

# Community structure of snakes in a human-dominated landscape

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## Abstract

We studied occupancy, species richness, abundance, and size distributions of snakes on habitat patches that ranged from 0.2 to 120 ha within a landscape undergoing substantial land-use changes. Additionally, we examined the role of intraguild predation in structuring snake communities by equipping five racers (*Coluber constrictor*, the largest snake in our study area) with transmitters, and then compared the abundance of smaller snakes within areas of intensive (75% isopleth home range) and limited activity (outside of 75% isopleth) by racers. As expected, small patches (< 1.5 ha) often were vacant or occupied by only one species (garter snakes, *Thamnophis sirtalis*). Species richness was greatest on large patches, and snakes also tended to be more abundant on large patches. Counter to our expectations, the proportion of large-bodied individuals on small patches was greater. The distribution of small-bodied snakes on one large patch may have been affected by racers because the proportion of small snakes was less in areas intensively used by racers. Additionally, the abundance of the most generalist species in our study (garter snakes) was less in areas of intensive use by racers. In the northeastern United States, populations from a variety of taxonomic groups (including insects, migratory songbirds, mammals, and snakes) are rapidly declining in response to the loss of early-successional habitats. Our study lends support to current initiatives that recommend restoration and maintenance of parcels of early-successional habitats to sustain regional biological diversity. © 2001 Elsevier Science Ltd. All rights reserved.

**Keywords:** Early-successional habitat; Fragmentation; Land-use changes; Reptiles; Snakes

## 1. Introduction

Since the development of the theory of island biogeography (MacArthur and Wilson, 1963, 1967) and its application to mainland systems (e.g. Harris, 1984), habitat loss and fragmentation have been implicated in affecting a number of demographic and community parameters among animal populations (Mühlenberg and Werres, 1983; Mader, 1984; Sarre, 1998). Although small patches typically contain few species (e.g. Klein, 1989), they may be characterized by a greater density of individuals than larger patches of similar habitat (Barbour and Litvaitis, 1993; Krohne and Hoch, 1999). Individuals on smaller fragments also may exhibit differences in body sizes (Klein, 1989), especially as a consequence of limited resources (Barbour and Litvaitis, 1993). Fragmentation also may result in the elimination of large predators because of their area requirements (Soulé et al., 1988), and greater mortality rates asso-

ciated with landscape modifications (e.g. roads) and more frequent encounters with humans (Litvaitis et al., 1996). As a result, populations of small predators may increase after being released from intraguild predation and competition (Polis et al., 1989; Palomares et al., 1995; Crooks and Soulé, 1999).

Responses by avian (e.g. Bayne and Hobson, 1997; Burke and Nol, 1998) and mammalian (e.g. Barbour and Litvaitis, 1993; Krohne and Hoch, 1999) populations to habitat fragmentation have received considerable attention. However, the effects of fragmentation on reptiles have not been investigated as extensively (exceptions include Shine and Fitzgerald, 1996; Cunningham and Moritz, 1997; Sarre, 1998). The consequences of habitat loss and fragmentation on reptiles are varied. Among species that are unable to traverse the matrix surrounding remnant patches of habitat, reduced fitness (inbreeding depression) has been detected (Madsen et al., 1996; Cunningham and Moritz, 1997). Other species may be able to persist in modified landscapes by avoiding encounters with humans (Shine and Fitzgerald, 1996).

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Snakes in particular may be suitable model organisms to investigate certain ecological questions (Shine and Bonnet, 2000), including responses to habitat fragmentation, because of their specific habitat requirements (Reinert, 1993), thermal constraints (Peterson et al., 1993), and limited mobility (Fitch and Shirer, 1971) in comparison to many other vertebrate taxa. Yet, we do not know of any investigation that examined how snake communities responded to extensive landscape modifications that are associated with expanding human populations. Therefore, we examined how populations of snakes responded to fragmentation by comparing species richness, abundance, size distributions, and the role of intraguild predation among populations of snakes on patches of early successional habitat that differed in size. Based on studies of other taxa, we predicted the following outcomes: (1) on small patches, occupancy rates by snakes would be less consistent, species richness would be less, there would be a greater proportion of small-bodied snakes, and the abundance of snakes would be greater than on large patches; (2) on large patches where large snakes (potential predators of small snakes) were present, the abundance of small-bodied snakes would be less in areas where large snakes concentrated their activity than in areas of limited activity.

## 2. Methods

### 2.1. Description of study area

We restricted our investigation to early successional habitats because these habitats are among the most productive for many of the snakes we were likely to encounter (Fitch, 1999). Our investigation was conducted within ca. 700-km<sup>2</sup> of Strafford County in southeastern New Hampshire (ca. 43°07' N, 71°00' W). Like many developing areas in the northeastern United States, Strafford County is presently characterized by a mosaic of forests, farms, and residential or industrial areas. In the early 1800s, widespread clearing for agriculture reduced forest coverage in New Hampshire to <50% (Litvaitis, 1993). However, subsequent abandonment of agricultural lands in the late 1800s and early 1900s resulted in a 'successional wave' where second-growth forests dominated the region (Litvaitis, 1993). Many species that occupy early-successional habitats expanded their geographic range and became abundant during the first half of the twentieth century. By the 1960s, however, most of these lands matured into mid-successional forests and the populations of animals associated with early successional habitats retracted and rapidly declined (Litvaitis, 1993).

Although New Hampshire is now the second most forested state in the United States (>80% forested;

Sundquist and Stevens, 1999), Strafford County is changing rapidly. Developed lands in this county increased to 27% of the area by 1983 (Befort et al., 1987), and human-population growth and forest fragmentation have accelerated (Vogelmann, 1995). New Hampshire currently has the fastest growing human population (increased by almost 7% from 1990 to 1998) in the northeastern United States, and much of this growth has been concentrated in the southeastern portion of the state (Sundquist and Stevens, 1999). Remaining patches of early-successional habitats are now small and patchily distributed (Litvaitis and Villafeurte, 1996).

We sampled early-successional habitats that ranged from 0.2–120 ha, including idle agricultural lands, edges of industrial sites, and powerline corridors. Small patches were consistently associated with intense habitat modifications (especially highway corridors). All patches were dominated by grasses, forbs (primarily goldenrod [*Solidago* spp.], milkweed [*Asclepias* sp.], vetch [*Vicia* spp.], Queen Anne's lace [*Daucus carota*], and cinquefoil [*Potentilla* spp.]), and low shrubs. Common shrub species included multiflora rose (*Rosa multiflora*), barberry (*Berberis* spp.), autumn olive (*Elaeagnus umbellata*), steplebush (*Spirea* spp.), blueberry (*Vaccinium* spp.), and common juniper (*Juniperus communis*).

### 2.2. Sampling snake communities

Eleven species of snakes are found in New Hampshire (Taylor, 1993), but eastern hognose snakes (*Heterodon platirhinos*) and timber rattlesnakes (*Crotalus horridus*) lacked confirmed sightings in our study area. Two of the other nine species (ringneck snakes [*Diadophis punctatus*] and water snakes [*Nerodia sipedon*]) were not considered common in the upland, early-successional habitats we sampled (Conant and Collins, 1991). Therefore, we based patch-size classes (small, intermediate, large) on home-range estimates of the species we were most likely to encounter. The two largest species, racer (*Coluber constrictor*) and milk snake (*Lampropeltis triangulum*), have home ranges estimated at 10–20 ha (Fitch, 1963; Fitch and Fleet, 1970; Plummer and Congdon, 1994). Consequently, we considered all patches >10 ha to be large. Home ranges of other snakes in the study area (e.g. brown [*Storeria dekayi*] and redbelly [*S. occipitamaculata*]) are typically <1.5 ha (Freedman and Catling, 1979; Semlitsch and Moran, 1984), so we considered patches <1.5 ha to be small. Those between 1.5 and 10 ha made up the intermediate-size class. Patches were delineated by dissimilar habitats (forest, water, residential) or non-habitat features (e.g. roads), and size was estimated from aerial photos or by perimeter pacing in the field.

We used sheets of black plastic (1.5×3.0 m×0.1 mm) pinned to the ground to sample snake populations

because this method was efficient and apparently less biased than known alternatives to capturing snakes (Kjøss and Litvaitis, 2001). Essentially, snakes congregated under these sheets during cool mornings and evenings and we were able to capture them by hand during routine checks. Sheets ( $n \approx 350$ ) were distributed among suitable locations in 1998, whereas in 1999, sheets ( $n \approx 400$ ) were placed 20–40 m apart along transects on each patch. On small and intermediate-sized patches, transects ran the lengths of the patches. On large patches, transects were placed in clusters. The area covered by these transects was roughly equivalent to small and intermediate-sized patches in an effort to increase sampling efficiency and to avoid habitat features that were only present on large patches (e.g. ponds and groves of trees). Density varied from 0.75–10 sheets/ha, with highest densities on small patches. Each sheet was checked a total of six times during both field seasons: three times during morning hours (between sunrise and 09:00) and three times in the evenings (between 16:00 and sunset). The distribution of sheet checks was scheduled among the three size classes of patches to avoid any temporal bias associated with high capture rates that occurred in the early portion of the field season (Kjøss and Litvaitis, 2001). Captured snakes were identified, weighed, measured (snout-to-vent length, SVL), and released. In 1999, all captured snakes were marked by clipping two ventral scutes. In 1999, we also characterized the habitat associated with each sheet by sampling features at each site that described coverage by herbaceous and woody vegetation, vegetation height, canopy closure, and distance to nearest road and habitat edge (Kjøss, 2000).

### 2.3. Occupancy, species richness, abundance, and size distributions

We examined the presence/absence of snakes on 38 patches (27 small, 7 intermediate, and 4 large) in 1998 and 22 patches (11 small, 8 intermediate, and 3 large) in 1999. Among occupied patches, the average number of species captured was calculated for each of the three size classes of habitat patches. To estimate abundance of snakes on each occupied patch, we initially used a mark-recapture estimator (Schnabel, 1938, method; Krebs, 1999). However, recapture rates were low ( $< 10\%$ ) and this resulted in very imprecise estimates. Therefore, we calculated an index of abundance based on the number of snakes caught per unit effort, where effort was the number of sheets on a patch multiplied by the number of times those sheets were checked. This index was then standardized to yield captures per 100 sheet checks. Because of the low recapture rates, we included all captures in our analyses. We used a Kruskal-Wallis test (Zar, 1999) to compare indices of abundance of snakes among patches in the three size classes.

We also tallied the number of individuals per SVL-size class ( $\leq 20$ , 21–30, 31–40, 41–50,  $> 50$  cm) on each patch and used a  $\chi^2$  test of independence (Zar, 1999) to compare size distributions among size classes of patches. Prior to all analyses, we excluded all brown and redbelly snakes  $< 10$  cm SVL and all garter snakes (*Thamnophis sirtalis*)  $< 20$  cm SVL because we considered these to be young-of-the-year (Blanchard, 1937; Wright and Wright, 1957; Conant and Collins, 1991). On several patches, the abundance of neonates would have overwhelmed any size and abundance comparisons we made.

### 2.4. Implications of intraguild predation

In fragmented landscapes, the elimination of large predators may allow the abundance of subordinate predators to increase if the large predators, at least occasionally, prey on the smaller predators (i.e. intraguild predation; Polis et al., 1989). The subsequent increase in populations of small predators (mesopredator release; sensu Soulé et al., 1988) may reduce the abundance and diversity of prey. To investigate the potential effects of intraguild predation on snake community composition, we used radio telemetry to monitor movements of racers on a single large patch (ca. 35 ha). We expected that racers, as the largest predator in our guild of snakes, would affect the local distribution and abundance of smaller-bodied snakes such that these snakes would be less abundant in areas frequently occupied by racers.

Five adult racers (4 males and 1 female, 91–130 cm SVL) were captured between May and July 1999. A transmitter (model SM1, AVM Instruments, Livermore, California, USA; 4 or 8 g with a 15-cm antenna) was surgically implanted into each racer by a cooperating veterinarian using the procedures described by Reinert and Cundall (1982). Individuals were monitored for 5–18 weeks and locations were recorded up to two times each day. Locations were marked, and the latitude and longitude of each were obtained with a global-positioning system receiver. The home range of each racer was estimated using the minimum convex-polygon method (Mohr, 1947) in conjunction with the program CALHOME (Kie et al., 1996). We considered that the 75% isopleth of each home range represented an area of intensive activity. This isopleth was the minimum area encompassed by a convex polygon that included 75% of the telemetry locations of an individual snake, and therefore, excluded areas that were infrequently visited. We considered areas outside of the 75% isopleths to be areas of limited activity by racers. We then compared the locations of cover sheets on this patch ( $n=63$ ) with respect to the 75% isopleth home range of each racer and sampled the microhabitat at each sheet using the procedures described in Kjøss (2000). Habitat features were compared between limited and intensive-use areas

Table 1

Snakes captured on 15 patches of early successional habitat in southeastern New Hampshire during 1998 and 1999 (neonates were not included)

Patch-size class	Garter	Brown	Redbelly	Milk	Racer	Green	Ribbon
> 10 ha ( $n = 3$ )	313	145	85	11	5	0	2
1.5–10 ha ( $n = 5$ )	78	7	6	3	0	1	0
< 1.5 ha ( $n = 7$ )	19	0	0	0	0	0	0

with a non-parametric Mann-Whitney test (Zar, 1999). We summarized the number of snakes caught by size classes in the intensive and limited-use areas. Finally, sizes of the most common species (garter snakes) captured in the two areas were compared with a Mann-Whitney test (Zar, 1999).

### 3. Results

#### 3.1. Occupancy, species richness, relative abundance, and size distributions

In both years, large patches had a higher percentage of occupancy (both years: 100%) than intermediate (1998: 88%, 1999: 75%) or small patches (1998: 11%, 1999: 64%). All remaining comparisons were based on the 15 occupied patches (large = 3, intermediate = 5, and small = 7) that were sampled in both years. We pooled data collected in both years.

We captured seven species (garter, brown, redbelly, milk, racer, smooth green [*Liochlorophis vernalis*], and ribbon [*Thamnophis sauritus*]; Table 1). Large patches contained more species ( $\bar{x} = 4.2$ ) than did intermediate ( $\bar{x} = 2.1$ ) or small patches ( $\bar{x} = 1$ ). In both years, we found only one species (garter snakes) on small patches. We recorded 675 captures (excluding neonates) on the occupied patches (small = 19, intermediate = 95, and large patches = 561; Table 1). Abundance of all species combined tended to be greater among large patches ( $\bar{x} = 20.6$  snakes/100 sheet checks), than among intermediate ( $\bar{x} = 12.3$ ), or small patches ( $\bar{x} = 9.4$ ). Although this difference was not significant (Kruskal–Wallis test statistic = 2.9,  $P = 0.235$ ), the limited number of patches sampled may have resulted in low statistical power. The abundance of the most frequently captured species, garter snakes, did not vary with patch size (large patches:  $\bar{x} = 11.0$ , intermediate patches:  $\bar{x} = 10.3$ , and small patches:  $\bar{x} = 9.4$  garter snakes/100 sheet checks; Kruskal–Wallis test statistic = 0.305,  $P = 0.86$ ).

Differences in size distributions of snakes among size classes of patches were detected ( $\chi^2 = 32.5$ , 8 d.f.,  $P < 0.0001$ ; Fig. 1). Almost half (44%) of the  $\chi^2$  statistic was attributed to the cell for snakes with a 41–50 cm SVL on small patches, indicating that large-bodied individuals represented a greater proportion of the snakes on small patches (Fig. 1). The pattern weakened, but persisted when restricted to garter snakes ( $\chi^2 = 11.9$ ,

6 d.f.,  $P = 0.064$ ). This was counter to our expectation that we would find more smaller-bodied individuals on small patches.

#### 3.2. Implications of intraguild predation

We recorded an average of 57 (range = 25–84) locations for each racer, and the mean 75% isopleth home range was 5.6 ha (range = 1.5–12.2 ha). Thirty-two sheets were within these intensive used areas, and 31 sheets were in areas of limited activity. We found a greater proportion of large-bodied individuals in areas of intensive use (Fig. 2). The most abundant species, garter snakes, was less abundant in the intensive-use areas (Table 2), and the average size of garter snakes was greater in areas of intensive activity ( $\bar{x}$  SVL = 61.4 cm, S.D. = 11.0,  $n = 7$ ) than in areas of limited activity by racers ( $\bar{x}$  SVL = 44.6 cm, S.D. = 14.2 cm,  $n = 14$ ; Mann–Whitney U statistic = 81.0,  $p = 0.017$ ). Too few individuals of other species were captured to make such comparisons. Microhabitat features also varied between these areas, where coverage by forbs was greater (Mann–Whitney U test statistic = 811,  $P < 0.0001$ ) and coverage by woody vegetation was less (Mann–Whitney U test statistic = 226,  $P < 0.0001$ ) among sheets in areas of intensive activity than among sheets in areas of limited activity by racers.

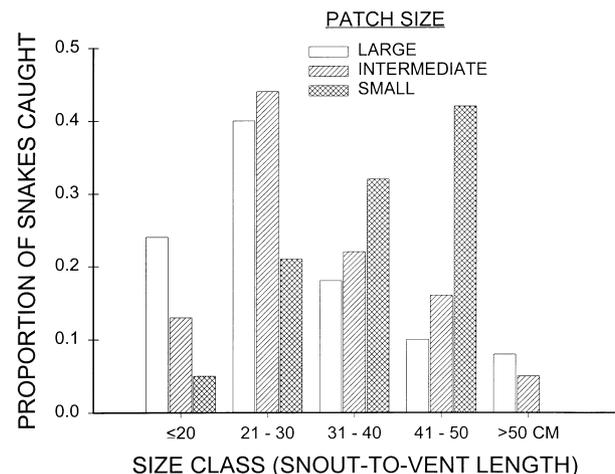


Fig. 1. Proportions of snakes captured on three large ( $n_{\text{snakes}} = 561$ ), five intermediate ( $n_{\text{snakes}} = 95$ ), and seven small ( $n_{\text{snakes}} = 19$ ) patches of early successional habitats in southeastern New Hampshire during 1998 and 1999. Neonates were not included.

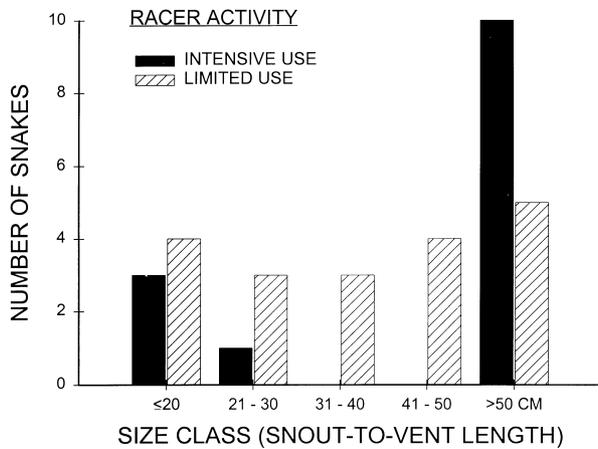


Fig. 2. Size-class distributions of snakes in areas of intensive (75% isopleth home range) and limited use (outside of 75% isopleth home range) by racers in southern New Hampshire, 1999. Neonates and racers were not included.

Table 2

Number and indices of abundance of snakes captured in areas of intensive and limited use by racers in New Hampshire, 1999 (neonates were not included)

Activity level	Number caught	Index of abundance (snakes captured/100 sheet checks)
<i>Intensive use</i>		
Brown	0	0.0
Garter	7	3.6
Milk	3	1.6
Redbelly	4	2.1
<i>Limited use</i>		
Brown	1	0.5
Garter	14	7.5
Milk	0	0.0
Redbelly	4	2.2

## 4. Discussion

### 4.1. Effects of habitat fragmentation

In accordance with the species-area hypothesis (MacArthur and Wilson, 1967), our results supported the predictions that populations on small patches would be volatile and characterized by few species relative to larger patches. We did not expect to find milk snakes and racers on small patches given the area requirements of these large species. However, the only snakes found on small patches (garter snakes) were not the smallest-bodied species encountered during our study. The lack of the smallest species (brown and redbelly snakes) was unexpected. To investigate this outcome, we compared habitat features between small patches sampled in 1999 and intermediate and large patches where we captured brown and redbelly snakes. Small patches were characterized by lower vegetation (mean lowest vegetation tier on small patches = 11.0 cm vs. 17.7 cm on inter-

mediate or large patches; Mann-Whitney U test statistic = 6.5,  $P=0.008$ ). This was likely a result of the frequent mowing that occurred at these sites (all small patches were associated with road corridors) and such disturbances may have rendered these sites less suitable for smaller snakes. Mowing may have reduced soil moisture, making these patches unsuitable to redbelly snakes that occupy a variety of moist, upland habitats (Klemens, 1993). Additionally, we speculated that frequent mowing reduced the diversity of vegetation and limited the abundance of potential prey of snakes that respond to ground-level moisture, especially gastropods. This conjecture was supported by a greater proportion of garter snakes (< 30 cm SVL) captured on small patches to be in poor physical condition. Physical condition was based on a regression of body weight to snout-vent-length (both log transformed, Weatherhead and Brown, 1996). Residuals were used as the index, where snakes with a positive regression residual were considered to be in good condition and those with a negative residual were considered to be in poor condition. We found that 77% of the garter snakes ( $n=14$ ) on small patches were in poor condition compared to 44% of garter snakes ( $n=177$ ) on intermediate and large-sized patches.

Garter snakes were the only species found among all occupied patches that we sampled in the two years of our study. Because garter snakes are extreme generalists (Wright and Wright, 1957; Rossman et al., 1996), they may not be as sensitive to habitat alterations. Habitat generalism is considered to be an important characteristic in determining the ability of a species to remain in an area following fragmentation (Sarre et al., 1995; Shine and Fitzgerald, 1996; Sarre, 1998). Blaesing (1979) found garter snakes inhabiting a semi-disturbed area to be at least as successful as those inhabiting relatively undisturbed areas and attributed this success to either decreases in populations of raptors in disturbed areas or to the ability of garter snakes to adjust to habitat modifications.

Several other habitat features also may have affected the diversity of snakes on small patches. For example, we found that sheets on small patches were closer to forest edges ( $\bar{x}=10.7$  m) than sheets on larger patches ( $\bar{x}=23.5$  m; Mann-Whitney U test statistic = 12.0,  $P=0.035$ ). Close proximity to forest edges may have increased exposure of snakes to potential predators, including raccoons (*Procyon lotor*) and raptors. Anecdotally, we detected raccoon tracks on sheets < 15 m from forest edges on the only patch in the intermediate-size class that had just one species (garter snakes).

Not surprisingly, sheets on small patches also were closer to roads ( $\bar{x}=13.6$  m) than sheets on larger patches where brown and redbelly snakes were captured ( $\bar{x}>30$  m, Mann-Whitney U test statistic = 1.0,  $P=0.001$ ). Roads are known to be effective barriers in

the dispersal of amphibians (Reh and Seitz, 1990) and mammals (Mader, 1984). Although we encountered few road-killed snakes during our study, snakes are often found dead on roads (Dodd et al., 1989; Bonnet et al., 1999). Furthermore, we did not recapture any snakes on small patches. So it is possible that mortality of snakes was greater on and adjacent to the small patches that we sampled. As a result, these habitats may function as population sinks (Pulliam, 1988).

Our results also support the hypothesis that predation by large snakes on small-bodied snakes affects the composition of snake communities. In areas of intensive use by racers, we captured more snakes (especially garters) in the largest size class (> 50 cm SVL), suggesting that these individuals escaped predation by larger snakes. Rosen (1991) found that garter snakes were the third most common food item in the stomachs of 28 Michigan racers. It is likely that the suitability of garter snakes as prey of racers is size dependent. In laboratory experiments, Weldon (1982) observed that garter snakes reacted strongly to the odor of racers in comparison to the odor of non-ophiophagous snakes. We must acknowledge, however, that there were other predators in our study area that likely preyed upon snakes, including raptors (e.g. *Buteo jamaicensis*) and generalist carnivores (e.g. *Canis latrans*). These predators are more wide-ranging than racers, thus making it difficult to assess their influence on a single patch.

#### 4.2. Implications to snake conservation and regional biodiversity

Populations of milk snakes and racers are declining in portions of the northeastern United States (Klemens, 1993; Vickery, 1999). In our study, racers utilized large areas (average 100% isopleth home ranges = 14.7 ha; range = 9.0–31.4 ha), and >95% of the locations of marked racers were associated with early-successional habitats or structures that bordered these habitats (e.g. rock walls). This explains their absence from small and intermediate-sized patches in our study area, and likely has contributed to their regional decline.

Although it is difficult to estimate the proportion of the region that was in early successional or shrub-dominated habitats prior to widespread human alterations, it is evident that the current abundance of these habitats is not sufficient to maintain the diverse species assemblage that is dependent on them. Early successional and shrub-dominated habitats are among the most rapidly declining communities in the northeastern United States (Vickery et al., 1995; Litvaitis et al., 1999). In New Hampshire, the area in seedling/sapling-sized forests declined from 344,000 ha in 1973 to approximately 159,000 ha in 1997 (Litvaitis et al., 1999). Large patches (> 10 ha) are especially rare (Litvaitis and Villafuerte, 1996; Fig. 1). We suspect that these

patches are essential to long-term survival of racers and other species in the region. As the second-growth forests that dominate the region mature, natural disturbances (e.g. wind, ice storms, defoliating insects) will generate small openings that allow understory vegetation to develop within the canopy gaps. However, we doubt that the addition of such patches will be sufficient to sustain all species that occupy early-successional habitats.

In pre-Columbian landscapes, small patches of early-successional habitat were probably common in mature forests. In some portions of the northeastern United States, especially areas near the Atlantic coast, large-scale disturbances (e.g., fires set by aboriginal peoples) also generated extensive (> 50 ha) grasslands, stands of early successional forest, or shrub-dominated habitats (including pitch pine [*Pinus rigida*] and scrub oak [*Quercus ilicifolia*] barrens; see Litvaitis et al., 1999 for a review). Wide-ranging species (including racers) likely moved among a number of small openings to satisfy their prey needs while other individuals occupied a single, large patch. In contemporary landscapes, canopy gaps are embedded in a habitat matrix that is very different from pristine conditions and large-scale disturbances have been substantially reduced or eliminated in space and time. Species with large-area requirements must traverse expanses of unsuitable habitat where generalist predators (e.g. raccoons) currently are abundant (Oehler and Litvaitis, 1996). Additionally, wide-ranging species frequently encounter and cross roads while moving between patches of suitable habitat. Relative to this point, it is worth noting that the only racer that we encountered away from the patch where we monitored movements of transmitter-equipped racers was an individual that we found dead on a road. Based on the surrounding habitat, we speculated that this snake was moving between small patches of early successional habitat that were associated with gravel mines on either side of the road. We did not detect any road crossings by transmitter-equipped racers that we monitored on a large patch.

The limitations of small patches of early successional habitats within human-dominated landscapes are not restricted to large snakes. For example, New England cottontails (*Sylvilagus transitionalis*) that occupied small patches (< 3 ha) in our study area encountered food shortages and were subjected to intense predation (Barbour and Litvaitis, 1993; Villafuerte et al., 1997). Long-term survival of this species would be unlikely if only small patches of habitat were present (Litvaitis and Villafuerte, 1996). Other species that require large patches of early successional and shrub-dominated habitats include golden-winged warblers (*Vermivora chrysoptera*) that do not nest in patches < 10 ha (Confer and Knapp, 1981), and buck moths (*Hemileuca maia*) that rarely persist in scrub-oak barrens < 100 ha in New England (Litvaitis et al., 1999).

We concur with recommendations made by Litvaitis et al. (1999), that efforts directed toward sustaining populations of animals that are dependent on early successional or shrub-dominated habitats be placed in the context of current land uses. In urbanized landscapes, maintaining native shrublands or creating patches of early successional stands will likely be most effective in sustaining populations of large snakes and other taxa if these habitats are clustered with similar habitats, including those that are a consequence of other land uses (e.g. powerlines corridors; Askins, 1998; Litvaitis et al., 1999). Such an approach will result in few, but large populations that are more resilient to short-term fluctuations than small populations. Patches of early successional habitat in these landscapes are likely to be fixed into place because of other land uses. As a result, consideration should be given to identifying potential dispersal corridors or positioning managed patches in relative close proximity. Fields that are taken out of agricultural production may be especially valuable because of their size and the ability to maintain them in early seral stages with minimal disturbances. Such sites also may support more diverse plant and animal communities than those generated by activities such as timber harvesting (DeGraaf et al., 1992; Litvaitis et al. 1999).

In conclusion, we advocate a response to the current limitations of early successional habitats in urbanized regions of the northeastern United States that includes the maintenance of large patches (> 10 ha) of this habitat. We acknowledge that such a recommendation may raise concerns over the issue of forest fragmentation. However, populations of many of the species that are dependent on early successional and shrub-dominated habitats have declined to levels where they are now vulnerable to regional extinctions.

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### References

Askins, R.A., 1998. Restoring forest disturbances to sustain populations of shrubland birds. *Restoration and Management Notes* 16, 166–173.  
 Barbour, M.S., Litvaitis, J.A., 1993. Niche dimensions of New England cottontails in relation to habitat patch size. *Oecologia* 95, 321–327.

Bayne, E.M., Hobson, K.A., 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11, 1418–1429.  
 Befort, W.M., Luloff, A.E., Morrone, M., 1987. Land use change: Strafford County, New Hampshire 1953–1982 (Agricultural Experiment Station Research Report 111). University of New Hampshire, Durham.  
 Blaesing, M.E., 1979. Some aspects of the ecology of the eastern garter snake (*Thamnophis sirtalis sirtalis*) in a semi-disturbed habitat in west-central Illinois. *Journal of Herpetology* 13, 177–181.  
 Blanchard, F., 1937. Data on the natural history of the red-bellied snake, *Storeria occipito-maculata* (Storer), in northern Michigan. *Copeia* 1937, 151–162.  
 Bonnet, X., Naulleau, G., Shine, R., 1999. The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* 89, 39–50.  
 Burke, D.M., Nol, E., 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *The Auk* 115, 96–104.  
 Conant, R., Collins, J.T., 1991. Reptiles and Amphibians — Eastern/Central North America. 3rd Edition. Houghton Mifflin, Boston, Massachusetts.  
 Confer, J.L., Knapp, K., 1981. Golden-winged warblers and blue-winged warblers: the relative success of a habitat specialist and generalist. *Auk* 98, 108–114.  
 Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400, 563–566.  
 Cunningham, M., Moritz, C., 1997. Genetic effects of forest fragmentation on a rainforest restricted lizard (Scincidae: *Gnypetoscincus queenslandiae*). *Biological Conservation* 83, 19–30.  
 DeGraaf, R.M., Yamasaki, M., Leak, W.B., Lanier, J.W., 1992. New England wildlife: management of forested habitats (General Technical Report NE-144). US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania.  
 Dodd Jr., C.K., Enge, K.M., Stuart, J.N., 1989. Reptiles on highways in north-central Alabama, USA. *Journal of Herpetology* 23, 197–200.  
 Fitch, H.S., 1963. Natural history of the racer *Coluber constrictor*. University of Kansas Publications. Museum of Natural History 15, 351–468.  
 Fitch, H.S., 1999. A Kansas Snake Community: Composition and Changes Over 50 Years. Krieger Publishing Company, Malabar, Florida.  
 Fitch, H.S., Fleet, R.R., 1970. Natural history of the milk snake (*Lampropeltis triangulum*) in northeastern Kansas. *Herpetologica* 26, 387–396.  
 Fitch, H.S., Shirer, W.H., 1971. A radiotelemetric study of spatial relationships in some common snakes. *Copeia* 1971, 118–128.  
 Freedman, B., Catling, P.M., 1979. Movements of sympatric species of snakes at Amherstburg, Ontario. *Canadian Field Naturalist* 93, 399–404.  
 Harris, L.D., 1984. The Fragmented Forest. The University of Chicago Press, Chicago, Illinois.  
 Kie, J.G., Baldwin, J.A., Evans, C.J., 1996. CALHOME: a program for estimating animal home ranges. *Wildlife Society Bulletin* 24, 342–344.  
 Kjoss, V.A., 2000. Community structure of snakes in a fragmented landscape. Thesis, University of New Hampshire, Durham.  
 Kjoss, V.A., Litvaitis, J.A. 2001. Comparison of two methods used to sample snake communities in early-successional habitats. *Wildlife Society Bulletin* 29 (in press).  
 Klein, B.C., 1989. Effects of forest fragmentation on dung and carrion beetles in central Amazonia. *Ecology* 70, 1715–1725.  
 Klemens, M.W. 1993. Amphibians and reptiles of Connecticut and adjacent regions. State Geological and Natural History Survey of Connecticut. Bulletin No. 112.

- Krebs, C.J., 1999. *Ecological Methodology*, 2nd Edition. Benjamin/Cummings, Menlo Park, California.
- Krohne, D.T., Hoch, G.A., 1999. Demography of *Peromyscus leucopus* populations on habitat patches: the role of dispersal. *Canadian Journal of Zoology* 77, 1247–1253.
- Litvaitis, J.A., 1993. Response of early successional vertebrates to historic changes in land use. *Conservation Biology* 7, 866–873.
- Litvaitis, J.A., Beltrán, J.F., Delibes, M., Moreno, S., Villafuerte, R., 1996. Sustaining felid populations in human-altered landscapes. *Journal of Wildlife Research* 1, 292–296.
- Litvaitis, J.A., Villafuerte, R., 1996. Factors affecting the persistence of New England cottontail metapopulations: the role of habitat management. *Wildlife Society Bulletin* 24, 686–693.
- Litvaitis, J.A., Wagner, D.L., Confer, J.L., Tarr, M.D., Snyder, E.J., 1999. Early-successional forests and shrub-dominated habitats: land-use artifact or critical community in the northeastern United States? *Northeast Wildlife* 54, 101–118.
- MacArthur, R.H., Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Mader, H.-J., 1984. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* 29, 81–96.
- Madsen, T., Stille, B., Shine, R., 1996. Inbreeding depression in an isolated population of adders *Vipera berus*. *Biological Conservation* 75, 113–118.
- Mohr, C.O., 1947. Table of equivalent populations of North American mammals. *American Midland Naturalist* 37, 223–249.
- Mühlenberg, M., Werres, W., 1983. Lebensraumverkleinerung und ihre Folgen für einzelne Tiergemeinschaften: experimentelle Untersuchungen auf einer Wiesenfläche. *Zeitschrift für Umweltschutz und Landespflege* 58, 43–50.
- Oehler, J.D., Litvaitis, J.A., 1996. The role of spatial scale in understanding responses by medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology* 74, 2070–2079.
- Palomares, F., Gaona, P., Ferreras, P., Delibes, M., 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Conservation Biology* 9, 295–305.
- Peterson, C.R., Gibson, A.R., Dorcas, M.E., 1993. Snake thermal ecology: the causes and consequences of body temperature variation. In: Seigel, R.A., Collins, J.T. (Eds.), *Snakes — Ecology and Behavior*. McGraw-Hill, New York, pp. 241–314.
- Plummer, M.V., Congdon, J.D., 1994. Radiotelemetric study of activity and movements of racers (*Coluber constrictor*) associated with a Carolina bay in South Carolina. *Copeia* 1994, 20–26.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20, 297–330.
- Pulliam, H.R., 1988. Sources, sinks and population regulation. *American Naturalist* 132, 652–661.
- Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* 54, 239–249.
- Reinert, H.K., 1993. Habitat selection in snakes. In: Seigel, R.A., Collins, J.T. (Eds.), *Snakes — Ecology and Behavior*. McGraw-Hill, New York, pp. 201–240.
- Reinert, H.K., Cundall, D., 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982, 702–705.
- Rosen, P.C., 1991. Comparative ecology and life history of the racer (*Coluber constrictor*) in Michigan. *Copeia* 1991, 897–909.
- Rossmann, D.A., Ford, N.B., Seigel, R.A., 1996. *The Garter Snakes — Evolution and Ecology*. University of Oklahoma Press, Norman.
- Sarre, S.D., 1998. Demographics and population persistence of *Gehyra variegata* (Gekkonidae) following habitat fragmentation. *Journal of Herpetology* 32, 153–162.
- Sarre, S.D., Smith, G.T., Myers, J.A., 1995. Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. *Biological Conservation* 71, 25–33.
- Schnabel, Z.E., 1938. The estimation of the total fish population of a lake. *American Mathematics Monthly* 45, 348–352.
- Semlitsch, R.D., Moran, G.B., 1984. Ecology of the redbelly snake (*Storeria occipitomaculata*) using mesic habitats in South Carolina. *American Midland Naturalist* 111, 33–40.
- Shine, R., Bonnet, X., 2000. Snakes: a new ‘model organism’ in ecological research? *Trends in Ecology and Evolution* 15, 221–222.
- Shine, R., Fitzgerald, M., 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal eastern Australia. *Biological Conservation* 76, 113–122.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinction of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2, 75–92.
- Sundquist, D., Stevens, M., 1999. *New Hampshire’s Changing Landscape — Population Growth, Land Use Conversion, and Resource Fragmentation in the Granite State*. The Society for the Protection of New Hampshire Forests, Concord, NH.
- Taylor, J.T., 1993. *The amphibians and reptiles of New Hampshire*. New Hampshire Fish and Game Department, Concord, NH.
- Vickery, P.D., 1999. Eastern racer. In: Hunter Jr., M.L., Calhoun, A.J.K., McCollough, M. (Eds.), *Maine Amphibians and Reptiles*, 2nd Edition. University of Maine Press, Orono, Maine, pp. 161–164.
- Vickery, P.D., Hunter Jr., M.L., Melvin, S., 1995. Effects of habitat area on the distribution of grassland birds in Maine. *Conservation Biology* 8, 1087–1097.
- Villafuerte, R., Litvaitis, J.A., Smith, D.F., 1997. Physiological responses by lagomorphs to resource limitations imposed by habitat fragmentation: implications to condition-sensitive predation. *Canadian Journal of Zoology* 75, 148–151.
- Vogelmann, J.E., 1995. Assessment of forest fragmentation in southern New England using remote sensing and geographic information systems technology. *Conservation Biology* 9, 439–449.
- Weatherhead, P.J., Brown, G.P., 1996. Measurement versus estimation of condition in snakes. *Canadian Journal of Zoology* 74, 1617–1621.
- Weldon, P.J., 1982. Responses to ophiophagus snakes by snakes of the genus *Thamnophis*. *Copeia* 1982, 788–794.
- Wright, A.H., Wright, A.A., 1957. *Handbook of Snakes of the United States and Canada, Volume II*. Cornell University Press, Ithaca, New York.
- Zar, J., 1999. *Biostatistical Analysis*, 4th Edition. Prentice Hall.