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Snowshoe Hares (*Lepus americanus*) in the Western United States

Movement in a Dynamic Managed Landscape

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Since the listing of the Canada lynx, *Lynx canadensis*, as threatened in the coterminous United States (U.S. Fish and Wildlife Service 2000), the effect of landscape-scale forest management on populations of snowshoe hares, *Lepus americanus*, has been a concern. Snowshoe hares are the central prey species of lynx (Aubry et al. 2000). Because snowshoe hare densities vary widely across different types of forested vegetation structure (Adams 1959, Dolbeer and Clark 1975, Wolff 1980, Wolfe et al. 1982), changes in forest vegetation structure through natural disturbance, succession, and silviculture can have dramatic impacts on populations. Snowshoe hare populations cycle with a regular 9- to 11-year period in the northern portion of the species range (Keith 1990), but evidence of a cycle to the south is mixed (Hodges 2000). Vegetative succession complicates population models (Johnson 2000). In western Montana, we have found highest snowshoe hare densities in regenerating forest stands with high sapling density and in uncut, late-seral-stage forest stands also with abundant saplings. This high-quality snowshoe hare habitat in Montana can be thought of as having a bimodal distribution relative to forest stand age, with only young and much older stands providing the "closed" understories with abundant cover and browse (Buskirk et al. 2000). The layer of abundant shrubs and saplings that regenerates following clearcuts or large fires later disappears as the lower limbs die on growing trees, but this layer may reappear when large trees die, creating canopy gaps (Oliver and Larson 1986). The potentially long period when the stand understory becomes and remains comparatively "open" is a time of lower habitat quality. Anthropogenic canopy gaps in partially harvested stands can also stimulate growth of a dense understory layer under an established canopy (DeBell et al. 1997, Tappeiner et al. 1997). Forest managers trying to maintain the prey base for lynx need to balance the maintenance of snowshoe hare and other prey habitats with other management goals (McKelvey et al. 2000). We used RAMAS GIS to explore the effects of timing and placement of one type of silvicultural treatment on a population of snowshoe hares that was highly connected by movement and distributed across many patches of varying quality.

In pre-commercial thinning of dense conifer regenerating stands in the western United States, live stem density is decreased from 3,000–6,000 per ha to 650–1,300 per ha to increase tree growth and yield, reduce future fuel load, and shift species composition (Seidel 1986, Johnstone 1995, Martin and Barber 1995). Through pre-commercial thinning, the sudden conversion of a "closed" understory to an "open" understory means the loss of cover and forage for hares. In preliminary results from a 3-year experiment, we have seen twofold to fourfold snowshoe hare density decreases during the 2 years after thinning (Griffin and Mills 2003). Because dense, young forest stands were known to hold high hare densities (Adams 1959, Wolfe et al. 1982, Hodges 2000), in 1999 the U.S. Forest Service halted pre-commercial thinning on lands defined as lynx habitat, although the practice continues on private and state-managed lands. Because pre-commercial thinning is a costly silvicultural investment, it may often be applied synchronously across large contiguous areas.

Current studies are addressing whether pre-commercial thinning could accelerate shrub and new seedling growth under the remaining trees, as well as what time scale is necessary for the regrowth of understory plants before a thinned stand is good habitat for snowshoe hares. Similarly, uncut mature stands may lose understory cover as a result of partial harvest operations. It is not clear how long a partially harvested mature stand must develop sufficient understory cover to consider it equivalent in hare habitat quality to uncut mature stands where shrubs and saplings are dense.

The montane forests of the study region are dominated by subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occcidentalis*), lodgepole pine (*Pinus contorta*), and Engelman spruce (*Picea engelmannii*), and they generally correspond to the "*Abies lasiocarpa / Menziesia ferruginea* warm phase" habitat type of Arno et al. (1985). Existing literature and successional models give a range of time necessary for development of a dense understory in our study region (Zamora 1982, Arno et al 1985, Moeur 1985).

We parameterized our demographic model with vital rate estimates (survival, birth, and movement) from ongoing studies in the Seeley-Swan region of western Montana, where we are evaluating snowshoe hare population dynamics in four forest vegetation structural types: uncut mature forest (henceforth referred to as "uncut mature"), partially harvested mature forest ("cut mature"), regenerating clearcut ("dense sapling"), and pre-commercially thinned or sparsely regenerating clearcut ("open sapling"). These structural types were determined in the field, based on sapling density, basal area, horizontal cover, and overhead canopy cover (Table 39.1). Both the cut mature and open sapling structural types generally had little understory cover. The preliminary data referred to in this chapter represent more than 4 years of intense work in 20 forest stands at five study sites (Griffin and Mills 2003).

Caution is appropriate in applying our data to larger spatial scales, for several reasons. First, by choosing four discrete vegetation structural types to study, we excluded many structure types of the forest matrix. For example, what we call the uncut mature structural type has dense understory, which should provide good cover and forage for hares; in reality, many mature stands have canopies of large trees without a dense layer

Table 39.1 A key to the vegetation structure attributes we used to delineate the four nominal structure types in this study

Habitat Type Name	Structural Attributes
Dense sapling	Dense stands of regenerating conifers with more than 5,600 saplings/ha
Open sapling	Open stands of regenerating conifers with fewer than 3,360 saplings/ha
Uncut mature	Uncut forest stands with more than 40% overhead canopy cover and a basal area greater than 13.8 m^2/ha (60 ft^2/acre)
Cut mature	Partially harvested forest with less than 30% overhead canopy cover and basal area greater than 13. 8 m^2/ha (60 ft^2/acre).

Note: These categories leave out a large number of vegetation structure types found in the study region. Saplings are defined here as trees over 0.5 m tall, but less than 10 cm diameter at breast height.

of shrubs or saplings. While our demographic research estimates vital rates in specific forest stands, hares can inhabit multiple structural types. Therefore, hares in our model occupy a "patchy metapopulation" (Harrison 1994) with a high degree of movement between contiguous patches, each of potentially different quality.

Our second concern for modeling our data in a RAMAS GIS framework was that the conditions and timing of succession that cause stands to change from one type to another can vary dramatically, depending on environmental factors, stand history, and site preparation (Arno et al. 1985).

Despite our considerable efforts in the field, the sample size and study duration are still not sufficient for us to evaluate carrying capacity and the type of density dependence. We also could not evaluate how dispersal varied according to patch type arrangement (Wiens et al. 1993). Finally, our preliminary data from a period of apparent decline give us no basis to evaluate whether vital rate estimates are close to average rates of the long term, especially for a species that may be cyclic.

Methods

Population Matrices

Our vital rate estimates are from the first 3 years of a 4-year study. Snowshoe hares born in the summer wean after 4 to 5 weeks (Keith 1990). Juveniles that survive to spring are reproductive adults. Adult females at our study area could have bred in each of three synchronous pulses per summer, with nursing taking place overall during ~15 weeks. Fertility, defined here as total number of young expected per summer per reproductive female, was estimated from observed values and ultrasonographic examinations (Griffin et al., in press). We detected no difference in fertility between vegetation structure types, although there were differences in litter size of newborns between the first, second, and third birth pulses.

Using known fates of 149 radio-collared hares, we estimated survival rates based on the candidate model with lowest AICc values computed in Program MARK (White and Burnham 1999). The 11 models for adult and juvenile survival ranged in complexity from simple models with one parameter to models with multiple parameters for season-specific and habitat-specific survival (Griffin and Mills 2003). The selected model structure had the lowest AICc value by 4.57 AICc units, indicating that it is more than 10 times as likely as all other models (after Burnham and Anderson 1998). Based on the selected model, survival rates were equal in all vegetation structure types in the summer and winter, but rates differed in fall and spring, when survival was lower in structure types with "open" canopies (the cut mature and open sapling structure types). Survival rates of adult and weaned juvenile hares were indistinguishable. There was no difference between male and female survival rates, so our matrix model reflects females only.

To reflect the seasonal differences in survival and movement, our matrix model has four time steps per year (Table 39.2). The 40-year simulations require 160 time steps. We account for juveniles starting in the first fall after birth, so the population vector includes three juvenile stages (fall, winter, and spring) and four adult stages (summer, fall, winter, spring). Because survival models for adult and juvenile hares were for 4-week time periods, mean seasonal survival rates were estimated by raising the 4-week rate to a power corresponding to the number of weeks in each season divided by 4 (Table 39.2). The fecundity term accounts for estimated survival of summer adults up to each birth pulse, fertility (number of female offspring per female per birth pulse), survival of newborns to weaning, and survival of weaned juveniles to the fall. To include all three 5-week nursing periods, our summer is 15 weeks and our spring is 11 weeks. Over 1 year (four time steps), population sizes decrease because of mortality then increase after each summer due to reproduction.

Movement rates were specified as a dispersal function in RAMAS Metapop, based on radio-collared hare movements. Observed maximum distances that hares moved every season were lognormally distributed with a mean of approximately 275 m per season (Griffin 2003). More individuals left natal home ranges during the fall, so we assigned highest relative dispersal weights to the fall stages.

Table 39.2 Our stage-based projection model for snowshoe hares makes explicit the seasonal differences in survival rates

	Juv (F)	Juv (W)	Juv (Sp)	Ad (Su)	Ad (F)	Ad (W)	Ad (Sp)
Juv (fall)	0	0	0	F[a]	0	0	0
Juv (winter)	S_{JFa}	0	0	0	0	0	0
Juv (spring)	0	S_{JW}	0	0	0	0	0
Adult (sum)	0	0	$S_{JSp}{}^{b}$	0	0	0	$S_{ASp}{}^{b}$
Adult (fall)	0	0	0	$S_{ASu}{}^{b}$	0	0	0
Adult (wint)	0	0	0	0	S_{AFa}	0	0
Adult (spring)	0	0	0	0	0	S_{AW}	0

Note: Survival rates are subscripted with J for juveniles and A for adults; then with Fa, W, Sp, and Su for fall, winter, spring, and summer. The fecundity term, F, accounts for survival of mothers up to each enumerated birth pulse, fertility per mother in each birth pulse (f_i), survival of baby leverets up to weaning in each birth pulse (S_{LevBPi}), and survival of weaned juveniles to the fall. Fertility is for female offspring only: half the total number of offspring. Adult survival rates in the fecundity term are raised to a power to indicate the number of weeks survived at that rate, out of the 15 in the summer. Juvenile survival after weaning until the fall is the same as adult summer survival (S_{ASu}).

[a]Fecundity term here is $(f_1 * S_{LevBP1} * S_{ASu}{}^{(10/15)}) + (S_{ASu}{}^{(5/15)} * f_2 * S_{LevBP2} * S_{ASu}{}^{(5/15)}) + (S_{ASu}{}^{(10/15)} * f_3 * S_{LevBP3})$

[b]Spring survival rates reflect an 11-week period; summer survival rates reflect a 15-week period.

In stochastic population models, variances of vital rates should reflect the temporal and spatial variation but should exclude sampling variance, which results from uncertainty in parameter estimates owing to incomplete sampling of the population (Burnham et al. 1987, Thompson et al. 1998, Gould and Nichols 1998, Ludwig 1999, White 2000). For survival rates, we could not partition out temporal variation from total variation because the most parsimonious survival model did not include parameters for year-to-year temporal variation. Instead, standard errors for survival rate estimates were taken from the survival model, and the corresponding standard deviations for seasonal survival rates used in RAMAS were found using the delta method (Agresti 1990). Similarly, because our fecundity data were limited in temporal scale, we could not partition temporal variance from total variance. We used the spatial variance in fecundity across all sites and vegetation structure types (0.75) as a proxy for temporal variance in fecundity. The implicit assumption that differences across sites are comparable to temporal variation at a single site is suspect because differences in parameter values at different sites can result from variation in abiotic and biotic factors (Tyre et al. 2000).

In the absence of dispersal, the population projection matrix corresponding to structure types with open understories ("open matrix" for cut mature and open sapling structure types) has a yearly rate of increase of $\lambda = 0.49$. The population projection matrix for structure types with more densely vegetated understories ("closed matrix" for uncut mature and dense sapling structure types) has a yearly rate of increase of $\lambda = 1.03$.

The data from 1998 to 2001 were from a period of overall decline (Mills et al. 2003). Average density estimates in summer 2001 were roughly 35% of summer 1998 values. Vital rate estimates for this period were probably influenced by whatever factor caused the declines. Because we do not know with certainty the cause of the declines, or how vital rates and movement would differ during population increases, we conducted simulations with the observed rates instead of increasing them arbitrarily to achieve stationary populations.

Model Landscapes and Succession

We limited model landscapes to four vegetation structure types (Table 39.1). We developed a single landscape, including a simple model of succession, and evaluated the population dynamics of snowshoe hares in three additional scenarios that varied only in the timing and placement of pre-commercial thinning. We used the Spatial Data module to create a single metapopulation map with 484 patches of 16 ha each, arranged in a square. Although snowshoe hare habitat is contiguous in reality, we included narrow 40-m boundaries so that RAMAS Metapop could distinguish patches.

Each patch was randomly assigned an initial forest vegetation structure type. The target proportions of patches in each structure type desired were approximately 60% uncut mature, 15% dense sapling, 10% cut mature, and 5% open sapling. Our model landscape is unlike managed landscapes in western Montana because few of those, if any, have 60% uncut mature forest. For example, in the Seeley Lake region the area of uncut mature forest is not more than 25%. When we initially allocated less uncut mature type, however, overall hare populations fell to 0 before the end of the 40-year simulations. This decline was unacceptable for meeting the objectives of this study because we wanted to explore the effects of timing and extent of pre-commercial thinning. By including so much uncut

mature type in the model, we ensured that some good-quality hare habitat in each scenario would remain as a source of snowshoe hares after thinning.

Each patch was associated with snowshoe hare vital rates, depending on the vegetation structure type found on the patch in each year. Uncut mature and dense sapling structure types had the higher survival rates of the "closed matrix." Cut mature and open sapling structure types had the lower survival rates of the "open matrix." The matrices for each patch at each time step were recorded in a "temporal change file," thereby reflecting the starting vegetation structure type of each patch and any changes in structure type that resulted from simulated succession or pre-commercial thinning.

We devised a simple model for forest succession allowing for transitions over time between the different vegetation structure types, and we recorded the successional trajectories of each patch. The successional simulation rules were used to represent probabilistic changes between types. Transitions between types were based on mean rates with a stochastic component analogous to demographic stochasticity, whereby transition occurred if a random number drawn from a uniform 0–1 distribution was less than the mean transition probability.

Any patch assigned initially as uncut mature type stayed in that condition; this simplifying assumption ignores possible logging, catastrophic fire, or insect damage that could convert mature stands to younger structure types.

Reflecting potential tree crowding and crown lift, dense sapling type patches could change to a vegetation structure type with an open understory with an annual probability of 0.015. After such a transition we left these patches with an "open" matrix of vital rates for the remainder of the 40-year simulation. The 1.5% probability reflects the assumption of a long residence time in the dense sapling type with the expectation that half the patches would change to the open-understoried type within 45 years, given a binomial distribution. Current management guidelines for preserving dense cover on U.S. Forest Service lands in potential lynx habitats recommend not thinning in regenerating stands until 45 years or older.

To signify regrowth of understory plants to the point that open sapling type patches support a high density of shrub and sapling cover, each patch of the open sapling type changed to a vegetation structure type with dense understory with annual probability 0.033, based on the expectation that half the patches of open sapling type should change to a structure type with a denser understory after 20 years, given a binomial distribution. Arno et al. (1985) indicate that high sapling coverage occurs 12 to 33 years after stand initiation, so the 20-year horizon is reasonable for dense growth of shrubs and small saplings.

To represent the growth of shrubs and saplings in patches starting as the cut mature type, such patches could change to and stay in a vegetation structure type with a dense understory with annual probability of 0.02, based on an expectation that half the patches of cut mature type should develop adequate cover within 35 years, given a binomial distribution. The cut mature type had a lower probability of developing a dense understory than did the open sapling structure type because large standing trees can reduce the light available for understory growth. Tree crown area, which intercepts light, can be approximated as a linear function increasing with tree diameter and height (Moeur 1981). Shrub cover value is predicted to decline with increased basal area of a stand (Moeur 1985).

Four Scenarios of Landscape Change

We refer to the single configuration of initial vegetation structure types and the time series of changes for that configuration as the "succession" scenario (no. 1). We used this configuration and time series, with changes only to those stands that were pre-commercially thinned in the three other scenarios: "upper half thin" (no. 2), "year 10 random thin" (no. 3), and "random thin" (no. 4). If a dense sapling type patch was thinned in a scenario, hares in that patch then had the lower survival rates associated with structure types with low understory cover. In all three scenarios with thinning (nos. 2, 3, and 4), thinned patches could potentially convert back to the "closed" matrix with the higher survival rate as a result of succession, but only after 3 or more years. All scenarios were simulated 100 times.

In scenario no. 2, upper half thin, we simulated spatial autocorrelation that could arise from patterns of land ownership. The randomly assigned configuration of vegetation structure types that initialized all four scenarios included either 54 dense sapling type patches in the 242 patches of the model landscape's upper half or 68 such patches in the lower half. In the upper half thin scenario, all 54 dense sapling patches were thinned at year 10. All 68 dense sapling patches in the lower half of the landscape were not thinned and kept the same temporal change files as in the "succession" scenario.

In scenario no. 3, year 10 random thin, 54 dense sapling patches were again thinned at year 10, but the placement of those patches was chosen at random from all 122 dense sapling patches.

In scenario no. 4, random thin, an equal amount of thinning occurs on the landscape as in other scenarios, but it is spread out across the 40-year time period and the 122 dense sapling patches. For this, we calculated the annual risk of thinning to patches in the other scenarios by dividing the 54 thinned patches by the 122 total patches and by the 40-year duration of the simulations, giving 1.106% mean annual probability of thinning per patch. For every dense sapling patch in every year, we evaluated a random number against this quotient (0.01106) to determine whether or not it would be thinned. Fifty-five patches were thinned in this process over the 40-year simulation, while unthinned patches maintained the same temporal change files as in the succession scenario.

Other Model Parameters

We used the ceiling model for density dependence because of its simplicity and lack of evidence for a better alternative. We could not evaluate carrying capacity from snowshoe hare time series at our sites, so we assigned it at $K = 42$ for all 16-ha patches based on the highest density we observed (2.63 hares/ha). This is within the upper range observed in experimental plots in the Yukon (Hodges et al. 2001).

For all scenarios, we initialized all patches at a density of 0.6 hares/ha (10 individuals per patch), approximately the mean density observed in 1998. The initial distribution to stages was according to stable age distribution, with hares only in the fall juvenile and fall adult stage classes.

Model Predictions

Of the four scenarios, the random thin scenario maintained the highest average total snowshoe hare population size across the 40 years simulated (Figure 39.1). The succession scenario without thinning had the next highest average number of hares. The predictions of these two scenarios overlap substantially for all years simulated.

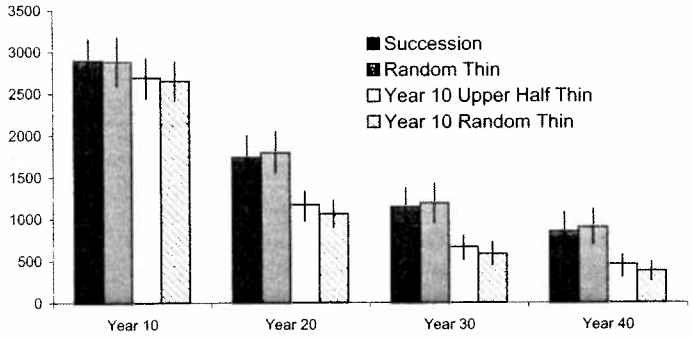

Figure 39.1 Overall abundance in four simulation scenarios for snowshoe hare populations at years 10, 20, 30, and 40. Scenarios in which thinning is applied in year 10 have lower trajectories than those with no thinning ("succession") or where thinning is spread out over time and space ("random thin"). Error bars are standard deviations from 100 simulations.

Both scenarios in which thinning occurred at year 10 maintained a lower total number of snowshoe hares than the other scenarios. On average, the abundance was marginally higher in the upper half thin scenario than in the year 10 random thin scenario; their standard deviation bars overlap substantially at all times.

Discussion

It is not surprising that overall abundance of hares was higher in the succession scenario than in the upper half thin and year 10 random thin scenarios. Both of the latter scenarios include synchronous conversions of 54 out of 122 high-quality dense sapling structure type patches to low-quality open sapling type patches, with at least a 3-year lag before they could convert back to a vegetation structure type with dense understory and higher hare survival rates.

More interesting is the possibility that, using our model assumptions, landscapes with a low level of pre-commercial thinning (the random thinning scenario) may support as many hares in the long term as do landscapes without any thinning (the succession scenario). One critical assumption driving this result is that young thinned stands can eventually provide the understory cover that is necessary for snowshoe hares. A scenario without thinning may have supported higher hare densities, however, if stand-replacing processes such as catastrophic wildfire, insect damage, or clearcutting had been included in the model; these would have led to regeneration of young, dense stands. Some outstanding research questions for models such as ours relate to successional rates: time for shrub and sapling growth to provide ample cover for hares; subsequent time until trees in the canopy reduce understory light levels such that shrub and sapling cover becomes insufficient for hare survival; and time to breakup of closed canopy so that understory cover is again favorable. Also, we raise the vexing question of whether uncut

mature stands can really be considered stable. For each of these successional rate questions, mean times will depend on many factors, including elevation, moisture, species composition, and disturbance history. For example, if the probability of changing from the open sapling type to a forest type with a dense understory were lower than the value we used, then negative effects of thinning could be more severe and longer lasting.

The simulation results also hinge on the initial proportions of structure types and the other rules for our simple model of thinning treatment allocation and succession. To maintain non-zero model populations over the 40-year simulated interval, we had to assign roughly 60% of patches as high-quality uncut mature structure type. Even though patches of the dense sapling structure type were converted to open habitats by thinning in the random thin scenario, these thinned patches were later available for dense understory growth. In contrast, during the 40-year simulation the 122 patches in the succession scenario starting in the dense sapling vegetation structure type could only change into a type with crowded trees and an open understory. After the creation of the starting arrangement of structure types in the landscape, the transition rates between structure types govern the overall availability of high-quality and low-quality patches. Furthermore, we simulated only one landscape arrangement in the succession scenario, which was then modified slightly under each of the thinning scenarios.

Our landscape contained only four of the many forest vegetation structure types in the region. Some other structural types may have higher vital rates than structure types with open understories. By assuming that pre-commercially thinned structure types had the same carrying capacity as all other structure types, we may have inflated the abundance that thinned patches could maintain.

Effects of our assumptions could be examined by linking randomized realistic models of succession to RAMAS GIS and by estimating demographic rates in more vegetation structure types. Successional rates, especially, are expected to have a large role in the long-term dynamics of populations living in successional landscapes (Johnson 2000). Before any model such as ours is used to make management recommendations, sensitivity analysis (as in Mills and Lindberg 2002) should be used to examine the effects of different landscape configurations and demographic and successional rates on projected hare population dynamics, perhaps with a program for generating large numbers of dynamic landscapes under different rules.

Populations declined over the 40-year duration of all four scenarios and remained at low but relatively steady levels in the latter decades of the simulations. This happened even though the proportion of uncut mature structure type started at a frequency not found in our study region. The overall decline reflects strong declines expected in the two vegetation structure types associated with the "open" stage matrix of vital rates and in the comparatively modest growth rates of the other two vegetation structure types associated with the "closed" matrix.

The field data leading to demographic rate estimates used here were from a period when the real snowshoe hare population declined in the study region. At this time it is not clear whether the apparent snowshoe hare declines in our study area occurred because of drought or other environmental factors, because of some underlying cyclicity, or because of habitat-specific demography linked to forest age and type composition in the real landscape. Evidence is mixed as to whether snowshoe hares cycle in the southern range (Hodges 2000, Malloy 2000). If (> 1 in all structure types during periods of increase, overall populations could periodically reach high levels despite pre-commercial

thinning. Even during periods of overall population increase, we would not expect vegetation structure types with open understories to have higher snowshoe hare survival than do vegetation structure types with dense understories.

Despite the caution necessary in interpreting our results, the landscape modeling framework in RAMAS GIS allows us to make tentative suggestions about the influence of pre-commercial thinning on snowshoe hare populations, pending more refined information about vital rates and dispersal distances in many vegetation structure types and about rates of successional change between structure types of varying quality for hares. For this model landscape where uncut mature forest was prevalent and stable, results suggest that snowshoe hare populations stay higher when pre-commercial thinning is not applied all at once in a landscape. In the context of less stable landscapes with a lower prevalence of favorable patches, successional transition rates should largely determine the dynamics of snowshoe hares.

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