

Niche dimensions of New England cottontails in relation to habitat patch size

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Abstract. We examined physical condition, niche dimensions, and survival of New England cottontails (*Sylvilagus transitionalis*) that occupied 21 habitat patches of different sizes during winter. Rabbits on small patches (≤ 2.5 ha) were predominantly males, and both sexes had lower body mass than individuals on large patches (≥ 5.0 ha). Niche indices (β , where β ranges from 0 to 1, and values approaching 1 indicate generalized resource use) of habitat use revealed that rabbits on small patches used a greater variety of microhabitats (based on understory stem density: $\beta_s = 0.81$, and proximity to cover: $\beta_c = 0.79$) than rabbits occupying large patches ($\beta_s = 0.65$, $\beta_c = 0.66$). Rabbits on small patches also consumed low quality forage more often and fed at sites farther from escape cover than rabbits on large patches. There were no significant correlations between rabbit densities and niche dimensions. Niche expansion was not a result of competitive release or relaxation of predator pressure. Rabbits on small patches apparently modified their niche dimensions in response to resource limitations. This response included occupying sites with limited understory cover that apparently resulted in rabbits on small patches having a lower survival rate (0.35) than rabbits on large patches (0.69) during a 10-week monitoring period. Skewed sex ratios and low survival rates among rabbits on small patches suggest that these habitats act as sinks to dispersing juveniles from large (source) patches. As a result, local populations of New England cottontails may become vulnerable to extinction if large patches of habitat are not maintained.

Key words: New England cottontail – Fragmentation – Niche expansion – Resource limitations

Much of what is known about the effects of habitat fragmentation on vertebrate demography is based on avian models that may not be relevant to other taxa.

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The use of artificial nests has been a principle method for evaluating the influences of habitat edges (Andrén and Angelstam 1988) or habitat-patch size (Wilcove 1985; Small and Hunter 1988). Predation on these nests is dependent exclusively on the predator locating a nest while foraging (Angelstam 1986), and nests may be incidentally encountered while predators are foraging for other food items (Vickery et al. 1992). Results from such studies may not be applicable to free-ranging animals that can evade predators. Birds also may ameliorate the effects of habitat fragmentation by combining several discrete patches of habitat into a functional home range (Rolstad 1991; Dunning et al. 1992), whereas other vertebrates often are restricted to forage and reproduce in a single patch. Thus, the effects of fragmentation may depend on the specific organism using the habitat, and it is unlikely that generalizations can be made on the demographic consequences without additional autoecological studies (Karieva 1987).

A number of small and medium-sized mammals are appropriate vertebrates to investigate additional effects of fragmentation because they are restricted to discrete habitats (e.g., Smith 1974; Weddell 1991). In southern New Hampshire, New England cottontails (*Sylvilagus transitionalis*) occupy patches of habitat in winter that vary from 0.2 to >15 ha (Litvaitis 1993). This medium-sized lagomorph (ca. 1 kg) occurs in the extreme north-eastern United States (Chapman et al. 1992), and is a candidate for threatened/endangered status by the U.S. Fish & Wildlife Service (Federal Register Vol. 54, No. 4:553–579, January 6, 1989). During a survey of suitable habitats, we observed that patches approximately 5 ha or larger were consistently occupied, whereas smaller patches had an occupancy rate of 60% (Litvaitis, unpublished data). Populations of rabbits occupying small patches were likely vulnerable to frequent extinctions simply because of their size (MacArthur and Wilson 1967; Verboom et al. 1991). Additionally, cursory observations of browse use by rabbits in small patches suggested that these habitats were food limited. We speculated that rabbits in small patches might attempt to

offset food limits by using a wider variety of foods, including those associated with elevated risks of predation. As a result, an additional consequence of habitat fragmentation to this species may be increased rates of predation that result from attempts to compensate the limitations imposed by small patches. To test this relationship, we specifically predicted that rabbits on small patches relative to those in large patches would: 1) have lower body mass, 2) occupy a greater diversity of microhabitats, 3) consume a greater variety and a lower quality of food resources, and 4) have lower winter survival rates as a result of utilizing less secure sites within a patch.

Methods

Study site

The study was conducted in ca. 80-km² portion of Strafford County, New Hampshire (43°07' N, 71°00' W). Mean annual temperature was 8 C and annual precipitation averaged 106 cm, including 137 cm of snow (NOAA 1970–92). Dominant overstory vegetation included northern hardwoods (*Fagus grandifolia*, *Acer* spp., and *Betula* spp.) and white pine (*Pinus strobus*). Understory species included red maple (*Acer rubrum*), beaked hazelnut (*Corylus cornuta*), viburnums (*Viburnum* spp.), raspberry/blackberry (*Rubus* spp.), and eastern hemlock (*Tsuga canadensis*). Strafford County is typical of many urbanizing areas and has a mosaic of forests, farmland, residential and industrial areas.

New Hampshire is at the northern range limit of New England cottontails. In this portion of their range, they are associated with habitats having dense understory vegetation (e.g., idle agricultural land, shrub-dominated wetlands, and regenerating woodlots; Litvaitis 1993). Two other lagomorphs also occur in this region, eastern cottontails (*S. floridanus*) and snowshoe hares (*Lepus americanus*).

Patch inventory and rabbit condition

We restricted our examination of resource use by cottontails to winter (December through April, 1990–91 and 1991–92). Previous research on northern populations of lagomorphs (primarily *Lepus americanus*) has indicated that winter survival may determine the persistence of a population, and that survival during winter is largely dependent on the availability of food and cover (Pease et al. 1979; Wolff 1980; Litvaitis et al. 1985a; Sievert and Keith 1985). Candidate patches of habitat were searched after snowfall for tracks of cottontails. Single-door box traps (90 × 30 × 30 cm) were baited with apples and placed in areas with substantial rabbit activity. Specific identity of captured rabbits was based on body mass, pelage and morphological characteristics (Litvaitis et al. 1991). Body mass, right hind-foot length, and sex were recorded prior to marking each rabbit with a unique ear tag. Body mass and an index (mass ÷ hind-foot length) were used to assess physical condition. Hind-foot length was used to examine age-class distributions (Bothma et al. 1972).

Patches were excluded from our study if they contained eastern cottontails or snowshoe hares because of the potential effects of competition on patterns of re-

source use. Boundaries of selected patches were delineated using nonhabitats (e.g., roads, railroads, and mowed pastures) or by a loss of woody understory vegetation. Area was estimated by pacing the perimeter and patches were classified as small (≤ 2.5 ha) or large (≥ 5.0 ha). We had originally planned to include an intermediate size (3.0–5.0 ha), but were unable to find a sufficient number of patches in this category. Because of practical constraints, we did not estimate rabbit densities using mark-recapture methods. On small patches, we believed that all individuals were captured. On large patches, we stratified our trapping effort by the distribution of rabbit activity and understory density. We then estimated the areas that contained traps, the density of rabbits within these areas (based on captures), and the proportion of the patch with similar understory density (see habitat sampling methods below). Using this information, we extrapolated rabbit density for the entire patch. Although we did not evaluate the accuracy of this method, we are confident (based on track distributions) that a high proportion of the rabbits on these patches were captured.

Habitat-use patterns

The distribution of fecal pellets was used to examine habitat use of rabbits relative to understory characteristics on each patch (Litvaitis et al. 1985b). Nested plots were used to sample pellet abundance (1-m radius) and understory-stem density (deciduous and coniferous plants >0.5 m tall and <7.5 cm dbh in a 2 × 5-m plot). Because coniferous stems provide more cover than deciduous stems during winter, we converted understory stems to stem-cover units, where: stem-cover units/ha = deciduous stems/ha + (3 × coniferous stems/ha) (Litvaitis et al. 1985a). Understory density at pellet plots was then placed into one of four categories (<25000; 25–50000; 50–100000 and >100000 stem-cover units/ha). Distance to cover was measured (<2, 2–5, 5–10 and >10 m) from each pellet plot to a clump of understory vegetation at least 1 m² that provided $\geq 50\%$ visual obstruction. We considered stem-cover unit density and distance to cover as habitat features that influence rabbit vulnerability to predation (Wolff 1980; Litvaitis et al. 1985a). A minimum of 32 plots were systematically distributed throughout each patch, with five additional plots sampled for each 0.25 ha increase in area among patches >0.5 ha. The center of each fecal pellet plot served as the center or reference point for all sampling.

Selection indices (percentage of use minus percentage of availability, Thomas and Taylor 1990) and simultaneous confidence intervals on habitat use were calculated to determine if rabbit use (based on pellet distributions) of categories of stem-cover unit density and distance to cover were greater or less than expected based on availability (Neu et al. 1974; Carroll 1988). Additionally, habitat niche dimensions were described relative to available resources using the following formula proposed by Feinsinger et al. (1981):

$$\beta = 1 - 0.5 \sum |p_i - q_i|$$

where p_i is the proportion of fecal pellets that are associated with habitat feature i and q_i is the proportion of an individual patch that is characterized by feature i . Values for this index range from 0 to 1, with values approaching 1 indicating use is equivalent to availability. Habitat-niche dimensions were based on density of stem-cover units (β_s) and distance to cover (β_c).

Forage-use patterns

Consumption of woody twigs was sampled using a modification of the point-center technique (Cottam and Curtis 1956), with pellet

plots serving as reference points. The nearest woody plant in each quadrat was identified and the browsed and unbrowsed twigs within 0.5 m of ground level were tallied. Wolff (1980) observed that snowshoe hares usually consumed twigs with a diameter ≤ 3 mm, apparently in response to the diminished protein content as twig diameter increased. Pease et al. (1979) also found that hares forced to consume twigs > 3 mm did not maintain body weight and starved. We recorded twig diameter at the point of browsing in three classes (< 3 , 3–6, > 6 mm) as an indication of the intensity of food use and food quality. Consumption of tree or shrub bark (presence/absence) within the 2×5 -m understory plots also was recorded as an additional index of the intensity of food use (Pease et al. 1979). Forage selection and food niche (β_f) were evaluated using the same procedures applied to habitat use. During 1992, the distance to cover from each woody plant used to sample forage use was measured to describe foraging habitat.

Rabbit survival

At least one rabbit per patch was equipped with a collar-mounted transmitter to monitor survival and determine causes of mortality. In patches with two or more marked individuals, transmitters were placed on males and females if both sexes were captured. Survival rates were calculated for a 70-day interval (Feb. 16 through Apr. 26) using program MICROMORT (Heisey and Fuller 1985). A staggered-entry analysis (Pollock et al. 1989) was used, and rabbits were eligible for entry each day if they were equipped with a transmitter. This approach is equivalent to the staggered-entry Kaplan-Meier method (Pollock et al. 1989). Survival was monitored during the winters of 1990–92 and included individuals from companion studies that used identical methods (Litvaitis and Brown, unpublished data). We grouped rabbits by patch-size classes prior to estimating survival. Individuals with unknown fates (signal loss) were considered alive on the last day they were monitored. As a result, survival estimates are liberal (Heisey and Fuller 1985).

Statistical analysis

Wilcoxon two-sample tests (SAS 1985) were used to compare rabbit densities, body masses, condition indices, hind-foot lengths, and niche indices between small and large patches. Because lagomorphs are sexually dimorphic, we grouped rabbits by sex prior to comparing mass, condition indices, and foot lengths. Contingency tables were used to examine differences in the intensity of food use (percent of browsed stems with a diameter at the point of browsing ≥ 3 mm and the percent of understory plots that contained evidence of bark consumption) and the distributions of browsed stems relative to distance to cover. Spearman-rank correlations were used to examine pairwise relations between rabbit density, patch size, and indices of niche width. Survival estimates were compared between patch-size classes using z statistics (Heisey and Fuller 1985). Statistical significance was set at $\alpha = 0.05$.

Results

Patch inventory and rabbit condition

New England cottontails were captured on 21 patches (12 small and 9 large). Seven patches (5 small and 2 large) were sampled during 1991 and 14 were sampled during 1992. Individuals captured per patch ranged from 1 to 7, and density estimates ranged from 0.3 to 7 rabbits/ha (Table 1). Females were captured on five (42%) of the small patches and 6 (67%) of the large patches. Mean densities differed between small (2.2/ha) and large (1.0/ha) patches ($z = -2.10$, $P = 0.04$), and density was correlated with patch size ($r = -0.66$, $P = 0.001$) (Fig. 1). Males on small patches had lower body masses ($\bar{x} = 955.6$ g) and lower condition indices ($\bar{x} = 10.1$) than males on large patches (\bar{x} mass = 1039.0 g, $z = -2.59$,

Table 1. Patch characteristics and indices of habitat and food niche parameters among New England cottontails occupying 21 patches of habitat in southern New Hampshire

Patch	Area (ha)	Rabbit density (%/ha)	Pellet plots	Niche indices ^a		
				β_s	β_c	β_f
Beech hill	0.3	3.0	32	0.97	0.97	0.93
Pinch hill	0.5	4.0	42	0.72	0.83	0.69
Route 4	0.5	2.0	40	0.79	0.78	0.86
Keefe's pond	0.8	1.4	48	0.85	0.77	0.58
Carlisle's	1.0	2.0	53	0.93	0.87	0.83
Crosby's	1.0	7.0	50	0.77	0.63	0.79
Lee circle	1.0	1.5	48	0.79	0.61	0.54
Deer point	1.1	2.0	48	0.67	0.61	0.81
Langley's	1.4	0.8	51	0.93	0.91	0.69
Back river	2.0	1.5	69	0.68	0.84	0.75
Turtle pond	2.0	0.5	72	0.94	0.86	0.71
Harris graphics	2.5	1.2	108	0.69	0.77	0.62
Keefe's barn	5.0	0.9	174	0.54	0.58	0.63
Condos	5.2	2.0	135	0.54	0.60	0.61
Windmill	5.8	1.0	152	0.95	0.85	0.59
Route 9 & 155	6.5	0.5	163	0.60	0.65	0.79
Wednesday Hill	8.0	1.8	191	0.54	0.50	0.68
Mill & Bartlett	8.5	0.4	212	0.62	0.65	0.70
Bunker creek	10.0	1.0	192	0.67	0.73	0.63
Wagon hill	10.0	1.0	270	0.70	0.65	0.55
White's	30.0	0.7	280	0.67	0.70	0.58

^a Niche indices based on understory cover (β_s), proximity to cover (β_c) and forage use (β_f)

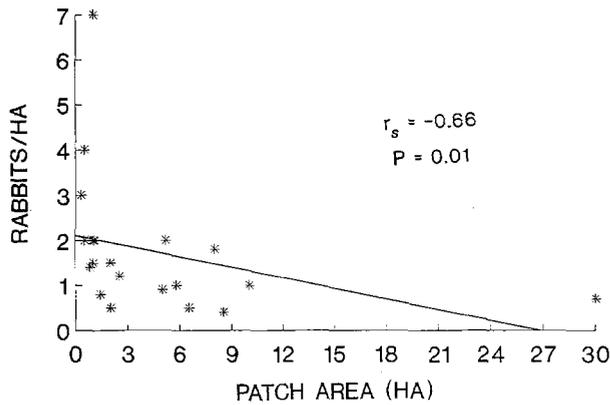


Fig. 1. Relationship between rabbit density and habitat patch size

Table 2. Average (and standard deviation) morphological characteristics of New England cottontails captured on small (≤ 2.5 ha) and large (≥ 5.0 ha) patches of habitat

Trait	Males		Females	
	Small	Large	Small	Large
Body mass (g)	955.6 ^a (99.0)	1039.0 (62.5)	1022.9 ^a (104.7)	1139.2 (71.5)
Hind-foot length (mm)	94.3 (4.9)	95.4 (2.6)	94.6 (3.1)	95.6 (3.0)
Mass ÷ hind-foot length	10.1 ^a (0.8)	10.9 (0.6)	10.8 ^a (1.1)	11.9 (0.9)
Sample size	13	20	10	9

^a Traits within a sex are different ($P < 0.05$)

$P = 0.010$; x condition index = 10.9, $z = -2.67$, $P = 0.008$) (Table 2). Body masses and condition indices also were less among females on small patches (\bar{x} mass = 1022.9 g and \bar{x} condition index = 10.8) than on large patches (\bar{x} mass = 1139.2 g, $z = 2.33$, $P = 0.020$ and x condition index = 11.9, $z = 2.00$, $P = 0.046$). Hind-foot lengths did not vary between patches for either sex ($z \leq -1.41$, $P \geq 0.160$); however, this technique may lack sensitivity for distinguishing age classes after rabbits are 3–4 months old (Bothma et al. 1972).

Habitat-use patterns

Pellet distributions on large patches indicated that rabbits generally used sites with dense understory cover (> 50000 stem-cover units/ha) more and sites with sparse cover less in relation to availability (Fig. 2). Rabbits on large patches also used sites in close proximity to cover (< 2 m) more and sites distant from cover (> 5 m) less than expected (Fig. 3). On small patches, rabbits exhibited a more generalized use of habitat relative to understory density (Fig. 2) and proximity to cover (Fig. 3), and these differences are reflected in larger habitat-niche indices (β_s : mean of small patches = 0.81 versus mean of large patches = 0.65, $z = -2.75$, $P = 0.006$; β_c : mean of small patches = 0.79 versus mean of large patches =

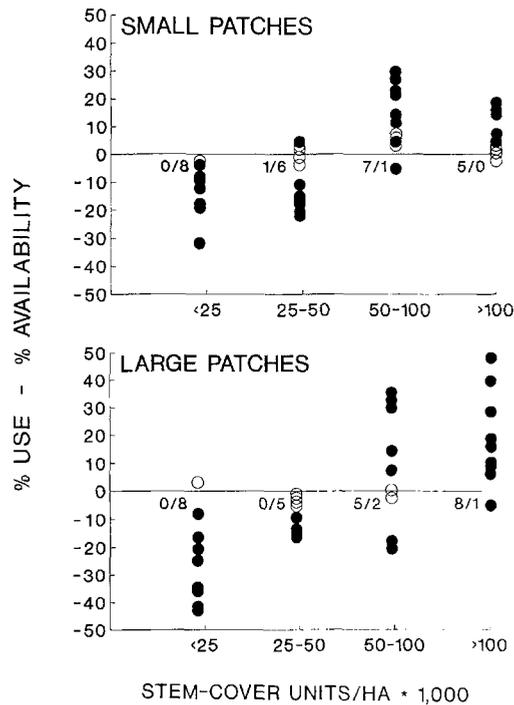


Fig. 2. Habitat selection by New England cottontails on 12 small (≤ 2.5 ha) and nine large (≥ 5.0 ha) patches. Selection was based on fecal pellet distributions in relation to understory density [stem-over units = deciduous stems + (3* coniferous stems)]. Filled circles indicate use that differed from expected ($P < 0.05$) and the numerals associated with a column summarize the number of patches where use was significantly greater or less than expected (i.e., +/-)

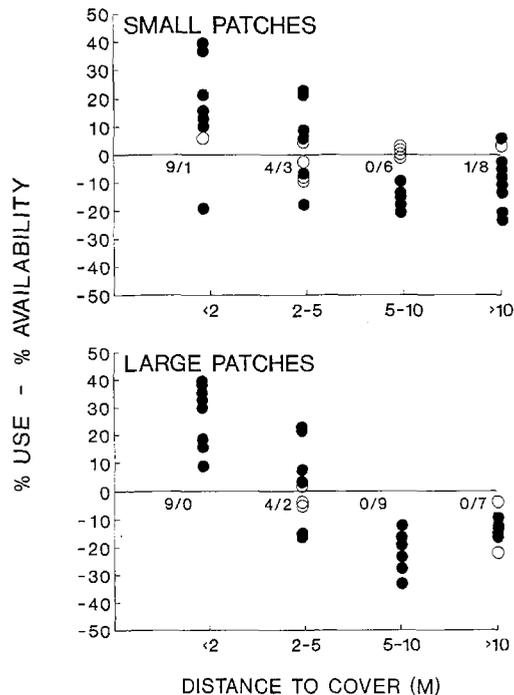


Fig. 3. Habitat selection by New England cottontails based on fecal pellet distributions in relation to distance from a clump of vegetation ≥ 1 m² that provided at least 50% visual obstruction. Filled circles indicate use that differed from expected ($P < 0.05$) and the numerals associated with a column summarize the number of patches where use was significantly greater or less than expected (i.e., +/-)

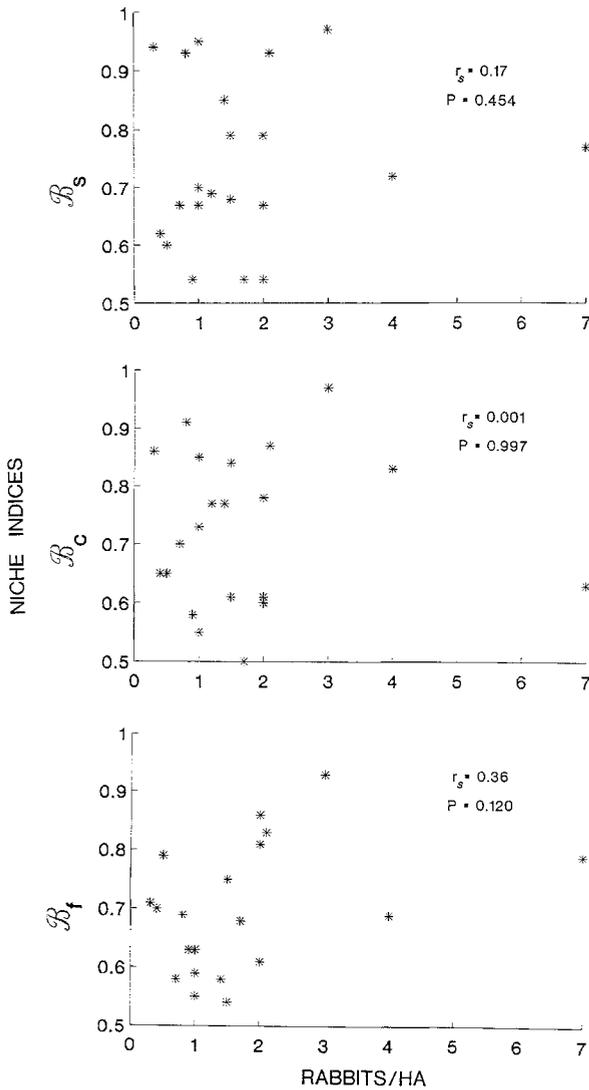


Fig. 4. Spearman-rank correlations between rabbit density and habitat (β_s and β_c) and food (β_f) niche indices

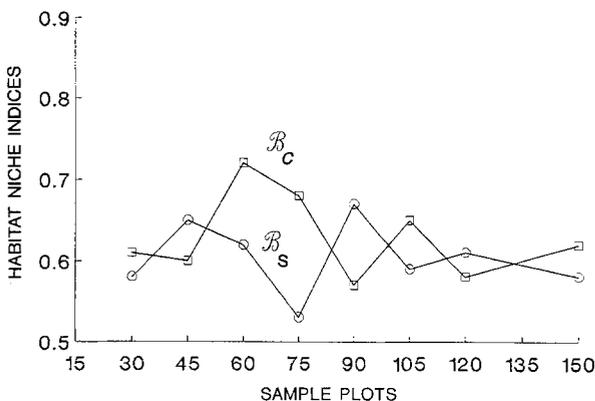


Fig. 5. Relationships between mean habitat-niche indices and number of habitat plots subsampled from large patches occupied by New England cottontails

0.66, $z = -2.17$, $P = 0.030$) (Table 1). There was no correlation between rabbit density and either habitat-niche index (Fig. 4). We also examined the relationship between the number of plots used to sample habitat-niche indices to determine if sample size influenced these pa-

rameters. The resulting correlations were inconsistent (β_s : $r = -0.57$, $P = 0.009$; β_c : $r = -0.38$, $P = 0.088$). Next, habitat-niche indices were calculated from subsamples (30–150 plots) taken from the nine large patches. These analyses did not reveal any consistent association between sampling size and niche indices (Fig. 5); therefore, we believe the niche indices did reflect actual selection patterns.

Forage-use patterns

Diet-niche indices indicated that rabbits on large patches were not more specialized (mean $\beta_f = 0.64$) than those occupying small patches (mean $\beta_f = 0.73$, $z = -1.81$, $P = 0.070$) (Table 1), and there was no correlation between rabbit densities and diet-niche indices (Fig. 4). However, rabbits on small patches did consume available forage more intensively and lower quality food more often, as indicated by a larger proportion of twigs that had a diameter at the point of browsing of ≥ 3 mm (31% versus 20% on large patches, $X^2 = 9.87$, $P < 0.005$). The percentage of plots with bark girdling also was higher on small (12.4%) than on large patches (2.1%, $X^2 = 14.2$, $P < 0.001$). During 1992, rabbits on small patches ($n = 7$) exhibited no selection among foraging sites relative to proximity to cover ($X^2 = 2.4$, $P > 0.50$), whereas differences were detected on large patches ($n = 7$, $X^2 = 270.2$, $P < 0.001$) with rabbits foraging more often within 5 m of cover (77% of foraging sites versus 48% on small patches) and less often > 5 m from cover than expected by the availability of these sites ($P < 0.05$).

Rabbit survival

Survival was monitored among 19 individuals on 15 small patches and 19 on 13 large patches. The pooled survival rate among rabbits on small patches was lower (0.35, 95% confidence interval = 0.16–0.74) than among rabbits on large patches (0.69, 95% confidence interval = 0.50–0.96, $z = 1.910$, $P = 0.028$). Nine of 10 verified mortalities on small patches and four of five mortalities on large patches were attributed to predators, primarily coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*).

Discussion

Previous research among insular populations of mammals has attributed niche expansion to a reduction in competition and predation (Cameron 1964; Grant 1972; Crowell 1973; Clough 1987), or to spillover of a population from preferred habitats into marginal habitats because dispersal was prevented (Grant 1969; Crowell 1983). In our study, we excluded patches that were occupied by lagomorphs other than New England cottontails. Additionally, all patches were surrounded by habitats that could have been used by predators while foraging or traveling between patches. Predators were the major mortality factor among all patches. Therefore, niche

expansion among New England cottontails was not a result of competitive release or relaxation of predator pressure.

Density may partly explain the differences in resource-use patterns among habitat patches. Although there was no correlation between rabbit density and niche indices, density was correlated with patch size. High densities were achieved with just one rabbit on very small patches (<0.5 ha). As a result, per capita resource abundance was probably less among small patches. Rabbits were reluctant to emigrate from small patches; however, we did detect movement to neighboring patches on several occasions. These movements by three rabbits occurred during late March and April, and may have been associated with reproduction, as well as food scarcity. All rabbits returned to their home patch within several days, perhaps in response to agonistic encounters with residents of these patches (Boutin 1984).

Recent studies among a variety of taxa have revealed that foraging behavior is not only motivated by maximizing nutrient acquisition, but also by predator avoidance (see review by Lima and Dill 1990). Among free-ranging vertebrates, these conflicting demands on fitness may result in individuals selecting sites where predation risks are low even if foraging opportunities are limited (Edwards 1983; Lima et al. 1985; Bland and Temple 1990). Physical condition, however, may mediate this response (McNamara and Houston 1987), and individuals may forage in sites with high risk of predation if they are under nutritional stress (Magnhagen 1988; Sweitzer and Berger 1992). We suggest that rabbits on small patches altered their foraging strategy in an effort to sustain physical condition and limit the loss of body mass. The subsequent increased predation rates among these rabbits, therefore, should be viewed as a consequence of habitat fragmentation.

Skewed sex ratios (or single occupant) and low survival among rabbits on small patches may effectively prevent reproduction from occurring on these sites. As a result, small patches should be viewed as sink habitats (Lidicker 1975; Van Horne 1982). Because of the high mortality rates of rabbits in small patches, these habitats are undoubtedly reliant on frequent colonization by juveniles dispersing from larger patches. Therefore, local populations of New England cottontails are likely to be extirpated if large (source) patches are fragmented or reduced to the size of sink habitats.

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