Habitat-dependent foraging in a classic predator–prey system: a fable from snowshoe hares

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Current research contrasting prey habitat use has documented, with virtual unanimity, habitat differences in predation risk. Relatively few studies have considered, either in theory or in practice, simultaneous patterns in prey density. Linear predator–prey models predict that prey habitat preferences should switch toward the safer habitat with increasing prey and predator densities. The density-dependent preference can be revealed by regression of prey density in safe habitat versus that in the riskier one (the isodar). But at this scale, the predation risk can be revealed only with simultaneous estimates of the number of predators, or with their experimental removal. Theories of optimal foraging demonstrate that we can measure predation risk by giving-up densities of resource in foraging patches. The foraging theory cannot yet predict the expected pattern as predator and prey populations covary. Both problems are solved by measuring isodars and giving-up densities in the same predator–prey system. I applied the two approaches to the classic predator–prey dynamics of snowshoe hares in northwestern Ontario, Canada. Hares occupied regenerating cutovers and adjacent mature-forest habitat equally, and in a manner consistent with density-dependent habitat selection. Independent measures of predation risk based on experimental, as well as natural, giving-up densities agreed generally with the equal preference between habitats revealed by the isodar. There was no apparent difference in predation risk between habitats despite obvious differences in physical structure. Complementary studies contrasting a pair of habitats with more extreme differences confirmed that hares do alter their giving-up densities when one habitat is clearly superior to another. The results are thereby consistent with theories of adaptive behaviour. But the results also demonstrate, when evaluating differences in habitat, that it is crucial to let the organisms we study define their own habitat preference.

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All naturalists know that species are restricted in the number of habitats that they occupy, and that their abundance is higher in some habitats than it is in others. Often, the differences in density reflect preferential occupation of habitats that yield the greatest fitness. If individuals possess perfect information about habitat quality, and are free to occupy any habitat that they choose, they will disperse among habitats until no single individual can improve its fitness by moving elsewhere (the ideal-free distribution, Fretwell and Lucas 1969,

Fretwell 1972). Ecologists should be able to use such ideal distributions to infer underlying similarities and differences in habitat quality.

Early approaches demonstrated, when an individual's fitness is proportional to its fraction of the total resources, that the number of foragers should match habitat differences in resource availability (the habitat-matching rule, Parker 1978, Pulliam and Caraco 1984, Fagen 1987, 1988, Recer et al. 1987, Kacelnik et al. 1992). But such perfect habitat matching is rarely

observed. Often there are more individuals in a habitat (especially poor ones) than expected from its resource quality (Van Horne 1983, Fahrig and Paloheimo 1988, Pulliam and Danielson 1991, Kennedy and Gray 1993, Tregenza 1995) and foragers frequently undermatch their consumption of resources by consuming proportionately more resources from poor patches than they do from rich ones (Kennedy and Gray 1993, Tregenza 1995).

Several mechanisms have been proposed to account for the mismatch between theory and nature, including, 1) incomplete information by foragers (Abrahams 1986, Ranta et al. 1999), 2) "errors" of patch assessment (reviewed by Tregenza 1995), 3) a lack of fit between foraging ability and the spatial or temporal distribution of resources (Ranta et al. 2000), 4) differences in competitive ability (Sutherland and Parker 1985, Milinski and Parker 1991, Hugie and Grand 1998, 2003), and 5) the influence of related individuals (Morris et al. 2001). But foragers are especially likely to mismatch resource harvest with patch productivity in different habitats when 6) fitness depends on predation risk as well as resource intake (Brown 1988, McNamara and Houston 1990, Moody et al. 1996, Houston and McNamara 1999).

The evidence for habitat-dependent predation risk is most convincing for numerous species of desert rodents that leave more resources (giving-up density, GUD) in risky foraging patches than in otherwise identical "safe" ones (Brown et al. 1992, 1994, 1999, Ziv et al. 1995), a result corroborated by carefully controlled experiments (Kotler et al. 1991, Kotler and Blaustein 1995, Kotler 1997, Morris 1997, Morris and Davidson 2000). Indeed, there are now so many examples of foraging-related differences between safe and risky habitats (e.g. crested porcupines, Brown and Alkon 1990; rock hyrax, Kotler et al. 1999; fox squirrels, Brown et al. 1992b; chipmunks and grey squirrels, Bowers et al. 1993; deer mice, Morris 1997; white-footed mice, Morris and Davidson 2000; voles, Jacob and Brown 2000; coho salmon, Grand and Dill 1996) that the connection between habitat and predation risk has become a virtual axiom in evolutionary ecology (Brown et al. 1999).

But should predation risk always vary between habitats? The answer is "yes" only if we assume that the predator's foraging cost always differs among habitats. The assumption that foraging costs vary among habitats is likely to apply to "stereotyped" predators that possess a single foraging strategy, but costs may be similar for adaptive predators that modify their strategy to meet the demands of different habitats. It is thus important to explore, more fully, the consequences of similar and different habitat-dependent predation risks on patterns of prey distribution. And it is equally important to assess whether natural predator–prey systems can break the "predation risk depends on habitat" rule. I address both issues by evaluating

patterns of prey distribution and patch use in the classic predator–prey system of lynx (and other predators) preying on snowshoe hares in Canada's boreal forests.

I begin by developing simple theory that integrates predation into evolutionarily stable strategies of habitat selection, then briefly review the connection to foraging strategies in small patches. I review conventional wisdom on snowshoe-hare habitat preference to develop competing predictions on hare distribution and foraging. My tests of the predictions demonstrate that hares (as well as their predators) are not bound by our expectations. Hare habitat preference between forest and cutover habitats is weakly density dependent, and mimics vague differences in predation risk. But obvious adaptive differences in habitat use and predation risk emerge along sharp ecotones separating shrubland from adjacent old fields. I conclude by revisiting the role that habitat-dependent predation plays in snowshoe-hare dynamics in particular, and in our general understanding of habitat selection.

Predation and the ideal free distribution

Habitat selection theory

The solution, in density space, of an ideal-free distribution can be revealed by plotting its isodar (Morris 1988). The habitat isodar is a graph of the density of individuals occupying one habitat against that in another when the expected fitness is equivalent in both. Isodars have often been used to explore intra and interspecific competition (Morris 1988, 1989, 1999). Several ecologists have explored the consequences of predators on ideal distributions of prey (McNamara and Houston 1990, Hugie and Dill 1994, Moody et al. 1996, Sih 1998, Abrams 1999, Grand and Dill 1999, Heithaus 2001, Grand 2003), but isodars have rarely been applied to predator–prey dynamics (Brown 1998, Morris 2003). Thus our first task is to build a "predation isodar" so that we know what signals to look for in the joint assessment of predation risk on population distribution and foraging behaviour.

To build the isodar, imagine two habitats that differ from one another structurally, as well as in resource abundance and renewal. Imagine further that a single predator population exploits the two habitats, but that the prey are more easily captured in habitat 1 than in habitat 2. A simple phenomenological fitness model that incorporates these assumptions for each habitat yields

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1\left(\frac{1-N_1}{K_1}\right) - Pa_1$$

and

$$\frac{1}{N_2}\frac{dN_2}{dt} = r_2\left(\frac{1-N_2}{K_2}\right) - Pa_2 \tag{1}$$

for habitats 1 and 2 respectively where N is the number of prey individuals, r is the prey intrinsic rate of increase, K is the carrying capacity, P is the number of predators, and a is the (linear) per capita attack rate (Morin 1999). The isodar is generated by setting the two fitness equations equal to one another and solving for N. If there are no predators, the isodar is given by

$$N_2 = \frac{(r_2 - r_1)}{r_2} K_2 + \frac{K_2}{K_1} \frac{r_1}{r_2} N_1 \qquad (2)$$

but when predators are present, the isodar becomes

$$N_2 = \frac{(r_2 - r_1) + (a_1 + a_2)P}{r_2} K_2 + \left(\frac{K_2}{K_1} \frac{r_1}{r_2}\right) N_1 \qquad (3)$$

from which we can see that the isodar intercept is increased when attack rates are greater in habitat 1 than in 2. The intercept is reduced when attack rates are less in habitat 1 than in habitat 2.

One of the lessons included in Eq. 3 is that a field ecologist is likely to observe a tight fit to a prey isodar only when predator numbers are linked closely to those of the prey. To make the lesson more transparent, imagine that the attack rate in habitat 2 exceeds that in habitat 1. Note that the isodar is linear at any given predator density. As the number of predators increases, the isodar intercept declines, but the slope is constant. Now imagine that predator numbers covary positively and instantly with prey density. The isodar in habitats where the predator is present will actually represent a composite of many different ideal-free distributions that produces a different intercept for each value of predator and prey densities. The prey isodar will thus diverge downward from that generated when predators are absent (Fig. 1A). And if the attack rate in habitat 1 exceeds that in 2, the "predation" isodar diverges from the "zero predator" isodar upward (Fig. 1B).

Note, if attack rates differ between habitats, that the predator's signature will often be revealed by a nonlinear isodar at low prey density (for example, if there are too few prey to support the predator's population, or if the predator switches to an alternative resource). When predators are absent at low prey density, the prey isodar tracks the prey's single-species habitat choice. Once prey become abundant enough to support predators, the predators cause either an increase or decrease in the isodar intercept (Eq. 3, assuming that the predator is more efficient in one habitat than the other). The slope of the composite isodar will change as it switches from the prey-alone isodar to the "prey + predators" solution (Fig. 1). The isodar slope at low prey density may, depending on attack rates and the set of predator and prey densities, even be negative. Strongly curved isodars at low prey densities can also occur when out-of-phase predator–prey dynamics force most prey into a single habitat (below).
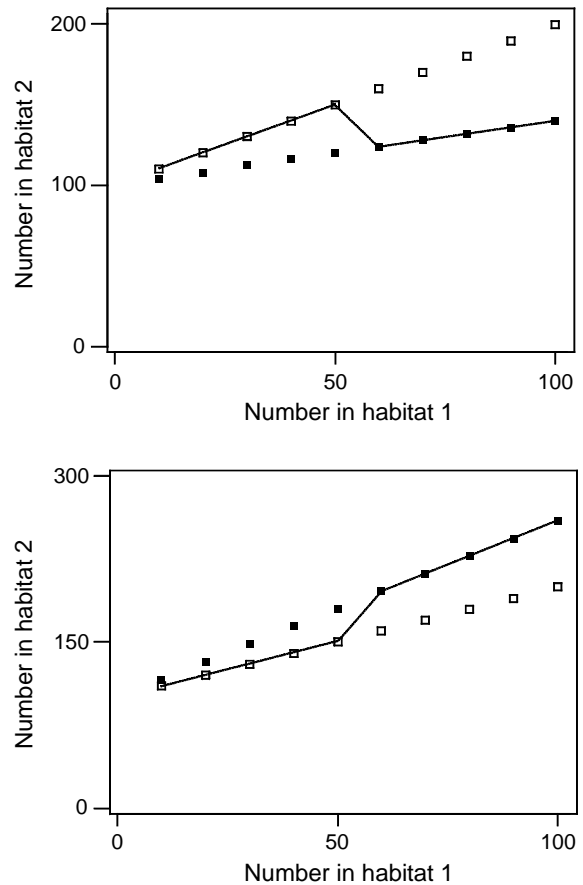

Fig. 1. A caricature of how predation risk, in concert with positively covarying densities of predators and prey, alters the shape of isodars. Dotted lines illustrate an example of the nonlinear discontinuities expected when predators are absent at low prey densities. Top: the predator's attack rate is greater in habitat 2 ($a_2 = 0.01$, $a_1 = 0.0025$). Bottom: The predator's attack rate is greater in habitat 1 ($a_2 = 0.0025$, $a_1 = 0.01$). Remaining parameter values and symbols as follows: $r_2 = 0.5$, $r_1 = 0.25$, $K_2 = 200$, $K_1 = 100$, $P = (0.2N_1)$, open squares = predators absent, filled squares = predators present, there has been no attempt to ensure that densities reflect predator–prey equilibria. Note that the scale for the ordinate varies between the two figures.

The difficulties of detecting differences in predation risk are complicated for an ecologist in the field who will not be measuring isodars with fixed predator numbers that can respond instantly to changes in prey density. Rather, she will be estimating the composite isodar that emerges with covarying time-lagged dynamics in predator and prey populations. A plot of the entire suite of individual prey isodars may not reveal the change in slope between "predator-free" and "predators-present" isodars at low prey density if the system is subject to frequent stochastic effects (Morris 2003). I illustrate an example in Fig. 2 where I simulate prey selection according to the discrete version of Eq. 1, namely
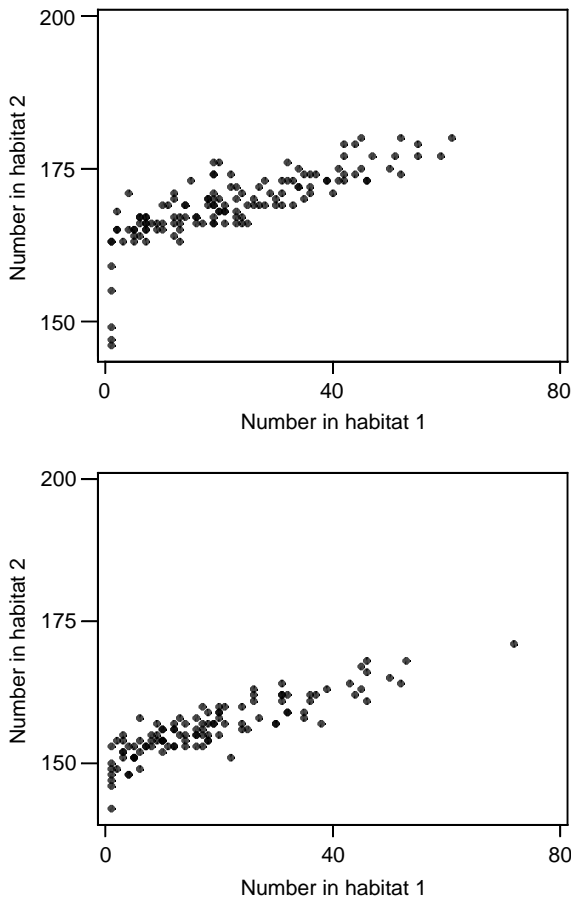
Fig. 2. An illustration of isodars produced when habitats differ in predation risk, and when predator–prey dynamics are linked with intrinsic time lags (Eq. 4 and 5). Top: predation risk is greater in habitat 2 ($a_2 = 0.007$, $a_1 = 0.006$). Bottom: predation risk is greater in habitat 1 ($a_2 = 0.006$, $a_1 = 0.007$). Remaining parameter values as follows: $\lambda_2 = 2.4$, $\lambda_1 = 1.2$, $K_2 = 200$, $K_1 = 150$.

$$\frac{N_{(t+1)i} - N_{(t)i}}{N_{(t)i}} = \lambda_i \left(\exp\left(-\frac{r_i}{K_i}\right) N_i - a_i P \right) - 1 \qquad (4)$$

where λ is the rate of discrete population growth in habitat i (modified from Comins and Hassell 1976). The solution to Eq. 4 yields the same isodar (Eq. 3) as that for continuous growth. I modelled the predator's growth in the two habitats as

$$P_{(t+1)} = N_{(t)1}(1 - \exp[-a_1 P]) + N_{(t)2}(1 - \exp[-a_2 P]) \qquad (5)$$

Equation 5 thus assumes that the same predators occupy both habitats where their overall population growth is the sum of reproduction associated with consuming the separate prey "populations" in the two habitats.

I simulated ideal-free habitat selection as follows: After initializing all parameters, I allowed both predator and prey populations to grow. Following growth, I estimated future fitness at time (t+2), (Eq. 4) and moved an individual to the habitat with higher fitness.

I then recalculated fitness as above and continued to move individuals until no individual could improve its fitness by moving to the alternative habitat. Next, I mimicked exogenous stochasticity by multiplying prey density in each habitat times a normally distributed variable with mean of 1 (values were truncated such that $0.7 \leq X \leq 1.3$; truncation ensured that fluctuating prey densities persisted for the entire simulation). Both populations were allowed to grow again, thus beginning another round of habitat selection by prey. Each simulation ran for 250 generations. I deleted the first 50 generations to exclude any effects caused by initial conditions, then used those remaining generations in which both habitats were occupied by predator and prey to generate the prey isodar (Fig. 2).

The simulations confirm our general understanding of how simple predator–prey models influence prey isodars. But the simulations also illustrate, clearly, how the intrinsic time-lagged dynamics of the predator–prey interaction lead to vague density-dependent habitat selection by prey. The jointly fluctuating, out-of-phase dynamics of predators and prey allow multiple solutions of N_2 for each value of N_1 (because each is associated with a different number of predators). The effect is most pronounced when prey populations decline before their abundant predators. But each decline is different from the one preceding it, and the variable densities of both species produce a series of different isodar solutions through time where only a single prey individual occupies the less-preferred habitat (Fig. 2). Thus, if an ecologist has a sufficiently long time series, the predator's effect on the prey isodar can be revealed by strong curvature at low density (Fig. 2). Of course, if the ecologist has data on predator density, the predator's effect can be tested directly (Eq. 3). Most prey data sets are likely to be of relatively short duration (relative to the joint predator–prey dynamics), and most will not include estimates of predator densities. Thus we know that predation alters the distribution of individuals between habitats, but we are unlikely to capture that effect uniquely with knowledge only of prey densities.

Optimal foraging theory

Theories of optimal foraging face the opposite problem. The theory demonstrates how we can assess predation risk with foraging experiments, but is not currently capable of mapping that risk uniquely onto population density. If we imagine, for example, that prey fitness is proportional to the harvest rate of energy from foraging patches (that will be discounted by predation risk while foraging), an optimal forager should discontinue using a foraging patch whenever

$$\gamma \frac{\partial V}{\partial x} < MV + C \qquad (6)$$

where γ is the net energy gain from foraging (equivalent to the rate of increase in the forager's energetic state, x), $\partial V / \partial x$ is the state-dependent value of energy in terms of reproductive value (V), M is the predation rate (roughly equivalent to Pa_i in Eq. 1), and C is the cost of staying in the patch when fitness could be enhanced elsewhere (Brown 1988, Houston and McNamara 1999). Thus, if two different habitats vary in predation rate, foragers will spend more time in patches located in the safer habitat, and thereby achieve a lower quitting-harvest rate, (there will be fewer resources left in patches in the safe habitat than in the riskier one, it will have a lower giving-up density).

The effects of density are complicated. Increasing prey density reduces the energetic state of individuals as well as the missed opportunities of not foraging elsewhere (Davidson and Morris 2001). Predictions are complex because the state of prey, and their missed opportunities, vary with changes in predator density.

To summarize, when habitats occupied by tightly-linked predators and prey differ in predation risk, we expect that risky habitats will be occupied by fewer prey individuals than will safer habitat. The pattern of density for such systems, revealed by the isodar, will depend on which habitat is riskier. Stochastic variation may obscure the isodar's shape and limit its ability to detect habitat differences in predation risk. The predator's effect can nevertheless be inferred from measurements of giving-up densities because prey foraging in riskier habitats will have higher quitting-harvest rates than where they forage in safe habitats (they will leave behind more resources in otherwise identical patches after foraging). And the best system to apply the theory will be one dominated by a habitat-selecting prey species locked into a definitive predator–prey interaction.

Methods

The study system and predictions

Snowshoe hares and their predators engage one another's dynamics in a legendary contest of prey capture and predator starvation (Elton 1924, Elton and Nicholson 1942, Keith 1963, Krebs et al. 2001). Snowshoe hares are key to the structure and dynamics of North America's boreal forests where they dominate the herbivore biomass that supports a rich and varied predator community (Krebs et al. 2001). Numerous studies document the preference of hares for young forest stands that provide food and protection from predators (Grange 1932, Meslow and Keith 1968, Buehler and Keith 1982, Wolfe et al. 1982, Pietz and Tester 1983, Litvaitis et al 1985, Wirsing et al. 2002), and

especially so in winter (Wolff 1980, Hoover et al. 1999). Where data on habitat-related predation rates exist, however, predator-induced mortality is as high (or higher) in densely-covered habitats as it is elsewhere (Keith et al. 1993, Wirsing et al. 2002). In the Yukon, lynx and coyotes preying on hares concentrated their activity in the same dense habitats preferred by the hares (Murray and Boutin 1994, O'Donoghue et al. 1998). And over longer time spans, both lynx and hares may be relatively stereotyped in their habitat preferences (Mowat and Slough 2003).

We can thus make the following suites of linked predictions. (1A) If snowshoe hares prefer densely-covered young forests over mature ones, then they should be more abundant in cutovers than in adjacent mature-forest habitats. The isodar intercept should be greater than zero, or its slope should be greater than one. (1B) And if cover acts to reduce predation rates, then giving-up densities should be less in regrowing cutovers than in adjacent forest. (1C) The isodar should have a general decelerating shape (at least for the range of predator densities where the functional response is more-or-less linear). (2A) But preference for one type of forest should disappear if the habitats have similar resource renewal rates for hares, and if they do not differ in predation risk. The isodar intercept should not be different from zero, and the slope should not be different from unity. (2B) And if predation risk is similar, then the more dense cover in cutovers does not act to reduce predation rates, and giving-up-densities should not differ between the two types of forest. Finally, H_0, if hares are not density-dependent habitat selectors, the isodar will not be statistically significant.

Field sites and methods

Snowshoe hares (*Lepus americanus*) are one of the most common vertebrates in regenerating conifer cutovers and adjacent conifer forests near my Sorrel-Lake study area in northwestern Ontario (approximately 100 km north of Thunder Bay [48°55′N, 89°55′W], the Sorrel-Lake camp and surrounding forest is owned and operated by Abitibi-Consolidated Inc.). The fire-origin forest is dominated by 80 yr old jack-pine (*Pinus banksiana*) and spruce (*Picea mariana*, *Picea glauca*) with interspersed balsam fir (*Abies balsamea*) and trembling aspen (*Populus tremuloides*), plus a scattering of paper birch (*Betula papyrifera*). The understorey includes a variety of shrubs such as alder (*Alnus viridis*), honeysuckle (*Diervilla lonicera*) and blueberries (*Vaccinium angustifolium*, *V. myrtilloides*) with occasional brambles (*Rubus idaeus*, *R. pubescens*) and roses (*Rosa acicularis*). Common herbs (bunchberry, *Cornus canadensis*; gaywings, *Polygala paucifolia*; goldthread, *Coptis trifolia*) grow on a lush and verdant carpet of feathermosses

(e.g. *Pleurozium shreberi*, *Ptilium crista-castrensis*, *Hylacomium splendens*). Adjacent 20 yr old cutovers vary from almost pure jack-pine (4 sites), to almost pure black spruce (1 site in a plantation used for family tests associated with tree 'improvement'). Tree densities on cutovers exceed those of the mature forest, but tree heights are much lower (approximately 5 m vs 20 m). Grasses (esp. *Calamagrostis canadensis*) and shrubs (*Alnus viridis*) are much more common in cutovers than in the forest.

Isodar analysis: do hares prefer densely-covered young forest?

My assistants and I began live-trapping hares along five 400 m transects that spanned the two habitats in the spring of 1998. Trapping along one of these transects was discontinued in 1999. Transects were trapped during late spring and summer (May–August) for three trapping periods in four years (1998, 2000, 2002, and 2003), twice in 2001, and once in 1999. Ten traps (five in cutover, five in mature forest) were located in hare runways at 40 m intervals along each transect. Though the number of traps was limited, each trap-set sampled hares from a wide area. Open traps were always available to hares even when hares were most abundant. Each trapping period included three consecutive trap nights. Traps were set in the evening of day 1 (usually Monday), checked at dawn and dusk on days 2 and 3, and collected at dawn on day 4. Hares were captured in collapsible Tomahawk live-traps baited with apple and (after 2000) alfalfa cubes. We marked individual hares with metal ear tags, determined their sex, recorded the length of their hind foot as an index of body size, and released them at the point of capture.

I estimated relative densities for the isodar regressions as the number of different hares captured in each habitat during each year. My intent was not to measure the absolute density of hares, but to ensure that my estimates in each habitat were equally comparable. Hares whose home ranges crossed the boundary between habitats were caught (and counted) in both. I contemplated excluding these animals from the isodars by using a census only from the distal segments of the transects. But reliable comparisons of predation risks from giving-up-densities require that the same foragers visit all patches so that other costs do not interfere with the estimate of predation risk (Brown 1988, 1992). It is thus crucial, in a test aiming to assess density-dependent differences in predation risk, that the density estimates apply to the same spatial scale as the foraging experiments. But even if all of the hares I censussed occupied both habitats, their probabilities of capture would be biased toward the habitat where they were most active, and would generate a reliable indicator of hare (activity) density.

Giving-up densities A: does predation risk differ between young and mature forest?

I searched for habitat-dependent predation risk in two different ways. In February and March 2003, I clipped 50 cm long boughs from jack-pine saplings in cutover habitat. It was impossible to completely standardize boughs by size or age, but I rejected those with cones. I then searched for winter runways near two of our transects where hares travelled between cutovers and adjacent forest. I wore snowshoes to minimize disturbance to the deep ($\sim$0.5–1 m) snow pack. I stuck four boughs 5 cm into the snow in each habitat along 11 different runways. I located boughs approximately 10 m from the boundary between the forest and cutover. All boughs were thus available to individual foraging hares moving along runways between the two habitats. I placed two boughs under the cover of large shrubs or drooping conifer branches. I placed the other two nearby (2–5 m) in the open. Individual boughs in each pair were approximately 25 cm apart. Pine-boughs were left in place for one week, after which I collected the remaining plant material. Snowshoe hares were the only animals that ate the boughs.

Protein content declines, and fibre increases, with increasing diameter of willow and birch twigs consumed by snowshoe hares (Hodges and Sinclair 2003). Accordingly, the diameter of twigs at the point of browse optimizes the balance between protein and the fibre required for proper digestion (Hodges and Sinclair 2003). A similar tradeoff can be expected with other browse species. Thus, I measured stem diameter of the pine boughs at the point of browse with digital calipers as an appropriate (inverse) giving-up density of hare diets in winter. I also measured the length of all residual boughs, and returned the samples to the lab where they were dried for six weeks (to a constant weight) before being weighed (biomass). I combined the data for each pair of boughs to create three metrics of giving-up density: mean browse diameter, total biomass, and mean residual length after browsing.

In June 2003 two assistants and I collected natural giving-up-densities from recently browsed shrubs along each transect. We collected one set of samples along a 100 m segment of each trapping transect (50 m in each habitat). We searched for browsed shrubs along a 3 m wide belt centred on the transect. We identified shrubs to species where possible (we could not distinguish reliably among different species of willow *Salix*, or "serviceberries", *Amelanchier*). We measured the browse diameter and height of the specimen of each species with the largest browse diameter (minimum GUD) within each 1 m linear segment of the belt. These data allowed me to calculate relative frequencies of browsed shrubs between habitats, and to assess whether there was any systematic difference in natural giving-up densities

between habitats and with increasing distance from the habitat boundary.

Next, we moved at least 50 m laterally from our trapping transects to find a hare runway bisecting forest and cutover habitats. We created a sinuous 3 m belt transect along the runway and measured the browse diameter and residual height of all browsed shrubs until we attained a sample size of ten in each habitat for each species. We stopped the search for new specimens approximately 75 m from the habitat boundary. Our combined data yielded only four "species" with sufficiently large samples for analysis (bush honeysuckle, *Diervilla lonicera*; wild rose, *Rosa acicularis*; *Salix* spp. and *Amelanchier* spp.).

My assessment of predation risk via giving-up-densities assumes that shrubs of each species represent comparable foraging patches between habitats. The assumption would be violated if shrub physiognomy, or anti-herbivore protection, varies between habitats (these potential effects can alter foraging costs, both were controlled in the pine-bough experiment).

Giving-up densities B: does predation risk differ between more extreme old-field and shrubland habitats?

There was no consistent difference in giving-up densities between cutover and forest habitats (below). The similar GUDs should reflect similar predation risks, but it is also possible that my design was incapable of detecting differences in predation risk between habitats. I tested the design with additional experiments at another site (approximately 100 km south) in winter 2004. Snowshoe hares were abundant in low-lying alder (*Alnus viridis*) shrublands adjacent to upland old-fields hand planted to red pine (*Pinus resinosa*, <1 m tall). The proportion of snow covered by hare tracks was highest in alder and declined noticeably toward zero in the middle of the old field. I observed tracks of several mammalian predator species in the study area (including lynx, *Lynx canadensis*; fox, *Vulpes fulva*; fisher, *Martes pennanti*, and wolf, *Canis lupus*). Differences in hare track density should correlate with differences in predation risk between the relative safety of cover in the shrubland, to the virtual absence of safe sites in the old field.

I cut 112 50 cm pine boughs in February 2004 from the same plantation as those used in 2003. I measured stem diameter at the base of each bough. Then I labelled every bough with a 2.5 cm square of flagging tape attached to the base with a thumb tack. I selected 14 sample sites with dense, fresh snowshoe hare spoor along the margin of the 10 ha old field. Distances between adjacent sites varied between 20 and 200 m (mean = 70.5). Each site was separated from others by areas of relatively unused (lower track density) habitat. I stuck a

pair of boughs into the snow under the protective canopy of hardwood shrubs (mostly alder), and in the open 1 m away. I placed one shrub-cover pair of boughs in dense brush along the habitat margin. I placed another shrub-cover pair (4 boughs) approximately 4 to 6 m away where sparse shrubs were invading the old field (Fig. 3A). The assignment of boughs to the two habitats was confirmed independently by an assistant (Michael Oatway). We collected the boughs after two nights of hare foraging and measured their browse diameters and lengths in my field laboratory (home workshop).

In March, I cut an additional 128 boughs to complement the alder-old-field experiment with two more. In one experiment, I assessed whether giving-up densities (browse diameters) depended on bough size (estimated by the stem diameter at the freshly cut base of the bough). I selected two sites in dense alder with numerous fresh snowshoe hare tracks. The sites were separated from each other by nearly 400 meters, and both sites were isolated from those used in the previous experiment (approximately 90 m). I placed a haphazardly chosen single pine bough every 2 m along an 8-station transect in each site (Fig. 3B, total of 16 different boughs). Boughs varied in size from the smallest (basal diameter = 6.28 mm, wet weight = 35.5 g) to the largest (10.84 mm, 113.9 g) in my samples. We collected the boughs after two nights of foraging.

I assessed the effect of distance from safety in a second "March hare" experiment at the same 14 sites as in February. I stuck two boughs into the snow under the canopy of large shrubs 2 m from the edge where thick brush merged with the old field. I placed two more at the edge, and stuck two subsequent pairs in the open field at 2 and 4 m distance from the edge. Each replicate was thus comprised of eight boughs arranged as pairs at 2 m intervals along a transect perpendicular to the edge, and bisecting the two habitats (Fig. 3C). The proper placement of all boughs was again confirmed independently by Mike Oatway. We collected these boughs following three nights of hare foraging. Boughs from both March experiments were measured in the field lab.

Analyses

I calculated the hare isodar by geometric mean regression (Krebs 1999), and searched the residuals for possible effects caused by collecting data among different transects or years. I tested for habitat and microhabitat (open vs cover) differences in pine-bough giving-up densities with repeated-measures analysis of variance with both habitat and microhabitat treated as within-subjects factors. I used separate analyses to evaluate differences in the three different estimates of giving-up density collected in 2003 (mean browse
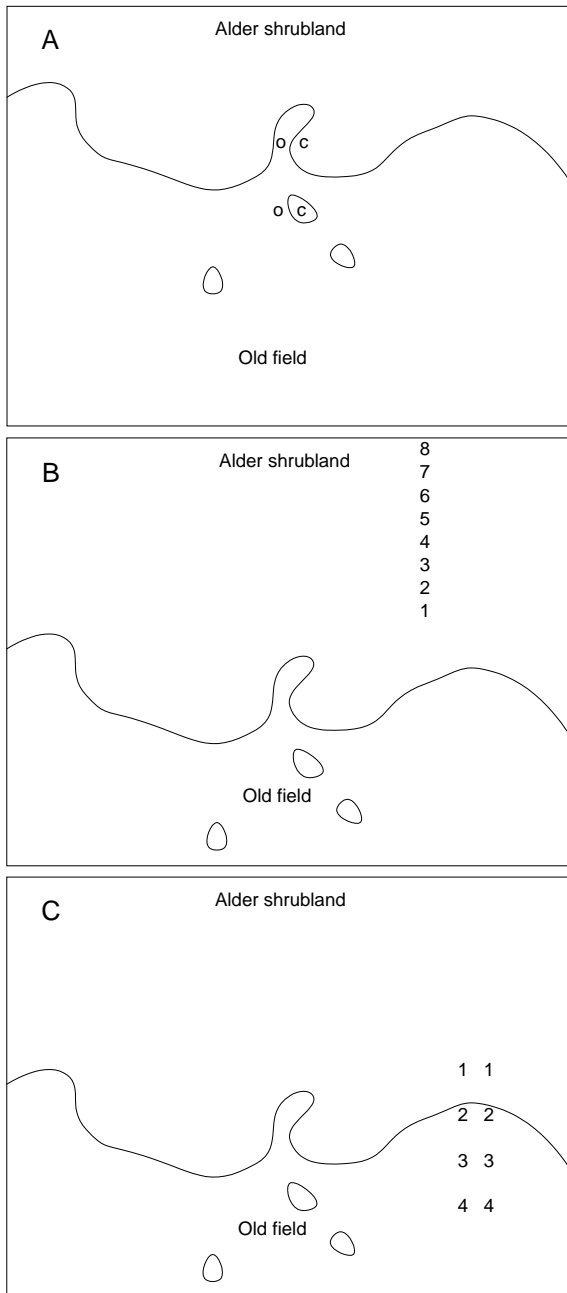
Fig. 3. A caricature of three field experiments to test whether giving-up-densities of snowshoe hares foraging on pine boughs differ, A) between shrubland and old field as well as between cover (c) and open (o) habitats, B) among boughs of different sizes, or C) with increasing distance from shrub habitat. Numbers correspond to either single or paired boughs along transects.

diameter, total biomass, and mean residual bough length after browsing).

I used contingency tables contrasting the number of 1 m segments containing each of the seven most common browse species to assess for relative differences in the number of foraging patches in each habitat. I tested for a distance effect in natural GUDs by two different mixed-model univariate analyses of covariance on browse diameter and browse height (habitat and species treated as fixed effects, transects as random effects) with distance from the boundary as the covariate. The covariate was not significant (below), so I grouped these data with those obtained from the second set of transects and again searched for significant differences in GUD with multivariate analysis of variance (MANOVA, but excluded the covariate). Species differed in browse diameter and height, an effect that depended on transect (below). I repeated each analysis separately on each species and adjusted significance levels with Bonferroni's correction. All analyses of variance were performed using the SPSS GLM procedure (version 11).

I also used repeated-measures ANOVAs to test for the effects of habitat and bough placement on browse diameters in the 2004 experiments. I used polynomial contrasts to assess whether giving-up densities varied along the transects from shrubland to open old field. Habitat and bough placement were included as within-subject effects in both designs.

I used linear regression on the data from the two transects in the "bough-size" experiment to test the assumption that foraging hares maximized their harvest rate in my experiments. Hares using a quitting-harvest-rate foraging rule should consume relatively more resource from "rich" than from "poor" resource patches if their harvest rates decline through time (Brown 1989, Brown and Mitchell 1989, Valone and Brown 1989). Diminishing harvest rates for hares in my experiments should be caused by changes in nutritional composition of boughs with increasing stem diameter. The thin tapered stems of boughs with small basal diameters are of higher quality than are the thick fibrous stems of boughs with large basal diameters. A foraging-strategy based on quitting-harvest rates would be implied if hares consumed more of the stem from thin than thick boughs. Browse diameters and residual stem lengths would both increase when regressed against increasing thickness of the bough (basal diameter).

Results

Isodar analysis: hares did not prefer young over mature forest

Snowshoe hares were common on all transects and occupied both habitats (Fig. 4), but densities varied among years (no hares were captured on the "black spruce" transect until 2000). The isodar was statistically significant but "noisy" ($F_{1,21} = 7.9$, $P = 0.01$, adjusted $R^2 = 0.24$). One cluster of three points with dramatically
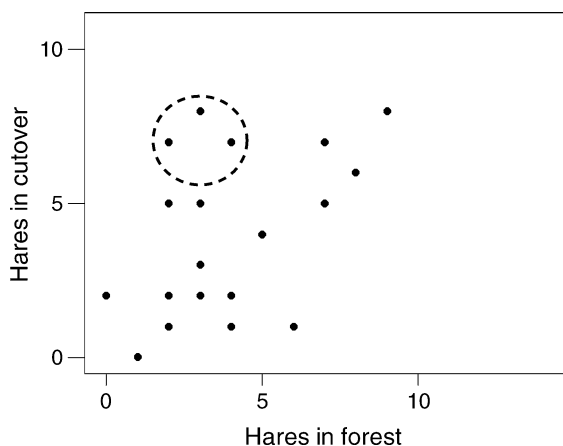
Fig. 4. The snowshoe hare isodar between regenerating 20 yr old cutovers and 80 yr old mature conifer forest in northwestern Ontario, Canada. Hares exhibited vague density-dependent habitat selection with no apparent preference for one habitat over the other. The dashed circle outlines three potential outliers with higher than expected hare density in cutover habitat.

Table 1. Summary of a repeated-measures analysis of variance on browse diameter, dry weight biomass, and residual length (GUD) of 50 cm pine boughs foraged during winter by snowshoe hares in open and covered microhabitats nested within cutover and mature forest habitats.

Source of variation	GUD measure	df	F	P
Habitat	browse diameter	1,9	0.12	0.74
	biomass	1,10	0.07	0.80
	length	1,10	0.06	0.81
Microhabitat	browse diameter	1,9	0.90	0.37
	biomass	1,10	0.002	0.97
	length	1,10	0.65	0.44
Habitat × microhabitat	browse diameter	1,9	1.32	0.28
	biomass	1,10	2.67	0.13
	length	1,10	2.04	0.18

higher density in cutover than in forest appears heterogeneous in comparison with the others (Fig. 4), but there was no common theme. The three data points came from two different transects and two different years. Hares had no preference for either habitat (Fig. 4). The isodar intercept (-0.51, $CI_{0.95} = -2.4–1.4$) was not significantly different from zero, and the slope (1.13, $CI_{0.95} = 0.69–1.56$) was not different from unity. Some readers might wonder, if the three "outliers" were removed, whether a quadratic isodar fits the data better than a linear model. The answer is no. A quadratic isodar calculated on the reduced data is redundant with the more parsimonious linear alternative ($R^2_{adj} = 0.473$ vs 0.465 respectively). Thus, snowshoe hare habitat selection, as revealed by the isodar, was weakly density dependent, there was no preference for one habitat over the other, and no convincing evidence of curvature to suggest differences in predation risk.

Giving-up densities A: there was no apparent difference in predation risk between young and mature forest

Pine-bough giving-up densities also implied that hares viewed the forest and cutover habitats as one. There were no significant differences in any of the three estimates of pine-bough giving-up-densities, either between habitats or between open and covered treatments (Table 1). Please note that sample size for the analysis of browse diameter was less than for the other GUD metrics. One twig was completely consumed (but not all of its needles) so I could not measure its diameter.

Hares browsed 14 different "species" of shrubs along our 100 m transects. Seven were common enough to be

included in the contingency-table analysis (Fig. 5). Relative shrub frequencies were greater in cutover than in forest (164 vs 109 specimens), but the ratio differed by species (Fig. 5, LR $\chi^2_6 = 22.24$; P <0.001). Six browsed species (*Amelanchier*, *Rosa acicularis*, *Rubus idaeus*, *Salix*, *Vaccinium angustifolium* and *V. myrtilloides*) were more common in cutovers. One species, *Diervilla lonicera*, was more frequent in forest.

Only four shrub species (*Amelanchier*, *Diervilla*, *Rosa*, *Salix*) were common enough to be included in the analyses of variance testing for differences in GUD. The two *Vaccinium* species were also common, but their twigs were too small for the reliable detection of differences in giving-up densities. The browse diameter of the four shrubs along the 100 m transects tended to covary with distance from the habitat boundary but the effect was not compelling ($F_{1,156} = 3.2$, P = 0.08). Browse height did not covary with distance ($F_{1,156} = 0.14$, P = 0.71). There were no differences in browse diameter, in the analyses including distance, between habitats, among species, or among transects. But the data hinted at a possible three-way interaction ($F_{4,156} = 2.03$, P = 0.09). Browse height differed among species ($F_{3,20.4} = 9.27$, P <0.001), but not
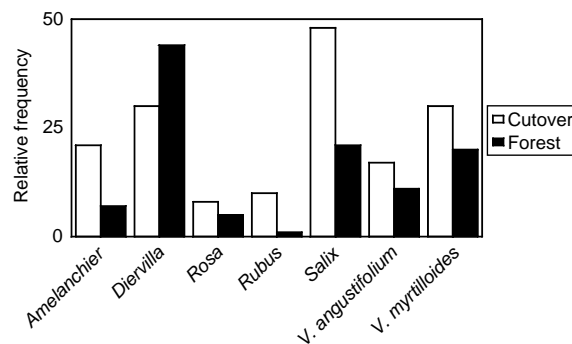

Fig. 5. The relative frequencies of seven "species" of shrubs browsed by snowshoe hares in 1 m segments along four 100 m long transects bisecting 20 yr old cutover and 80 yr old mature conifer forest in northwestern Ontario, Canada. *Amelanchier* and *Salix* specimens were not identified to species.

with any other factor or interaction. I eliminated the covariate of distance, combined the data from the two sets of techniques (shrubs with the largest browse diameter within 1 m segments along 100 m transects plus those where we measured the first 10 browsed shrubs along hare runways), and tested whether browse diameter and browse height differed among species or between the two techniques (multivariate analysis of variance). Both measures of giving-up density differed dramatically among species (diameter, $F_{3,368} = 17.82$, $P < 0.001$; height, $F_{3,368} = 43.41$, $P < 0.001$), but not among techniques (diameter, $F_{1,368} = 0.12$, $P = 0.72$; height, $F_{1,368} = 0.87$, $P = 0.35$) or their interaction (diameter, $F_{3,368} = 2.42$, $P = 0.07$; height, $F_{3,368} = 1.53$, $P = 0.21$). So I tested for a significant habitat effect with each species separately (Fig. 6).

Browse diameters of *Salix* and *Rosa* were significantly greater in cutover habitat (lower GUD, $F_{1,131} = 14.54$, $P_{Bonferroni} < 0.001$ and $F_{1,38} = 8.03$, $P_{Bonferroni} = 0.03$ respectively). But the browse diameter of *Amelanchier* was similar between habitats ($F_{1,69} = 0.99$, $P_{Bonferroni} = 1$), while that of *Diervilla* was suggestive of differences, but not significantly so ($F_{1,130} = 6.19$, $P_{Bonferroni} = 0.06$).

Browse heights of *Salix* were taller in cutovers ($F_{1,131} = 10.68$, $P_{Bonferroni} = 0.004$), but so too were those of *Amelanchier* ($F_{1,69} = 12.93$, $P_{Bonferroni} = 0.004$). There was no clear and uniform evidence that the two habitats differed in predation risk.

Giving-up densities B: upland old-field habitat was riskier than was the alder shrubland

Snowshoe hares harvested pine boughs in a manner consistent with a quitting-harvest rate foraging strategy. Hares foraging on thick-stemmed boughs tended to leave behind thicker and longer residual stems than they did when foraging on thin-stemmed boughs (experiment outlined in Fig. 3B, $F_{1,14} = 5.52$, $P = 0.03$, $R^2_{adj} = 0.23$; $F_{1,14} = 5.1$, $P = 0.04$, $R^2_{adj} = 0.22$ for browse diameter and residual stem length respectively, Fig. 7). Both regressions were influenced by a potential outlier from the thickest bough. I removed the "outlier" and repeated the analysis. The regression of browse diameter on basal diameter was nonsignificant ($F_{1,13} = 0.4$, $P = 0.55$) while that of browse length was improved ($F_{1,13} = 12.7$, $P = 0.003$, $R^2_{adj} = 0.46$). Nevertheless, hares
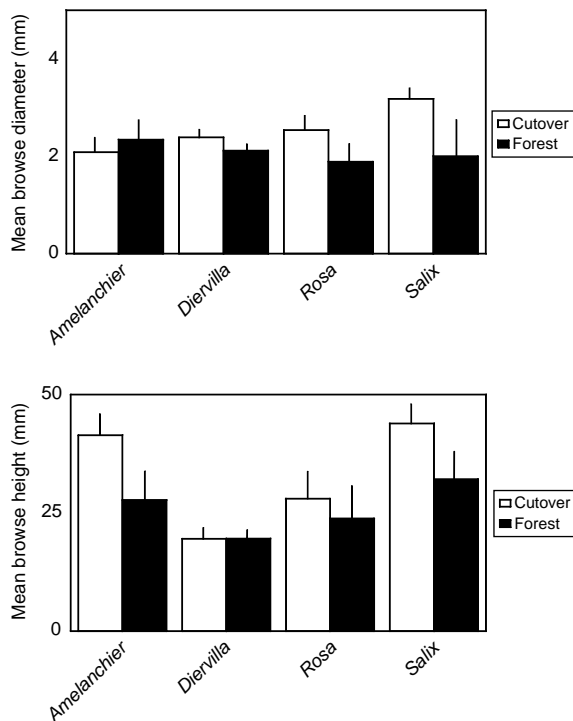

Fig. 6. Mean browse diameters and mean browse heights (each with upper 95% confidence intervals) of four species of shrubs commonly browsed by snowshoe hares in cutover and forest habitats in northwestern Ontario, Canada. Note that the confidence intervals exclude Bonferroni corrections used to assess statistical significance.
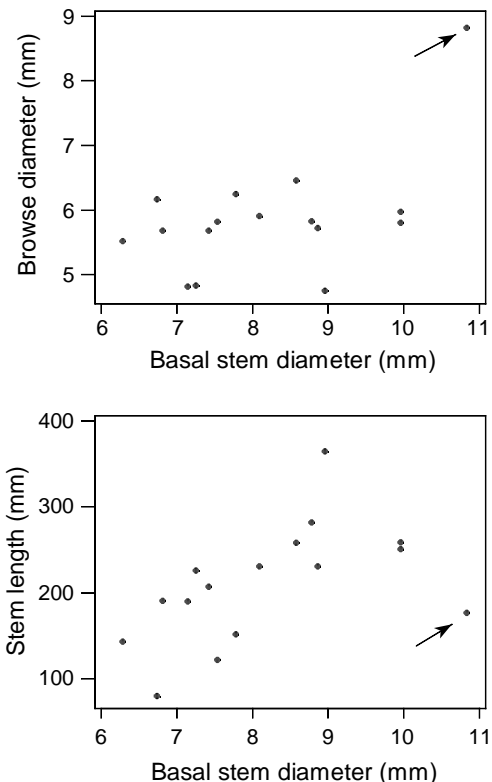

Fig. 7. The relationships of browse diameters and stem lengths with the basal stem diameter of pine-boughs consumed by snowshoe hares in a dense alder shrubland habitat in 2004. The arrows identify a common outlier in both graphs.

consumed more of the stem from thin, than from thick, boughs.

Predation risk was lower in the shrub habitat than in the old field. Giving-up densities (inverse of browse diameters) were significantly smaller when hares foraged in the alder shrubland than when they foraged nearby in the adjacent old field (experiment outlined in Fig. 3A, $F_{1,13} = 16.71$, $P = 0.001$, Fig. 8A). There was no difference in giving-up density between boughs located under the canopy of shrubs and those in the open 1 m away ($F_{1,13} = 0.13$, $P = 0.7$).

The habitat difference in predation risk was confirmed in the second experiment (Fig. 3C) where browse diameters on pine boughs declined linearly with distance from the protective cover of the shrubland (overall analysis, $F_{3,11} = 8.8$, $P = 0.003$; linear contrast with distance $F_{1,13} = 23.05$, $P < 0.001$; quadratic and cubic contrasts both non-significant [$P > 0.7$], Fig. 8B). Thus, the lack of significant differences in giving-up densities between young and mature forest in 2003 was not because the design was incapable of detecting real habitat differences.
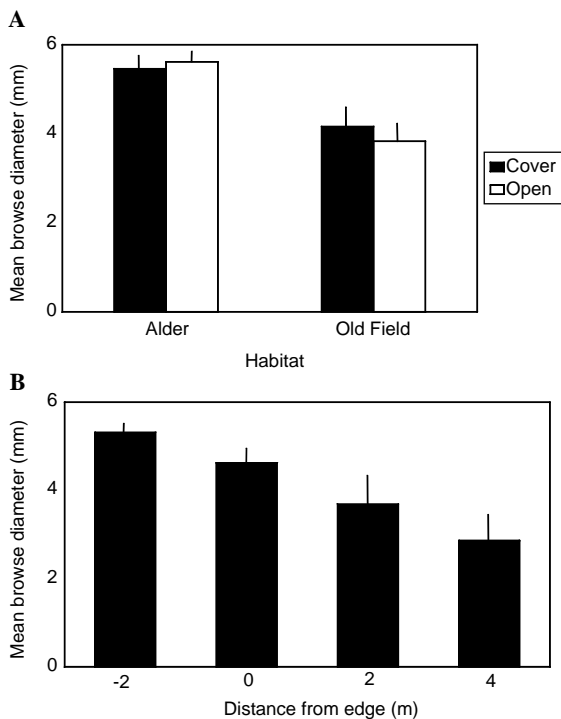

Fig. 8. Mean browse diameters ($\pm$one standard error) of pine boughs consumed by snowshoe hares were larger in alder shrubland than old field habitat, but were similar under shrubs and in the open (A). Mean browse diameters declined linearly with increasing distance into the old field (B).

Discussion

Hares confirmed predictions from habitat-selection and optimal-foraging theories

Snowshoe hares occupied adjacent 20 yr old cutover and 80 yr old mature forest habitats in Northwestern Ontario with no apparent preference for one over the other. The relative number of hares in each habitat was more or less constant over a range of population sizes, and there was no hint of a nonlinear or curving isodar that would implicate habitat differences in predation risk. But even though the isodar was highly significant statistically, there was substantial residual variation. Hares appear to be rather vague density-dependent habitat selectors.

A similarly vague pattern emerged in my attempts to document differences in predation risk between cutover and forest habitats. Hares did not consume pine-boughs located under cover preferentially to those in the open, or those located within the habitat with the greatest cover (cutovers).

Natural browse is a complex indicator of predation risk

Natural browsing of shrubs suggested that predation risks may be less in cutover habitat, but the pattern was inconsistent among common browse species. The utility of using natural browsing to assess habitat differences is compromised whenever the quality of forage differs between habitats. Two of the common browse species possessed clear habitat-related differences in their quality. Browsed willow stems were thicker and taller in the cutover than in the forest. Serviceberry browse diameters were similar between habitats, but browse heights were, as for willow, taller in the cutover. It is thus clear, 1, that the shrubs in the cutover were taller than those in the forest, or 2, that the physiognomy (e.g. the relationship between stem diameter and height) of the cutover shrubs differed from those in the forest. I cannot distinguish between the two alternatives because the hares ate the evidence.

Interpretation of the browse data are further compromised by the different histories of cutover and forest plots (naturally-browsed shrubs may, for example, be more "youthful" on the cutovers), and through the equal use of runways by hares. Though I collected no data, the number of winter runways, as well as the intensity of hare spoor, were much greater in cutovers than in forest. But hares that construct or use a runway in dangerous habitat when a safer alterative is available are not only short-sighted, they are bound to be short-lived. It is thus possible, even if forest habitat is more risky than cutover, that hares equalize the risks by careful selection of safe routes. Runway density (and hare density km^{-2}) may be

higher in one habitat than in another, but runways might receive equivalent use at the ideal-free distribution.

It is also possible that equal use of runways could tend to equalize the hare densities that I used for the isodar. Note, however, that the interpretation of equal habitat use and GUD does not change. True, traps were placed in runways. But GUDs were also collected along runways. The spatial scale of the experiment, relative to the unit of replication, was the same in both habitats.

Experimental patches provide clear evidence of similarities and differences in predation risk

Hares do not have the option of safe passage between shrubland and old-field at the second field site. Hares foraging on pine boughs along the margin between dense shrubland and adjacent old field consumed more browse in relatively safe shrubland than in the risky and more open field. Hares appeared to possess a limited "comfort zone" of about 1 m. Giving-up densities were not different between boughs located under the protective canopy of shrubs and those open to the sky 1 m away. But when stations were located along safe-to-risky transects, GUDs differed consistently over a spatial scale of only 2 m. The difference probably reflects, 1, the ability of hares to assess and modify predation risk over short intervals (as along runways), as well as 2, dramatic differences in visibility and susceptibility to predators as hares move from dense shrubland into the zone of sparsely distributed shrubs along the old field ecotone.

Two additional points should be emphasized from the shrubland vs old field experiments. 1) Hares appear to base their browsing decisions on quitting-harvest rates. Hares consumed more of the stem from thin high quality boughs than from thicker boughs of lower quality. 2) Giving-up densities (inverse of browse diameter) increased linearly with increasing distance from safety. It is tempting to speculate that the linear pattern reflects a similarly linear distance-from-safety increase in predation risk. We should be cautious of such an interpretation because giving-up density in patches with diminishing returns does not scale linearly with quitting-harvest rate.

While it is clear that hares can adjust their foraging to habitat differences in predation risk, it is also clear that hares did not associate the obvious structural differences between cutover and forest habitats with differences in risk. The result complements the data from two earlier studies that attempted to merge habitat-selection theory (represented by isodars) with optimal-foraging theory (represented by GUDs). An isodar for deer mice living in prairie and badland habitats in western Canada indicated that the mice preferred badland at all densities even though badland habitat is remarkably less

productive than prairie (Morris 1992). The badland preference was confirmed by mouse foraging. Deer mice had higher giving-up densities in prairie than badland, and proportionately higher GUDs in open prairie microhabitats than in similar sites in the badland (Morris 1997). Another isodar, for white-footed mice living in interior forest and edge habitats in southern Canada, documented essentially equivalent densities in the two habitats (Morris 1996). But white-footed mice are territorial during the reproductive season, and their despotic habitat selection (Fretwell and Lucas 1969) captured by the isodar represents sets of densities where fitness is greater in forest than edge. Demographic estimates of fitness were indeed higher in forest, weasel predation was less, and so too were giving-up densities (Morris and Davidson 2000). Most importantly, the difference in GUD between safe and risky sites was greater in the risky edge habitat than in forest. And now we see the exceptions that "prove the rule" for hares. Similar densities between cutover and forest habitats for nonterritorial hares suggests similar predation risks. Estimates of those risks from giving-up densities generally agreed. And in other sites with obvious differences in hare density between shrubland and old-field habitats, GUDs revealed dramatic differences in predation risk.

Prey habitat preference depends on their predators' strategies

Predation risk for snowshoe hares appears similar between densely-covered "regenerating" forests and adjacent mature-forest stands. Why can the risk be the same when habitats differ in structure? Much of the answer must depend on the foraging strategies employed by predators. Year-round predators of snowshoe hares at our location include lynx, bobcats (*Lynx rufus*), red foxes, coyotes (*Canis latrans*), wolves, fisher, and marten (*Martes americana*). Hunting strategies vary from the stalk and rush method used by coyotes to ambush predation that is often practised by lynx (O'Donoghue et al. 1998). Both coyotes and lynx, the dominant hare predators throughout the boreal forest, alter their use of habitats with hare abundance (O'Donoghue et al. 1998). In the Yukon when hares were at, or just beyond, their peak density coyotes and lynx hunted predominantly in densely-covered habitats that supported large densities of hares. When hares were less abundant, they tended to occupy more open habitats (but the differences were not dramatic (Murray et al. 1994, O'Donoghue et al. 1998, Fig. 7), and so did their predators.

Habitat and prey-switching predators alter predictions for the shape of prey isodars because attack rates (e.g. Eq. 1) vary with prey density. Thus, an increase in attack

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rates in the prey's preferred habitat when prey are abundant, will either counterbalance or accentuate the predator's effect on the isodar (depending on the relative qualities and predation risks in the two habitats, Eq. 3). The opposite will occur when prey are less abundant. The combination of habitat selection and prey switching by predators may explain the preference of hares for dense cover, as well as high predation rates in the same habitats (Keith et al. 1993, Wirsing et al. 2002). Alternative hunting strategies and habitat preferences among the entire suite of snowshoe hare predators will also tend to equalize predation risk between habitats.

Hik (1995) evaluated hare responses to increased risk during the decline in snowshoe-hare populations by manipulating food and safety. Time-lagged predator–prey dynamics yield the highest predator-to-prey ratios (and predation risk to hares) while hare population density declines. Female body mass and fecundity on food-supplemented and control areas was greater than on nearby plots excluding predators (Hik 1995). Hares also increased their use of safe habitats. Hares were thus able to balance the body condition and reproductive benefits of food against the survival costs of predation (Hik 1995). The "similar" patterns of density and GUDs for hares in northwestern Ontario suggest that hares can fine tune their adaptive foraging to local differences in predation risk. Isodars and giving-up densities both documented that the young and mature forest "habitats" were perceived as one. When hares can travel and forage along safe corridors in different habitats they do so. The runways equalize risks, so hare densities and GUDs in adjacent habitats are also equalized. But when one of the habitats is too risky for safe passage, hares avoid the habitat and reduce their foraging effort.

Can we unite demographic theory with adaptive foraging?

The local habitat- and density-dependent behavioural responses by hares, and their agreement with theory, are highly encouraging to those ecologists who hope to link population dynamics and behaviour. The union of demographic theories of predator–prey dynamics with complementary ESS models of adaptive foraging yield striking, and yet sometimes conflicting, insights. Consider the case where habitat 2 is more productive (higher r) than 1, and that prey face a tradeoff between food and safety because predators have a lower attack rate in habitat 1. Equation 3 demonstrates that the isodar's intercept will be reduced, and that the composite isodar will diverge from the predator-free alternative (Fig. 1). But Joel Brown (1998), in a typically creative and unique contribution, modelled a similar scenario as

an evolutionary game and reached a different conclusion (Brown actually imagined that habitat 1 was riskier). According to Brown's behavioural model, prey should prefer habitat 1 at low density because they are relatively safe and have a high resource-harvest rate. The isodar intercept is reduced (as it is in the demographic model). But as prey density increases, each individual can expect to harvest less energy, and the marginal value of energy in terms of fitness is likely to increase. Meanwhile, the marginal value of safety declines. Individuals will be more willing to occupy risky habitat 2 to secure their required energy for survival and reproduction. The isodar slope is increased and converges on the predator-free alternative.

Why do the two models differ in their isodar predictions? The behavioural model assumes a constant difference in predation risk. As prey increase in density, the net fitness rewards of the two habitats are bound to converge. The demographic model assumes that predation risk covaries with prey density. As prey become more abundant, predator numbers increase, and the relative differences in predation risk between habitats diverge.

Which model is closer to the truth? The answer will again depend on the predator community, and the predators' abilities to exploit different habitats. Models with constant differences in predation risk will most likely apply when much of the predation on the target species is incidental. The dynamics of the predator(s) will be determined by the interaction with other prey (but this could also produce 'unpredictable' predation risk as predator numbers covary with other prey species). Models with variable (but predictable) risks will most likely apply to tightly-linked predator and prey dynamics such as that suspected for snowshoe hares. The predictions of both models become somewhat more complicated (and valuable) in communities with additional interacting species (Brown 1998, Morris 2003, 2004).

Ecologists interested in using isodars and GUDs to infer relative habitat qualities of prey species should do so with care. The mechanisms underlying the two sets of theories differ, and so too does the scale of their application. Isodars yield only the net pattern of density between habitats. Isodars should be effective at detecting density-dependent habitat selection, but are rather dull scalpels for dissecting out causal processes (Jonzen et al. 2004; but mechanisms can often be inferred by including additional terms in the regressions, Morris 1999, Morris et al. 2000a,b). Patterns in giving-up densities can give clear indications about predation risk, but at least in the case of natural "patches" (=shrubs) exploited by snowshoe hares, the answer could depend on the type of patch chosen for study. Moreover, GUDs are reliable indicators of predation risk only when the same individuals equalize marginal

values between habitats. Changes in hare diets at larger scales, such as that reported for hares living within and outside of predator exclosures (Hodges and Sinclair 2003), are difficult to interpret because the analysis contrasted different hares living at divergent population densities. The assessment of foraging cost is complicated by differences in the state of foragers and their respective evaluations of energetic costs, predation risk, and missed opportunities for alternative fitness-related activities (Brown 1988, Houston and McNamara 1999). Tests of habitat differences in predation risk, at the scale where density can vary between habitats, is best done with a combination of isodars and giving-up densities. But both habitat selection and foraging reflect the adaptive density-dependent behaviours of individuals. While we are not yet able to move seamlessly between patterns in demography (isodars) and patterns in foraging (GUDs), it is nevertheless clear that we must incorporate their joint effects on behaviour into our understanding of population dynamics and spatial distribution.

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