cycles in their range well north of the US – Canada border make them the 'poster child' for population dynamics studies (Elton 1924, Moran 1953, Keith 1990, Krebs et al. 1995,

Krebs et al. 2001). As generalist herbivores with a wide range and large trophic influence in boreal and montane forests, snowshoe hares repeatedly move between and use adjacent patches over short time periods of hours, days, weeks, and seasons. Not only is the mechanism of snowshoe hare population change in a patchy landscape of interest in its own right, an understanding of hare dynamics also underlies insights into US federally threatened Canada lynx (US Forest Service 2007), which rely heavily on hares as prey (Squires and Ruggiero 2007).

Snowshoe hares are generally found at highest densities where understory vegetation is dense (US Forest Service 2007), but density alone may not be an indicator of favorable survival rates (van Horne 1983). The matrix of montane and subalpine forests in the southern landscapes they inhabit is made heterogeneous by elevation and moisture gradients, vegetation succession and disturbances including fire, insect outbreaks and industrial forest management. In this southern range, snowshoe hares may cycle with low amplitude, irregularly, or not at all (Keith 1990, Hodges 2000, Malloy 2000, Murray 2000). The mountain hare, *Lepus timidus*, which occupies a similar ecological niche in Eurasia, also has inconsistent patterns of population dynamics in its southern range (Newey et al. 2007).

Dolbeer and Clark (1975), Wolff (1980) and Keith et al. (1993) echoed Howell (1923) when they proposed that high quality habitat patches in the southern range can produce a net surplus of snowshoe hares, but low reproduction and/or high mortality in poor quality habitat types prevent synchronous, high population densities across large landscapes in the southern range. The ensuing 'refugium' model for snowshoe hares (Wolff 1980) predicts that source–sink dynamics prevent cyclic population dynamics in the southern range. One study that has evaluated this conceptual model in the snowshoe hare southern range found such uniformly low survival rates in the habitat types studied that it appeared hare populations there were supported by immigrants from elsewhere (Wirsing et al. 2002).

Here, we apply a novel extension of the contribution metric to snowshoe hare vital rates in order to quantify whether different habitats in a heterogeneous landscape act as sources and sinks. By determining how the composition of different habitat types in a landscape influences snowshoe hare population growth rates, we apply an analytical source–sink framework to the long-standing question of whether cyclic dynamics are dampened by habitat heterogeneity.

Methods

Forest stand structure types, study areas and seasons

In the Seeley-Swan region of western Montana, forests are dominated by Douglas-fir *Pseudotsuga menziesii*, subalpine fir *Abies lasiocarpa*, western larch *Larix occidentalis*, lodgepole pine *Pinus contorta* and Engelmann spruce *Picea engelmannii*. To simplify the diversity of stand histories, successional stages, stem densities and species compositional mixes typical of montane coniferous forests in Montana, we chose four distinct forest stand structure (FSS) types from

opposing ends of the ranges of stand age and tree stem density: dense young, open young, dense mature and open mature. Dense young and dense mature FSS types are putative sources because hares are known to typically favor young (20–45 years), dense stands providing ample cover and forage (Hodges 2000), as well as mature stands (>150 years old and with average DBH >30 cm) with dense understories. In contrast, what we term open young and open mature FSS types with less horizontal and/or vertical cover generally support lower hare densities (Hodges 2000). We operationally classified stands into one of the four FSS types based on criteria for sapling density, basal area, horizontal cover and overhead canopy cover (Griffin and Mills 2004).

We used air photos of the Seeley-Swan region to choose three replicate study areas each with all four target FSS types in close proximity (within 1.5 km of one another), and where the stands were >30 ha and within 1 km of a forest road: Inez (~1400 m a.s.l.), Placid (~1250 m a.s.l.), and Spring Creek (~1700 m a.s.l.). The three study areas were 22–30 km from each other, well above published snowshoe hare dispersal distances (Hodges 1999).

Trapping and density estimation

We used live traps to capture snowshoe hares for three purposes: density estimation, radio telemetry and fertility rate estimation. We baited traps with apple, alfalfa and horse pellets, and checked traps every morning. Hares were tagged in both ears, weighed, sexed and released.

When trapping to estimate density (Mills et al. 2005) in a particular FSS type stand, we arranged 50 live traps in a 5 × 10 grid, with traps 50 m apart. The result was a 200 × 450 m trapping grid that also had a buffer of 50 m or more to any stand edge. Primary sessions were four to six nights, and we trapped all four FSS type stands at a study area simultaneously. On each trapping grid, we trapped three primary sessions per summer in 1998 and 1999, two primary sessions in summer 2000, and one primary session per summer in 2001, 2002 and 2003. We trapped one primary session at Inez and Spring Creek study areas in the winter of 1999–2000, and one primary session at each of the three study areas in winter 2000–2001 and in winter 2001–2002.

We used the Lincoln–Petersen estimator with small sample size correction (Chapman 1951) for abundance estimation because of a low number of recaptured animals (McKelvey and Pearson 2001); we increased the number of individuals per sample period by creating two sample periods from the first half and last half of the 4–6 trap nights (Mills et al. 2005). Our estimates of density accounted for the 'effective area' over which animals were available for trapping by estimating the mean maximum distances moved (Mills et al. 2005).

Telemetry

We conducted intensive study with radio telemetry at the four FSS stands on the Inez study area. We trapped extensively on permanent trapping grids and on auxiliary trap lines covering over ~5.3 km² of the site throughout 1999–2002. Adult hares and juveniles over 500 g were individually fitted with 30 g radio collar transmitters. Switches on the transmitters signaled mortality after ~6 h of motionlessness. Snowshoe hares are generally crepuscular or nocturnal (Keith 1964, Hodges 1999), so we relocated hares at all hours. UTM coordinates were recorded with handheld geopositioning system recorders (<10 m inaccuracy). Locations before April 2000 were differentially corrected, with reference to a GPS base station. In most cases, FSS type for each snowshoe hare location was recorded in the field, then cross-referenced against a geographic information system (GIS) database that also had spatial data layers for elevation, forest stand boundaries, roads and LandSat 7 satellite imagery. Some hares entered stands that were not trapped or formally sampled with vegetation plots; we judged whether the vegetation structures in those stands matched any of the four FSS type designations, based on GIS layers and our experience in sampled stands. The four target FSS types occupied most of the Inez study site, but early successional riparian vegetation structures were also found in patches totaling ~4% of the ~5.3 km² study area. For analyses of survival and emigration rates, we pooled hare locations from riparian stand structures with the dense young FSS type because they were dominated by young aspen trees *Populus tremuloides* and alder *Alnus tenuifolia* shrubs <10 cm DBH.

We determined the majority of snowshoe hare locations by sight (n >1664), or by hearing transmitter signals without an antenna (n >1050), indicating location error of <15 m (N. Olson and P. C. Griffin unpubl.). We did not record a location if radio signals indicated that a hare flushed as we approached. We also estimated 204 snowshoe hare locations from triangulation, using program TelLoc7 (G. McDaniel, US Forest Service Rocky Mountain Research Station, Missoula, MT unpubl.). Mean triangulated location uncertainty was 46 m (SE = 2.0 m), based on the location error method (Zimmerman and Powell 1995) and field trials with 43 triangulations of hidden radio-collars (P. C. Griffin, A. Landro and C. Waroquiers unpubl.).

Survival rates of adults and post-weaning juveniles

We attempted to monitor the location and survival status of all radio-collared hares once per week, with 144 weekly time periods included in the survival analysis from 26 July 1999 to 28 April 2002. The frequent relocation of radio collared hares allowed us to estimate the proportion of time each hare spent in each FSS type for 7-day time periods. If we located an animal twice or more in a given 7-day period, then we assumed that the animal was found in each FSS type in proportion to the fraction of locations observed. For example, an animal observed twice in one FSS type and once in a second would have estimated use during that 7-day period of 0.67 for the first and 0.33 for the second. If no location was recorded for an animal in a 7-day period then we assumed that it had remained in the same FSS type as its last observed location. When a radio-collared hare's remains were found in a given FSS, that mortality was also recorded as a location in that FSS.

For each individual hare there was a unique compositional use vector for each time period, **u**, with four values that summed to one. For each time period of the study this was the vector of the proportions that an individual used the four different FSS types. In this way, the proportion of each hare's estimated use in each FSS type was recorded as a time-varying individual covariate (MacKenzie et al. 2002, Schwartz et al. 2006) that represented time-specific habitat type use separately for each week the hare was monitored. Weekly survival for juveniles ($S_{Juv\ \mathbf{u}}$) or adults ($S_{Ad\ \mathbf{u}}$) could then be estimated as a function of snowshoe hares' proportional use of different FSS types in each time period.

We used known-fate models in program MARK (White and Burnham 1999) to estimate survival rates. Hares were added to the data set starting from the first date when they were radio-collared, were followed through to mortality, and were right-censored if we lost their signal (i.e. due to collar failure or dispersal beyond the ~ 15 km range of radio reception). In candidate models, survival rates were potentially influenced by season and by individual covariates for sex, age and FSS type use. All survival models that included effects of FSS type included logit link functions with parameters that were multiplied by the time-varying individual covariates specifying the proportion (0–1) of animal use in each FSS type during that time period. In some models only one FSS was modeled as an additive effect, with all others pooled. In other models, open FSS types were pooled and compared to dense FSS types. A third set of models compared mature FSS types to young FSS types.

We differentiated four seasons for survival analyses, based on local climate. Snow was likely to cover the ground completely during the 16 week winter (~ 13 December to ~ 2 April). Spring (~ 3 April to ~ 25 June), summer (~ 26 June to ~ 17 September) and fall (~ 18 September to ~ 12 December) were each 12 weeks long. In models with seasonal effect parameters, the effect was additive across all FSS types. Some models included an effect of two season groups, where spring and fall were combined, and summer and winter were combined. This grouping reflected biological processes that may reduce survival in spring and fall – for example where molting hares may not match background colors in the environment (Litvaitis 1991). Also, in the fall herbaceous foliage has senesced yet no snow gives access to higher conifer branches, while in the spring forage may still be poor while energy demands prior to reproduction increase.

Sex was included in some models as an additive effect throughout the year. In other models the effect of sex was limited to the reproductive season (~ 21 April to ~ 30 September). Age was modeled as an additive effect throughout the year; hares were considered juvenile from weaning until the end of their first spring.

We used AICc to rank model parsimony (Burnham and Anderson 1998), then used model averaging to estimate the weekly survival rates and the associated 95% confidence intervals for snowshoe hares living in different FSS types, based on models with $\Delta AICc < 4$. We also used model averaging to estimate the effect size on weekly survival rate of age, sex, season and proportional FSS usage. Because bootstrap goodness-of-fit testing is not possible in program MARK for models with individual covariates, we tested the goodness-of-fit for the highest ranked model by assuming that the deviance of the model was χ^2-distributed, with degrees of freedom equal to the difference in the number of parameters in the saturated model and the highest ranked model (White and Burnham 1999).

Movements and dispersal

Based on radio telemetry locations, we calculated the distances between all points where each individual was located within a given season, and over all dates monitored. For each hare and time period, we call the largest of those distances the maximum displacement. We tested for variation in the average maximum displacement that hares moved in each season, and used the distribution of observed maximum displacements to estimate the spatial scale of the ecologically interacting population.

We defined emigrants as radio-collared hares that permanently dispersed greater than 500 m in one direction, a distance more than two times the diameter of a reasonably large (20 ha) home range (Hodges 1999). For adults, because natal location was not known, we required $>$ five locations prior to dispersal to detect a >500 m shift in home range.

Individual covariates used in the known fate models for emigration (Bennetts et al. 2001) included season, age, sex and FSS type usage. We analyzed (using Program MARK) known fate data from 141 radio-marked adult and juvenile hares compiled in 36 4-week periods, during which each monitored hare was recorded as having stayed or having emigrated, to estimate E, the per-capita annual probability that an individual permanently disperses from a FSS type.

We removed the effect of survival on emigration probability by right-censoring hares that died prior to emigrating. Emigration rates for 4-week intervals, along with the effect sizes of age, sex, season and FSS type usage, were estimated by model averaging. Goodness-of-fit for the highest ranked model was assessed as with survival models. We could not directly measure immigration rates into each FSS type because it was possible that unmarked hares that were trapped on our study areas may have come from adjacent unsampled forest stands.

Fecundity rates and survival rates of leverets

Snowshoe hares are born in the spring and summer, and are reproductively mature the following spring. Pregnant snowshoe hares give birth roughly synchronously, in birth pulses (Keith 1990, Murray 2000). In this study there were three synchronous pulses per summer.

For each of the three birth pulses, we considered fecundity, f_1, f_2 and f_3, to be the number of female offspring in each birth pulse per reproductive age female; this value is the product of pregnancy rate and litter size for that birth pulse, both estimated at the three study areas and two nearby sites (trapping grids 36 and 102 in Mills et al. 2005) using ultrasound as described in Griffin et al. (2003). Total fecundity (of female offspring) from all three birth pulses was 4.2 (Table 1); by comparison, total fecundity ranges between 3.5 to 9.5 in cyclic populations (Cary and

Table 1. Parameter estimates for fertility in each of three birth pulses ($\hat{f}_1$, $\hat{f}_2$, $\hat{f}_3$), leveret survival rate ($\hat{S}_{Lev}$), and annual emigration rate ($\hat{E}_1$)were common to all FSS types. Fertility in each birth pulse, the number of female leverets per adult female, is the expected product of pregnancy rate and litter size divided by 2. Standard errors are in parentheses.

$\hat{f}_1$	$\hat{f}_2$	$\hat{f}_3$	$\hat{S}_{Lev}$	$\hat{E}$
1.40 (0.071)	1.87 (0.092)	0.89 (0.087)	0.56 (0.082)	0.21 (0.071)

Keith 1979, Stefan and Krebs 2001) and between 3.2 to 5.8 in non-cyclic populations (Murray 2000).

Newborn snowshoe hares (leverets) wean after four to five weeks (Keith 1990). For population projection models we used leveret survival-to-weaning rate estimates from Griffin (2003), who followed methods of O'Donoghue (1994). Briefly, radio transmitters were glued on newborn leverets born to temporarily captive females, then radio-marked leverets and their mothers were located daily until 35 days after birth, or until found dead. We applied the same estimate for leveret survival rates (mean = 0.56; 95% CI 0.40–0.72; n = 41) to all FSS types.

Projected growth rates accounting for routine movement

In the absence of emigration and immigration, and in a landscape with spatially uniform quality, a simple model (Eq. 1) for discrete exponential population growth, $\lambda_{no\ migrants}$, incorporates the annual survival rate of adults, $S_{Ad\ Annual}$, and the fertility rate, F, the number of female offspring present at time $t+1$ per female alive at time t. Fertility reflects both fecundity and survival of reproducing females up to parturition and of subsequent newborns to time $t+1$. This value of λ is the expected growth rate if the population is closed to movement, and also describes the mean individual fitness for the population (McGraw and Caswell 1996); values over 1 indicate that individuals leave more than one surviving offspring and also that they contribute to an increasing population.

$$\lambda_{no\ migrants} = S_{Ad\ Annual} + F \tag{1}$$

Individual snowshoe hares move, however. They do not necessarily remain in one FSS type and their routine movements through heterogeneous forest in an interconnected matrix expose them to variable risk. If survival rates vary as a function of the vector that represents the proportional use of different FSS types, $\mathbf{u}$, then Eq. 1 can be generalized to include this survival rate, $S_{Ad\ Annual\ \mathbf{u}}$, and describe the individual fitness for a hare using FSS types in the proportions $\mathbf{u}$.

We modeled expected population growth rates for snowshoe hares that varied in the compositional use of different FSS types they occupied ($\lambda_{\mathbf{u}\ matrix}$), using Eq. 2. The annual population growth rate ($\lambda_{\mathbf{u}\ matrix}$) incorporates adult survival ($S_{Ad\ \mathbf{u}}$) through all seasons, and fertility ($F_{\mathbf{u}}$; Appendix 1). Equation 2 yields the expected individual fitness (McGraw and Caswell 1996) for hares with a particular vector, $\mathbf{u}$, of proportional use in different FSS types. $\lambda_{\mathbf{u}\ matrix}$ also approximates the snowshoe hare

population growth rate for a landscape that is closed to immigration or emigration, and which is composed of FSS types in the proportion $\mathbf{u}$.

$$\lambda_{\mathbf{u}\ matrix} = S_{Ad\ Annual\ \mathbf{u}} + F_{\mathbf{u}} \tag{2}$$

This equation can also be expanded to allow for seasonal variation in survival rates, so that adult survival is decomposed into the weekly adult survival rate in each of the four seasons, raised to the power corresponding to the length of each season, in weeks (Eq. 3).

$$\lambda_{\mathbf{u}\ matrix} = (S_{Ad\ Spring\ \mathbf{u}}^{12} \times S_{Ad\ Summer\ \mathbf{u}}^{12} \times S_{Ad\ Fall\ \mathbf{u}}^{12} \\ \times S_{Ad\ Wint\ \mathbf{u}}^{16}) + F_{\mathbf{u}} \tag{3}$$

To estimate the annual expected growth rate of single FSS types in isolation, $\lambda_{Single\ FSS}$, for each of the four FSS types, we calculated $\lambda_{\mathbf{u}\ matrix}$ using expected survival rates for individuals occupying only single FSS types. That is, Eq. 4 describes $\lambda_{Single\ FSS}$ only for the following vectors of $\mathbf{u}$: (1,0,0,0), (0,1,0,0), (0,0,1,0) or (0,0,0,1).

$$\lambda_{Single\ FSS} = \lambda_{\mathbf{u}\ matrix} \tag{4}$$

Considering the frequent movements that hares make between adjacent and nearby FSS types, it may not seem realistic to assess $\lambda_{\mathbf{u}\ matrix}$ as if a single FSS type is used exclusively. Nonetheless, this approach does allow us to explore what factors could increase population growth rates in landscapes where particular FSS types dominate. For example, we used Eq. 4 to ask what increase in fecundity rates would lead to stable populations (e.g. $\lambda_{Single\ FSS} = 1.0$) in a landscape composed only of a single FSS type. Both $\lambda_{Single\ FSS}$ and $\lambda_{\mathbf{u}\ matrix}$ are equivalent to the Runge et al. (2006) 'contribution' or C^r metric (Introduction), quantifying the per capita contribution to the greater metapopulation of a member of a focal population (in this case hares occupying either a single FSS type, or a mixed landscape composition $\mathbf{u}$). We used the delta method (Agresti 1990) to estimate standard error terms.

Projected growth rates including emigration and immigration

Real snowshoe hare populations consist of hares that move between nearby stands and that are 'open' to the outflow of emigrants and the arrival of immigrants. Expected population growth for hares using a single FSS type type $\lambda_{Single\ FSS}$ (Eq. 4) can be expanded to account for connectivity, or per-capita emigration (E) and immigration (I) rates:

$$\lambda_{Single\ FSS\ with\ connectivity} = \lambda_{Single\ FSS} - E + (I \times \lambda_{Single\ FSS}) \tag{5}$$

If Eq. 5 is used to project population size at time $t+1$, then E and I are rates per individual hare that is present in the FSS type at time t. Equation 5 is structured as if movement occurs just after time t. That is, the population declines by the per-capita emigration rate, but the per-capita immigration rate must be multiplied by $\lambda_{Single\ FSS}$ because the animals that arrive potentially survive and reproduce in the interval before time $t+1$.

Immigration is difficult to estimate in any open population in the wild because immigrants by definition come from outside the population (at least 500 m away in our case), and can come from any patch type (FSS type

in our case). We could not reliably estimate immigration rate from our field work; untagged hares trapped on our study grids could have been immigrants or could have been present but not trapped in previous trapping occasions.

We could, however, directly estimate annual emigration rate (E), the probability that an individual will emigrate during the year. Thus we could estimate the dynamics of a population losing emigrants but not gaining immigrants (Eq. 6).

$$\lambda_{\text{Single FSS}-\text{emigrants}} = \lambda_{\text{Single FSS}} - E \qquad (6)$$

This equation is equivalent to the self-recruitment rate (R^r) for a population r; that is, the ability of the population to maintain itself in the absence of immigration (Runge et al. 2006).

For FSS types with $\lambda_{\text{Single FSS}-\text{emigrants}}$ less than 1, we rearranged Eq. 5 to ask what values of immigration rate, I, would be necessary to make $\lambda_{\text{Single FSS with connectivity}}$ stationary ($=1.0$):

$$I = \left(\frac{1+E}{\lambda_{\text{Single FSS}}} \right) - 1 \qquad (7)$$

Observed growth rates

We used the density time series to estimate the average observed population growth rates, $\bar{\lambda}_{\text{Observed}}$, for each trapping grid. These realized rates reflect actual survival, emigration, and immigration. We calculated $\bar{\lambda}_{\text{Observed}}$ as the geometric mean across all years of the observed annual growth rates in population density, (D_{t+1}/D_t) for each trapping grid. We used the first estimated density value from every summer in these calculations (i.e. from May or early June), because only adult snowshoe hares were caught in these trapping sessions and because these estimates of density reflect the size of the adult population around the time of parturition for the first birth pulse. We also calculated an average observed growth rate for each study area, $\bar{\lambda}_{\text{Observedstudyarea}}$, estimated from changes in total density of the study area for each year based on the summed total of estimated hare abundance in the four FSS types divided by the summed total of the effective trapping areas for the four trapping grids.

Results

There were consistent differences in snowshoe hare density among FSS types. The highest summer densities at each study area were generally in the dense young FSS type, and the next highest in most years and study areas was in the dense mature FSS type (Fig. 1, Table 2). Only stands of dense mature consistently had densities that were as high or higher in winter as in the preceding summer (Fig. 1). Estimated $\bar{\lambda}_{\text{Observed}}$ varied with study area and FSS type (Table 2). At the Placid and Spring Creek study areas, where in most years we caught no snowshoe hares on the open young and open mature trapping grids, the highest average $\bar{\lambda}_{\text{Observed}}$ estimates were in the dense young type. The $\bar{\lambda}_{\text{Observed}}$ estimate was highest in the dense mature type at
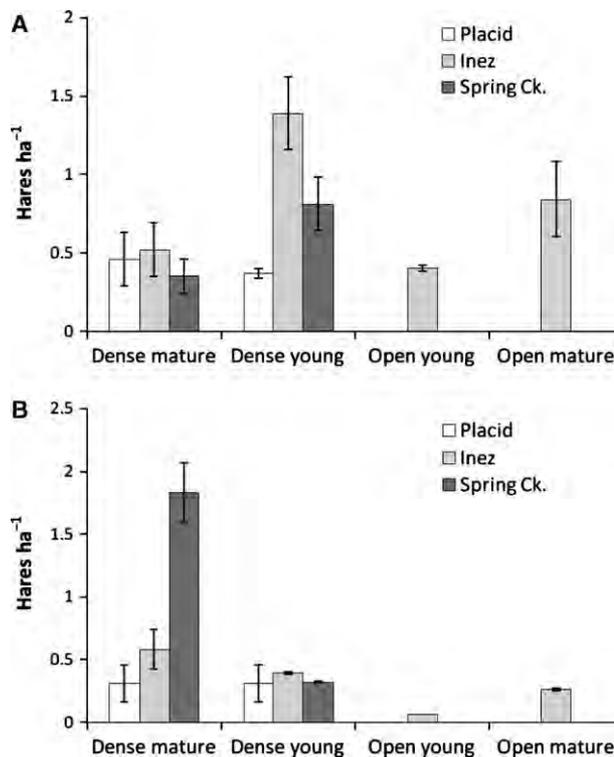

Figure 1. Initial snowshoe hare density estimates (hares ha^{-1}) on trapping grids in four FSS types at each of three study areas. Study areas are: Placid (white bars), Inez (grey bars), and Spring Creek (black bars). (A) Initial summer densities, from 1999. (B) Initial winter densities, from winter 1999–2000 at the Inez study area and Spring Creek dense mature and dense young stands, and from 2000–2001 at the Placid study area and Spring Creek open mature and open young stands. Error bars are standard errors.

the Inez study area. This study apparently coincided with a regional decline in snowshoe hare densities; $\bar{\lambda}_{\text{Observed study area}}$ was less than one at the Placid and Spring Creek study areas, but slightly greater than one at the Inez study area (Table 2).

We monitored 175 snowshoe hares with radio-telemetry at the Inez study area from 26 July 1999 to 26 April 2002, recording 3240 locations. The median number of locations per hare was ten (range = 1 to 205). Movement among FSS types was common. Of 128 hares that were located five or more times, 118 were recorded in more than one FSS type (Fig. 2). Nearly 70% of hares were located at least once in the dense mature FSS type and roughly half of radio-collared hares were located at some point in the dense young or open young FSS types, but only ∼30% of hares were located once or more in the open mature FSS type (Fig. 2).

Weighting equally all hares that were radio collared, the average proportional occupancy rates of the dense mature, dense young, open young and open mature FSS types were 0.37, 0.30, 0.21 and 0.12, respectively.

From the observed distribution of annual displacements, 50%, 75% and 90% of maximum annual displacements were less than 470 m, 780 m and 1800 m, respectively. We found slightly greater maximum movement distances for hares in the fall (730 m, SE = 150 m) than in spring (430 m, SE = 50 m), summer (440 m, SE = 50 m), or winter (420 m, SE = 40 m).

Table 2. The observed geometric mean $\bar{\lambda}_{Observed}$ values estimated from annual changes in estimated summer densities on individual trapping grids from 1999–2003 varied from study area to study area. The same was true of overall values for the observed rates of growth for each study area, $\bar{\lambda}_{Observed\ study\ area}$, based on annual changes in average estimated density across all trapping grids at a study area. The average proportional densities ($\hat{D}_{Proportional}$) observed in summer at each of the four FSS types did not vary greatly from study area to study area in 1999, the year of the study with the highest average observed hare densities. Standard errors are in parentheses.

	$\bar{\lambda}_{Observed}$ Placid	$\bar{\lambda}_{Observed}$ Inez	$\bar{\lambda}_{Observed}$ Spring Ck	$\hat{D}_{Proportional}$
Dense mature	0.58 (0.40)	1.34 (1.33)	0.23 (0.39)	0.340 (0.113)
Dense young	1.04 (1.26)	1.01 (0.31)	0.54 (0.17)	0.528 (0.084)
Open young	*	0.76 (0.25)	*	0.043 (0.043)
Open mature	*	0.94 (0.49)	*	0.089 (0.089)
$\bar{\lambda}_{Observed\ study\ area}$	0.85 (0.63)	1.09 (0.45)	0.63 (0.10)	

*No values for these trapping grids could be estimated because initial densities were zero.

For radio collared animals with enough locations to distinguish emigration from routine movement, we recorded emigration in 13 of 34 radio-collared juveniles and 7 of 107 adults. There were 23 emigration models with AICc < 4, all of which included an effect of season, with higher estimated emigration rates in fall and winter than spring and summer. The model averaged 4-week emigration rate estimates were 0.0070 {95% CI: 0.0020–0.020} for spring and summer versus 0.027 {95% CI: 0.016–0.043} in the fall and winter. For hares that survived an entire year, the annual emigra-

tion rate, E, was 0.21 {95% CI = 0.12–0.35}. The most parsimonious emigration model had acceptable goodness-of-fit ($\chi^2 = 183.4$, DF = 575, p = 1.0).

In projections, we used a single value for E in every FSS type, because models with different emigration according to FSS type were not well supported by the data. Although effects of each FSS type, age and sex were included in some of these 23 models, the effect sizes for all of the FSS, age, and sex covariates were close to zero, with 95% CI overlapping zero. Differences in the absolute number of
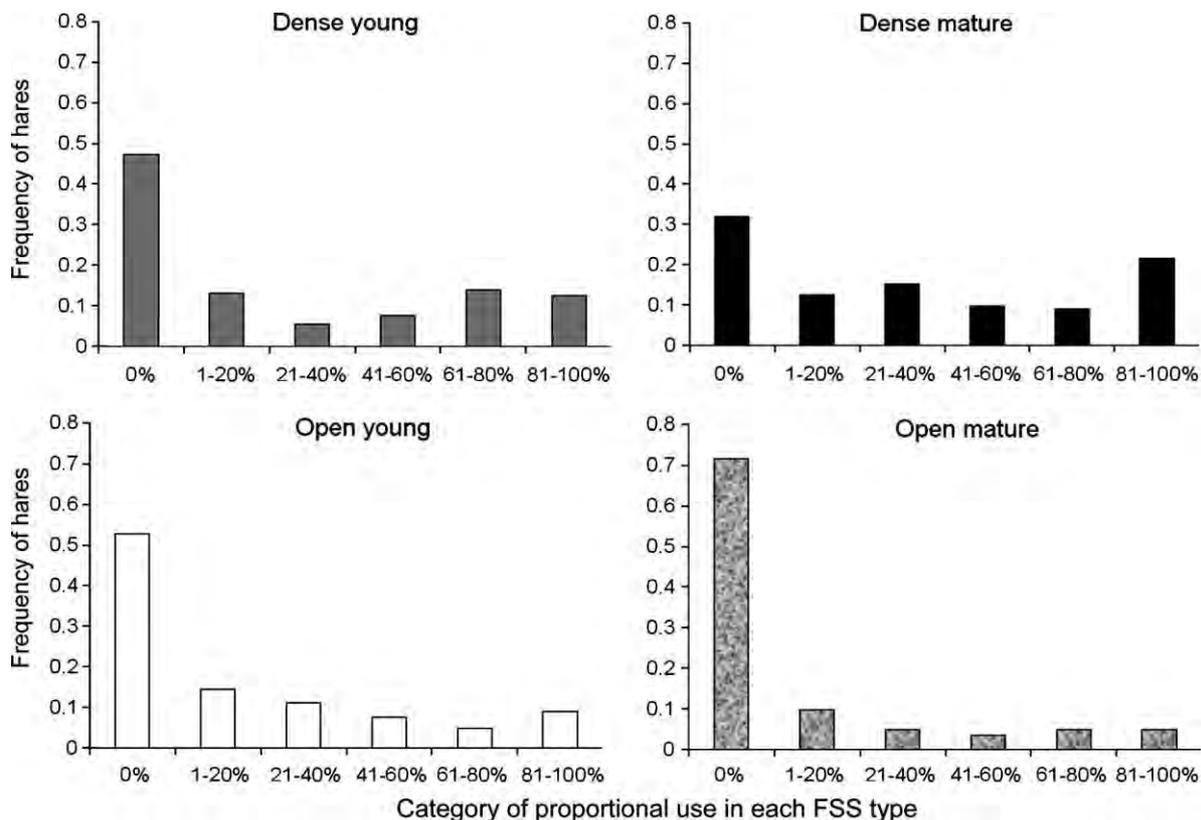

Figure 2. Histograms showing the frequency of FSS type use by snowshoe hares show that individuals frequented many FSS types. The overall proportion of locations from which a hare was located in a particular FSS type are grouped here into six categories of proportional use, shown on the x-axes. The height of each bar represents the frequency of hares whose total fraction of locations fell within that range of percentages. For example, 12% of observed hares had between 1–20% of their locations in the dense mature FSS type; 22% of observed hares had between 81–100% of their locations in the dense mature FSS type, and 53% of observed hares had no locations in the open young FSS type.

Table 3. Twenty of 141 radio collared snowshoe hares with well documented home ranges emigrated, representing permanent dispersal more than 500 m in one direction. The column at left indicates the number of emigrants that departed from each of the four FSS types in this study. The column at right indicates the number of those twenty which settled into each of the four FSS types.

	No. emigrants	No. emigrants, settled
Dense mature	7	11
Dense young	10	5
Open young	3	2
Open mature	0	2

individuals that emigrated from each FSS type (Table 3) may be partially explained by the associated differences in snowshoe hare density.

Emigrants did not settle into FSS types in the same proportions as the proportions of FSS types from which they came; twice as many emigrant hares originated in the dense young FSS type as settled there (Table 3). However, the proportions in this small sample were not statistically significantly different (Fisher's exact test p = 0.19) so we cannot conclude that any one FSS type was a preferred destination for emigrants.

Adult and post-weaning juvenile survival

Survival analyses were based on 163 radio-collared snowshoe hares at the Inez study area. Weekly snowshoe hare survival was heavily influenced by season and the relative use of different FSS types, and was less influenced by individual age or sex. The 12 models with the lowest AICc values all included parameters representing effects of season and FSS type (Table 4). Goodness-of-fit for the most parsimonious model, based on model deviance, was adequate ($\chi^2 = 964.4$; DF = 1148, p = 1.0).

The estimated weekly survival rate for an adult snowshoe hare inhabiting the dense young FSS type in spring was 0.96 (95% CI 0.97–0.95). In seasons other than spring, weekly female survival rate in dense young was estimated to be 0.022

higher in summer (95% CI of effect size 0.011–0.028), 0.022 higher in winter (95% CI of effect size 0.012–0.028), but only 0.0003 higher in fall (95% CI of effect size –0.0006–0.0009). Compared to adults, there was a 0.0019 lower weekly estimated survival rate for juveniles (95% CI of effect size 0.00090–0.0020); across the entire duration of the fall, winter and spring seasons this difference equates to a survival rate for juveniles that is lower by 0.017–0.036, depending on the FSS type occupied. Model averaged estimates did not indicate an influence of sex on annual survival rate.

The proportional use by hares of the various FSS types influenced weekly survival rates. The estimated weekly survival rates in the dense mature FSS type was highest of the stand types, and was 0.0090 higher (95% CI effect size 0.003–0.013) than in the dense young FSS type. Weekly survival in the dense young FSS type (0.96 for an adult in spring) was 0.019 higher (95% CI of effect size 0.0050–0.038) than in the open young and open mature FSS types. For adult female hares inhabiting only one FSS type, estimated annual survival rates were 0.42 for hares in dense mature, 0.25 for hares in dense young, and 0.091 for hares in either open young or open mature (Fig. 3). Because of the estimated effects of FSS type use, it is possible to estimate the seasonal or annual survival of snowshoe hares that used any combination of the various FSS types. For example, a hare that spent half its time in dense young and half in open young would have an annual survival rate of 0.15.

Population projections and observed population trends

Variation in weekly survival rates led to large differences in population growth rates for animals living exclusively in a single FSS type (Table 5). Survival, fecundity, and $\lambda_{\text{Single FSS}}$ rate estimates were the same for open young and open mature FSS types. Only the dense mature FSS type was projected to have a mean positive $\lambda_{\text{Single FSS}}$ for hares living exclusively there.

Hares inhabiting multiple FSS types were projected to have variable $\lambda_{\text{u matrix}}$ values according to their proportional use of different FSS types; this pattern resulted from

Table 4. The best-fitting known fate models tested against survival data for 175 radio-collared hares at Inez included effects of FSS, season, age and sex on weekly survival rates. The 'Summer and winter' effect had one pooled parameter describing the effect those seasons on survival, in contrast to pooled survival rates in Fall and Spring. The models shown here had ΔAICc values within four units of the best fitting model, indicating relatively good fit to the data compared to other models considered. For estimation of survival rates with model averaging, we used AICc weights from these models only.

| Model rank and effects included in the model	ΔAICc	AICc weight	No. parameters
1. Summer and winter; open FSS types; sex in summer	0.00	0.17	4
2. Summer and winter; dense mature FSS type; sex in summer	0.30	0.15	4
3. Summer and winter; open FSS types; sex in summer; age	0.64	0.12	5
4. Summer and winter; open FSS types	0.66	0.12	3
5. Summer and winter; open FSS types; age	0.85	0.11	4
6. Summer and winter; dense mature FSS type	1.49	0.08	3
7. Summer and winter; dense mature FSS type; sex in summer; age	1.93	0.065	5
8. Summer and winter; open FSS types; sex year round	2.36	0.052	4
9. Summer and winter; dense mature FSS type; age	2.93	0.039	4
10. Summer and winter; dense mature FSS type; sex year round	2.93	0.039	4
11. Four different seasons; dense mature FSS type; sex in summer	3.53	0.029	6
12. Four different seasons; open FSS types; sex in summer	3.87	0.024	6
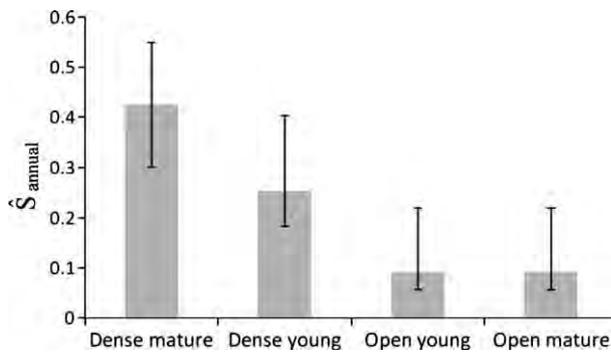
Figure 3. Annual survival rate estimates for adult female snowshoe hares living exclusively in one of the four FSS types in the study, $\hat{S}_{annual}$. FSS types are shown on the x-axis. Error bars represent one standard error.

variation in survival rates that were a function of individual hares' proportional FSS type use in the dense mature, dense young or open FSS types. Because survival rate estimates were highest for time periods when individuals occupied dense young or dense mature FSS types, $\lambda_{u\ matrix}$ increased along with increasing proportional use of either of those FSS types. As survival rate was the only vital rate to vary as a function of FSS type, the $\lambda_{u\ matrix}$ values resulting from the range of possible vectors for **u** can be modeled as a surface in three dimensions (Fig. 4), which approximates the population growth rate expected in a landscape composed of the FSS types in the proportions of the vector **u**.

The differences in $\lambda_{Single\ FSS}$ mean that emigration differentially affects projected population growth rates for single FSS types. For example, for the dense mature FSS types the product of the estimated annual emigration rate of 0.21 and the 1.14 value of $\lambda_{Single\ FSS}$ yields a larger absolute decrease in $\lambda_{Single\ FSS-emigrants}$ than in the case of open mature FSS type, where $\lambda_{Single\ FSS}$ is only 0.41. Thus, the relative difference between $\lambda_{Single\ FSS-emigrants}$ and $\lambda_{Single\ FSS}$ appears greater for the dense mature and dense young FSS types than for the open FSS types.

Not surprisingly, FSS types that already have relatively high $\lambda_{Single\ FSS}$ rates need relatively low immigration rates to increase the $\lambda_{Single\ FSS\ with\ connectivity}$ population growth rates to values above 1.0. Based on Eq. 8, and observed values for $\lambda_{Single\ FSS}$ and emigration rate (E), immigration rates (I) would need to be 0.061 into the dense mature FSS type, 0.49 into the dense young FSS type, and 1.95 into the open mature or open young FSS types.

Table 5. Projected contribution rates, C, in each of the four FSS types of this study. The contribution rate is equivalent to the annual population growth rates for populations of snowshoe hares living exclusively in one of the four FSS types, $\lambda_{Single\ FSS}$. Also shown are the self-recruitment rates, R, for each FSS type, which are equivalent to $\lambda_{Single\ FSS-emigrants}$. Standard errors are in parentheses

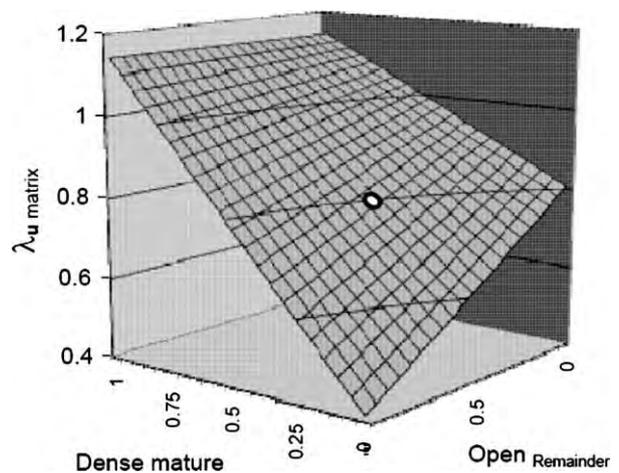| FSS type	C	SE(C)	R	SE (R)
Dense mature	1.14	(0.26)	0.93	(0.27)
Dense young	0.81	(0.21)	0.60	(0.22)
Open young	0.41	(0.18)	0.20	(0.19)
Open mature	0.41	(0.18)	0.20	(0.19)

Figure 4. Projected individual growth rates, $\lambda_{u\ matrix}$ (z-axis) for snowshoe hares inhabiting up to three FSS types (dense mature, dense young and open) with varying proportions. Highest $\lambda_{u\ matrix}$ values above 1 are predicted for hares with high occupancy in dense mature FSS type (x-axis). The y-axis is the proportion of the remaining occupancy that is in the open FSS type; lowest $\lambda_{u\ matrix}$ values are for hares inhabiting only open FSS types. The circle is the point representing $\lambda_{u\ matrix}$ for the observed average proportional occupancy of different FSS types, based on all radio-collared snowshoe hares. In this example, $\lambda_{u\ matrix} = 0.79$ and occupancy of dense mature $= 0.37$; because occupancy of the open and dense young types are 0.33 and 0.30, respectively, the value of the y-axis is $(0.33/0.63) = 0.52$.

Discussion

Our novel extension of an operational source–sink definition to quantify fitness effects in a heterogeneous, fragmented landscape has confirmed the fundamental mechanism that could dampen cycles for snowshoe hares in their southern range. Our equations for $\lambda_{Single\ FSS}$, and for $\lambda_{u\ matrix}$ in general, are equivalent to the metric C^r, which Runge et al. (2006) define as the per-capita contribution to the population growth of the greater connected metapopulation that comes from a particular local population; a population with $C^r \geq 1$ defines a source, while $C^r < 1$ denotes a sink. In our case, the individual is defined by a vector describing its proportional use of different FSS types, **u**, rather than its geographic location in a particular patch.

Our quantification of the contribution metric, and other empirical data, unequivocally establishes a source–sink dynamic for snowshoe hares in our study areas. The contribution metric $\lambda_{Single\ FSS}$ was 1.14 for dense mature, exceeding the 1.0 threshold to be considered a source. The contribution metric for the dense young FSS type was 0.81, but would have been >1.0 if fecundity in the second and third birth pulses were $\sim 50\%$ higher, which would be well within the range of recorded fecundity for other cyclic and stable hare populations (Adams 1959, Murray 2000, Stefan and Krebs 2001, Wirsing and Murray 2002). In addition, we could couple our estimated emigration rates with within-population vital rates to conclude that even accounting for emigration by hares using exclusively these dense FSS types, abundance trajectories would be stationary ($\lambda_{Single\ FSS\ with\ connectivity}$) with the importing of 0.061

(dense mature) or 0.49 (dense young) immigrant hares per year per hare present. The average observed growth rates, $\bar{\lambda}_{Observed}$, were positive at two of three trapping grids for both of the dense forest types (Table 2). Thus, the dense mature FSS types acted as a demographic source during this study, and we expect that the dense young FSS type would be a source under conditions that lead to slightly higher fecundity, survival or immigration.

In contrast, all evidence from the field points strongly to the open young and open mature FSS types being population sinks. For these FSS types, the self-recruitment ($\lambda_{Single\ FSS-emigrants}$) was 0.33, implying that immigration into them is required for persistence. If these open FSS types were strong producers of emigrant hares to other populations they could still be sources (Runge et al. 2006); however, their per-capita contribution metric ($\lambda_{Single\ FSS}$) was only 0.41. In fact, 1.95 immigrant hares per year per hare present in these stands would be necessary to support a stationary population size; this level of immigration would be roughly nine times the estimated annual emigration rate (0.21). The $\bar{\lambda}_{Observed}$ (Table 2) at the INEZ site – the only site where $\bar{\lambda}_{Observed}$ could be estimated for the open sites – was 0.76 for open young and 0.94 for open mature, implying also that these sites were maintained by a high per-capita immigration rate. Likewise, our modeling indicated that in the absence of immigration, annual survival or fecundity would need to increase dramatically for populations of hares living exclusively in open FSS types to persist. To bring the open FSS types up to a $\lambda_{Single\ FSS}$ value of 1.0, annual reproduction in the second and third birth pulses would need to increase by an improbably high $\sim 320\%$, or adult survival increase by 140%.

Our documented source–sink dynamic for this southern snowshoe hare population strongly supports predictions of the refugium model (Wolff 1980) related to dampened cycles in a heterogeneous landscape. The vegetation structure in open FSS types, lacking sufficient hiding cover, dramatically reduced snowshoe hare survival rate for hares that used it even as only part of their routine movements. The differences in projected $\lambda_{u\ matrix}$, as a function of the proportional use of different FSS types, implicated routine movement between favorable and unfavorable FSS types as a potential cause of depressed growth rates in the overall population. Although we cannot yet resolve whether or not these populations cycle, our quantification of the relative importance of the densely forested stands (often called high density young and high density multistory in forest management contexts; US Forest Service 2007) to overall hare population growth has implications not only for understanding hare population dynamics but also for conservation of threatened Canada lynx.

The survival rate estimates we obtained may not be typical for all years. Indeed, our study apparently took place during a period of decline, when one would expect to see relatively low survival rates in most FSS types. Ongoing population monitoring with mark–recapture live trapping at the study areas (Mills unpubl.) indicates that snowshoe hare abundance has still not rebounded to the levels observed in 1998 and 1999.

The greater the proportion of open FSS types in the landscape, the more often snowshoe hares will use those dangerous FSS types, incur a higher mortality, and contribute to a lower overall population growth rate. Indeed, we have found that after pre-commercial thinning, whereby dense young FSS type stands are converted to open young FSS type stands, snowshoe hare density declined (Griffin and Mills 2007). Given the spatial scale of observed routine movements, we predict that habitat type heterogeneity in the southern range could lead to asynchronous local snowshoe hare population dynamics if barriers more than a few km effectively separate potentially interacting groups of hares.

Application of our findings to snowshoe hare management indicates that an efficient action to increase snowshoe hare population growth in a landscape of mixed FSS types would be to increase the proportion of dense young and dense mature FSS types, within landscapes that are defined spatially by the scale of snowshoe hare movements. One might, for example, conserve clusters of favorable FSS type forest stands within 5–10 km^2 areas. The dense young FSS type successional stage lasts only for only a short time, while dense mature FSS type stands are presumably closer to an ecological steady state (McKelvey et al. 2000); with their long residence time, dense mature stands can act as demographic refugia for longer periods of vegetational succession. We note that we sometimes found very high hare densities in these older stands in winter, up to 1.8 hares ha^{-1}. Dense mature FSS type stands in isolation, however, may not yield high snowshoe hare densities. More than 65% of radio-collared hares ever located in the dense mature FSS type routinely used other FSS types, from which we conclude that adjacent stands complement food or cover resources available in the dense mature FSS type. Recognizing that an individual's proportional use of different habitat types influences its fitness and the overall population growth rate, the adjacency of dense mature with dense young FSS type stands would be more valuable than adjacency of either with open FSS type stands.

The conceptual approach we developed to quantify snowshoe hare population dynamics in a complex landscape has broad implications for wild populations of mobile species living where sinks (or sources) have no borders. Movement through various habitat types can affect individual fitness and vital rates, and our method links field estimates to time-varying individual contributions to population growth, and ultimately to the expected contribution of different habitat types to overall population growth. The combination of advances in vital rate estimation and the framework developed here means that analyses of sources and sinks no longer needs to be limited to artificial discrete patch types. Rather, source–sink analyses can be extended to the real-world context of movements among heterogeneous habitats in fragmented landscapes.

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Appendix 1. Estimating fertility

Fertility, $F_{\mathbf{u}}$, incorporates: season-specific weekly survival rates for mothers that use FSS types in the compositional use vector $\mathbf{u}$ up to the birth of leverets in each birth pulse ($S_{\text{Ad Spring } \mathbf{u}}$ and $S_{\text{Ad Summer } \mathbf{u}}$); fecundity rates in each of the three birth pulses (f_1, f_2, f_3); the survival of leverets to weaning (S_{Lev}), and weekly survival rates for weaned juveniles occupying FSS types in the compositional use vector $\mathbf{u}$ in the different seasons ($S_{\text{Juv Summer } \mathbf{u}}$, $S_{\text{Juv Fall } \mathbf{u}}$, $S_{\text{Juv Wint } \mathbf{u}}$, $S_{\text{Juv Spring } \mathbf{u}}$).

$$
\begin{aligned}
F_{\mathbf{u}} = [&f_1 \times S_{\text{Lev}} \times S_{\text{Juv Summer } \mathbf{u}}^{10} + f_2 \times S_{\text{Ad Spring } \mathbf{u}}^{3} \\
&\times S_{\text{Ad Summer } \mathbf{u}}^{2} \times S_{\text{Lev}} \times S_{\text{Juv Summer } \mathbf{u}}^{5} + f_3 \times S_{\text{Ad Spring } \mathbf{u}}^{3} \\
&\times S_{\text{Ad Summer } \mathbf{u}}^{7} \times S_{\text{Lev}}] \times S_{\text{Juv Fall } \mathbf{u}}^{12} \times S_{\text{Juv Wint } \mathbf{u}}^{16} \\
&\times S_{\text{Juv Spring } \mathbf{u}}^{9}
\end{aligned}
$$

(A1)

Parturition in the first birth pulse was approximately in the ninth week of spring ($\sim$ 1 June), and leverets born in the 1st birth pulse must survive as juveniles through 10 weeks of summer after weaning. Adult females must survive through 3 weeks of spring and 2 weeks of summer before parturition for the 2nd birth pulse, and leverets born in the 2nd birth pulse must survive as juveniles through 5 weeks of summer after weaning. Adult females must survive through 5 more weeks of summer before the 3rd birth pulse and leverets born in the 3rd birth pulse must survive to weaning. After the end of summer, all juveniles must survive 12 weeks of fall, 16 weeks of winter and 9 weeks of spring. The three products in Equation 7 that are added inside the brackets represent the birth and survival through the summer of leverets born in the first, second and third birth pulses. That sum is multiplied by juvenile survival throughout the fall, winter and early spring.