

**COMMUNITY STRUCTURE OF SNAKES IN A FRAGMENTED LANDSCAPE**

BY

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THESIS

Submitted to the University of New Hampshire  
in Partial Fulfillment of  
the Requirements for the Degree of

Master of Science  
in  
Natural Resources – Wildlife Ecology

May, 2000

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## ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. John Litvaitis, for his help, encouragement, patience, and trips to Young's Restaurant. Many thanks also to my thesis committee, Dr. Kim Babbitt, Dr. Chris Neefus, and Dr. Jim Taylor, for their advice.

Thanks to the following people and entities for help in and contributions to various aspects of my research: Toby Currier and Brian Gilbert (field assistance), Dr. John Means and assistants (transmitter implantation), NH Fish and Game Department, UNH Center for International Studies (conference funding), UNH Department of Natural Resources (conference funding), UNH Department of Natural Resources Office Staff, UNH Graduate School (funding), UNH Instructional Services Staff, UNH Kendall Library Staff, U.S. Fish and Wildlife Service, and all landowners whose properties were sampled.

Finally, much appreciation to all fellow graduate students at UNH and to my globally-distributed friends for countless hours of "being there"; thanks to my family in New England and Germany for their encouragement, financial support, and chocolate; and last but not least, thanks to Christopher Somers for all of the above.

V.A.K.  
Durham, New Hampshire  
March 2000

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## ABSTRACT

### COMMUNITY STRUCTURE OF SNAKES IN A FRAGMENTED LANDSCAPE

by

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Habitat fragmentation has been implicated in affecting a variety of ecological processes that may alter biological diversity. The objective of my study was to identify community parameters (e.g., species composition, size structure, and abundance) of snakes that may be sensitive to variations in size of habitat patches. Based on studies of other taxa, I expected species diversity to be less on small patches. I predicted that on small patches, there would be a higher abundance of snakes and a higher proportion of small-bodied snakes, and that snakes on small patches would show shifts in microhabitat use. I also predicted that the abundance of small-bodied snakes would be less in areas where large snakes (racers [*Coluber constrictor*]) concentrated their activity. I sampled populations of snakes on patches of early-successional habitats in southern New Hampshire in 1998 and 1999 using plastic cover sheets. Compared to trap-drift fence arrays, cover sheets sampled a lower richness but higher evenness of species and a wider range of individual sizes, were less costly and easier to use, and resulted in fewer mortalities than traps. Among the 15 occupied patches (0.2-120 ha) sampled in both years, I recorded 675 captures (not including young-of-the-year) of seven species. Small patches (<1.5 ha) were occupied by only one species, common garter snakes (*Tham-*

*nophis sirtalis*). The abundance of garter snakes did not differ among patch-size classes, but I found a greater proportion of larger individuals on small patches than on intermediate (1.5-10 ha) or large (>10 ha) patches. Moreover, garter snakes on small patches tended to have lower indices of physical condition than snakes on intermediate and large patches, possibly due to limited resources on small patches. I was unable to assess differences in microhabitat use by small snakes among patch size classes. In areas of intensive activity by racers (as determined by radio telemetry and subsequent home-range analysis), I found fewer but larger garter snakes than in areas of limited activity by racers, suggesting that predation by racers may affect the distribution of small garter snakes. The results of my study suggest that snake populations may be responding to habitat fragmentation. Additional loss of habitats and reductions in patch sizes will likely eliminate large species such as racers. Such losses in turn may alter the structure of snake communities and their prey on small patches. Habitat losses may be countered by implementing management programs that establish and maintain early-successional habitats.

## **CHAPTER 1**

### **INTRODUCTION**

One of the major factors causing change in natural communities is habitat fragmentation (Harris 1984, Saunders et al. 1991). Previously continuous biotic communities are now patchily distributed within a mosaic of agricultural fields, managed forests, and urban sprawl. Remaining patches of habitat vary in size, shape, and degree of isolation (Saunders et al. 1991). Any combination of these factors may lead to changes in abiotic properties, including changes in wind movement, increased irradiation, and greater edge-to-interior ratios (Saunders et al. 1991). Additionally, if a network of roads or railroads fragments an area, pollutants and noise will increase (Mader 1984). In response, biotic communities are changing.

#### **Changes in Species Diversity**

Ecological theory holds that small patches of habitat should harbor fewer species than larger patches of similar habitat (MacArthur and Wilson 1967). However, this species-area relationship is not consistently supported in fragmented systems. Klein (1989) found that populations of dung and carrion beetles in central Amazonia were sparser and less diverse following fragmentation of their original habitat. Similarly, Mühlenberg and Werres (1983) found a reduction of spiders and carabid beetles following a fragmentation experiment. In contrast, other studies have reported an increase in the diversity of carabid populations in fragmented forest patches following increased isolation and reduction of patch size (Mader 1981, 1984). This increase was

attributed to an encroachment of species from surrounding agricultural areas that were able to outcompete forest species, thus reducing their population sizes and resulting in an unstable species composition (Mader 1981, 1984).

Laan and Verboom (1990) found a positive correlation between amphibian community diversity and sizes of pools that amphibians inhabited. Similarly, McCoy and Mushinsky (1994) determined that patch sizes of Florida scrub habitat were correlated with vertebrate species richness. Although these researchers found that hypothetical “archipelagoes” composed of small patches often hosted more taxa than single large patches, the conclusions were based on presence-absence data, without consideration for species distribution or abundance.

### **Abundance and Density**

A corollary of the species-area hypothesis is that smaller remnants should hold fewer individuals than large remnants. Support for this hypothesis comes from field data. Sarre (1998), for example, found a strong positive correlation between population sizes of geckos (*Gehyra variegata*) and sizes of remnant habitat patches. However, although population size may be smaller in small fragments, density of individuals may be greater on small patches (e.g., Barbour and Litvaitis 1993). Furthermore, small individuals are expected to occur at higher densities than large individuals (Peters and Wassenberg 1983).

The reduction or elimination of large predators from a landscape caused by fragmentation may result in populations of potential prey species characterized by smaller individuals living at higher densities, whereas in the presence of predators, prey populations may consist of fewer but larger individuals as a result of reduced intra-specific competition (Tonn et al. 1992). This trophic cascade effect, wherein predation

depresses consumer populations and indirectly leads to an increase in resource abundance, has been well-studied in aquatic systems (e.g., Power 1992).

A special case of a trophic cascade is proposed by the mesopredator release hypothesis (Soulé et al. 1988). The elimination of large carnivores (e.g., wolves [*Canis lupus*]) may allow populations of subordinate medium-sized carnivores (e.g., gray foxes [*Urocyon cinereoargenteus*], raccoons [*Procyon lotor*], and skunks [*Mephitis mephitis*]) to increase. In turn, these intermediate predators exert intensive predation pressure on prey species occupying remnant patches of habitat (Soulé et al. 1988, Rogers and Caro 1998, Crooks and Soulé 1999). Although this hypothesis makes intuitive sense, it has received relatively little critical evaluation (Litvaitis and Villafuerte 1996, but see Palomares et al. 1996). However, it is plausible that the mesopredator-release hypothesis may be applicable to any ecological system.

### **Variations in Body Sizes**

An increasing amount of evidence supports the notion that many species exhibit “island syndrome” following isolation from larger, mainland populations. Some taxa (e.g., bears, rodents, iguanas, and tortoises) may be represented by larger-bodied species on oceanic islands, whereas other groups (e.g. artiodactyls, bats, elephants, foxes, lagomorphs, raccoons, snakes) tend to be represented by smaller forms on islands (Case 1978). These size differences are likely evolutionary responses to initial resource conditions encountered on islands by colonizing individuals (Case 1978). Lindell and Forsman (1996), for example, found a negative relationship between adder (*Vipera berus*) densities and their growth rate on islands in the Baltic Sea, suggesting that these snakes suffered a reduction in growth rates as a result of intensive exploitative competition. In contrast, King (1989) found that populations of northern water snakes

(*Nerodia sipedon*) on islands in Lake Erie were composed of larger individuals than mainland populations of the same species, whereas common garter snakes (*Thamnophis sirtalis*) showed no difference in body sizes between island and mainland populations. Andrews (1976) found that island populations of anoline lizards (*Anolis* spp.) grew more slowly and matured later than mainland lizard populations. These differences were attributed to food resource limitations on islands.

Although oceanic islands have been separated from the mainland for long periods, it is possible that similar trends could be apparent on more recent, anthropogenically-created habitat islands. In particular, species that produce multiple generations within relatively short periods of time (e.g., many insects or small mammals) could develop such morphological symptoms. Following a fragmentation experiment, Klein (1989) found that beetles in fragments were smaller than those in surrounding contiguous areas or than those that had been found in unmanipulated patches prior to the experiment. Barbour and Litvaitis (1993) found that New England cottontail rabbits (*Sylvilagus transitionalis*) in small patches of early-successional habitat had lower body masses and condition indices than rabbits on larger patches. Survival rates of rabbits on small patches were lower than those of conspecifics on large patches. The researchers attributed these results partly to higher densities and consequently lower per capita available resources on small patches.

### **Shifts in Microhabitat Use**

Sarre (1998) found that habitat use differed substantially between geckos (*Gehyra variegata*) in large vs. small forest remnants; geckos on small patches used less variable microhabitats than conspecifics on large patches did. This species is considered to be a habitat generalist, a characteristic that may be critical in allowing it to persist following fragmentation (Sarre et al. 1995, Sarre 1998).

In contrast, Barbour and Litvaitis (1993) compared niche breadth indices of New England cottontail rabbits on small and large patches of early-successional habitat and found that rabbits on small patches exhibited larger habitat-niche indices than rabbits on large patches. This was a result of a more generalized habitat use (relative to understory stem density and proximity to cover) by rabbits on small patches; these animals also consumed lower quality food more often and foraged more intensively on available resources. The researchers attributed differences in resource-use patterns between the two habitat patch sizes to rabbit density, which was inversely correlated to patch size. Other studies (e.g., Cameron 1964) have suggested that a reduction in competition and predation can lead to niche expansion on islands.

### **Further Consequences of Fragmentation**

In the absence of colonizing populations, sink populations are more prone to localized extinctions from stochastic events (Harrison 1991). Atypical changes in environmental and climatic conditions, disease outbreaks, or unfavorable demographic conditions (such as extremely skewed sex ratios) can quickly lead to the demise of an isolated population (Harrison 1991). For example, prickly skinks (*Gnypetoscincus queenslandiae*) in forest fragments showed substantial inbreeding coefficients compared to skinks in continuous forests (Cunningham and Moritz 1997). Similarly, Madsen et al. (1996) concluded that an isolated population of adders (*Vipera berus*) in Sweden suffered from a lower degree of genetic heterozygosity and high genetic similarity among individuals, and that inbreeding depression resulted in smaller litter sizes and relatively more stillborn and deformed young. If several isolated populations experience such conditions at the same time, extinction may seriously threaten local populations.

Empirical data on white-footed mice (*Peromyscus leucopus*) support this prediction (Fahrig and Merriam 1985). These researchers found that mouse populations in isolated woodlots of Ontario had lower growth rates that made them more prone to extinction than conspecifics living in connected woodlots. A general model predicts that when immigration rates are high relative to extinction rates, turnover rate is directly related to the distance between an island and the source of colonizing species (Brown and Kodric-Brown 1977). Thus, extinction is inversely related to island size and recolonization is inversely related to inter-island distance. Support for this model comes from field studies of the distribution of arthropods among isolated plants (Brown and Kodric-Brown 1977) and pikas (*Ochotona princeps*; Smith 1974).

### **Implications of Fragmentation to Snake Ecology**

Since the development of the island biogeography theory in the 1960s (MacArthur and Wilson 1963, 1967), the issue of habitat fragmentation has received much attention (e.g., Harris 1984), particularly in regards to avian (e.g., Soulé et al. 1988), mammalian (e.g., Barbour and Litvaitis 1993), and invertebrate (e.g., Klein 1989) communities. Amphibians only recently have been considered more closely, especially in relation to forest management practices (e.g., Gibbs 1998), but reptiles largely have been overlooked (e.g., Sarre 1998). Snakes in particular have received very little attention (e.g., Lindell and Forsman 1996). However, snakes often have specific thermal (Peterson et al. 1993) and habitat requirements (Reinert 1993) and often are less mobile than birds or some mammals (Fitch and Shirer 1971); they may therefore be appropriate models to test the influence of habitat fragmentation.

In the northeastern United States, losses through increased urbanization and forest maturation have led to the decline of early-successional habitats used by a number of

species (Litvatis 1993, Askins 1998). Early-seral or disturbed habitats are dominated by forbs, grasses, and shrubs, and secondary succession has progressed less than 25 years (Kricher and Morrison 1988, Litvatis 1993). Populations of several snake species known to use this type of habitat (including racers [*Coluber constrictor*], milk snakes [*Lampropeltis triangulum*], and smooth green snakes [*Liochlorophis vernalis*]) seem to be declining in response to the loss of these habitats in New England (racers: Klemens 1993, Vickery 1999, P. Mirick, Massachusetts Division of Inland Fisheries and Wildlife, personal communication; milk snakes: Ritter 1999; smooth green snakes: Arbuckle 1999). Species such as racers and milk snakes have relatively large area requirements (Fitch 1963, Fitch and Fleet 1970) and may not be able to maintain home ranges in small fragments of habitat. Therefore, large-bodied snakes may be restricted to large patches of habitat. Small-bodied snakes (e.g. brown snakes [*Storeria dekayi*] and redbelly snakes [*S. occipitamaculata*]) with smaller area requirements may be able to better exploit smaller patches (Freedman and Catling 1979), especially in the absence of large snakes. In isolated patches, however, this may lead to resource limitations that could affect population profiles. To evaluate whether differences exist in the community structure of snakes among habitat fragments of different sizes, I sampled snake populations in patches of early-successional habitats in southern New Hampshire during 1998 and 1999.

### **Questions Addressed**

The objectives of my research were to investigate several parameters of snake communities that may be sensitive to variation in habitat patch size. Specifically, I asked the following questions.

1. Do abundance and species diversity of snakes vary with sizes of habitat

patches?

2. Does the proportion of small-bodied snakes vary with patch size?
3. Do small snakes show shifts in microhabitat use on small patches where large snakes are absent?
4. On large patches, does the presence of large snakes (e.g., racers) that prey on small snakes influence snake community structure?

### **Organization of the Following Chapters**

The following chapters were written to address these questions. Chapter 2 provides a comparison of the relative efficiency of methods used to sample snake communities in early-successional habitats. Chapter 3 considers the variation in species richness, abundance, size distributions, and microhabitat use of snakes in relation to habitat patch size.

## CHAPTER 2

### COMPARISON OF TWO METHODS USED TO SAMPLE SNAKE COMMUNITIES IN EARLY-SUCCESSIONAL HABITATS

Researchers have relied on a variety of methods to sample snake populations, including focused searches of suitable microhabitats and hibernacula (Burger and Zappalorti 1988, Rosen 1991, Weatherhead and Prior 1992), and use of funnel or box traps in combination with drift fences (Fitch 1951, Plummer and Congdon 1994, Zappalorti and Torocco 1997, Zappalorti et al. 1998). Most investigators using these methods were likely attempting to capture a subset of the snakes in an area and therefore may not have been concerned with the inherent differences in capture success associated with each method. During an investigation of snake community structure in early-successional habitats (Chapter 3), I attempted to assess the abundance, species diversity, and size distribution of snakes occupying habitat patches of different sizes. In doing so, I required a method of capture that would provide representative samples of snakes that occupied a discrete patch of habitat.

Initial field efforts indicated that focused searches provided few captures. Trap-drift fence combinations yielded more captures than focused searches, but seemed biased toward larger snakes. Therefore, I developed a sampling method similar to the shelterboards used by DeGraaf and Yamasaki (1992) to sample the distribution of redback salamanders (*Plethodon cinereus*). Shelterboards apparently simulated fallen logs used by salamanders as cover, and DeGraaf and Yamasaki (1992) reported that these

boards provided an efficient method to sample the abundance of salamanders in different habitats. I used sheets of black plastic similar to those used by horticulturists to limit weed growth. Incidental observations by colleagues indicated that snakes congregated under such sheets, possibly attracted to the elevated temperature and moisture. In this chapter, I report the relative efficiencies of plastic cover sheets and trap-drift fence arrays that were used simultaneously to sample snake populations during 1998 and 1999.

### **Study Area**

I conducted the study within a 700-km<sup>2</sup> portion of Strafford County, New Hampshire (ca. 43°07' N, 71°00' W). Like many developing areas in southern New England, Strafford County is characterized by a mosaic of forests, farmland, and residential or industrial areas. Between 1953 and 1983, the area covered by developed lands in this county increased from 12 to 27% (Befort et al. 1987). Dominant overstory vegetation in forests of the area included northern hardwoods (American beech [*Fagus grandifolia*], birches [*Betula* spp.], maples [*Acer* spp.]), eastern white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*). Understory species included red maple (*Acer rubrum*), beaked hazelnut (*Corylus cornuta*), viburnums (*Viburnum* spp.), raspberry/blackberry (*Rubus* spp.), and eastern hemlock (*Tsuga canadensis*). I sampled patches ranging from approximately five to 120 ha of early-successional habitat, including idle agricultural land and edges of industrial sites. These patches were dominated by grasses and forbs (primarily goldenrods [*Solidago* spp.]) with low shrubs. Common shrubby species included *Rubus* spp., multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellata*), *Spirea* spp., blueberry (*Vaccinium* spp.), and common juniper (*Juniperus communis*).

## Methods

### Trap-Drift Fence Arrays

In 1998, I placed 41 traps along 330 m of commercial siltation fence on five patches (approximately one to two traps/ha), and in 1999, I used 17 traps along 170 m of the original fences on three patches (approximately two traps/ha). Fences (30-m and 60-m sections) were erected in a linear fashion, and were 90 cm tall with the lower 10 cm spaded into the ground to limit movement of snakes under the fence. Initially, I placed cylindrical funnel traps (constructed from 1.3-cm mesh hardware cloth) parallel to and against each fence (Fitch 1951). Because these funnel traps captured few snakes in 1998, I replaced them with box traps (31 x 31 x 92 or 122 cm constructed from rough-cut lumber; after Zappalorti et al. 1998) that were placed perpendicular to the fences. I inserted a funnel made of 0.6-cm mesh hardware cloth into one end of the trap and sealed the other end with hardware cloth. The funnel end was then inserted into a hole that was cut in the fence at ground level. Funnels and traps were lined with fly screening to reduce the number of snakes injured by the mesh. Traps were checked daily when temperatures exceeded approximately 26°C and every other day during cooler periods.

Captured snakes were placed into plastic bags and weighed to the nearest 0.5 g, and snout-to-vent length (SVL) was measured to the nearest 0.5 cm. In 1999, trap-caught snakes were marked by clipping three ventral scutes. All snakes were released  $\geq 5$  m from the fence. Traps were active on a patch for 30-55 days between July and September 1998, and all traps were operational for 90 days from May to August in 1999.

### Cover Sheets

I used 1.5 m x 3 m x 0.1-mm black plastic sheets staked with four to six plastic pegs or metal sod staples. In 1998, I distributed sheets ( $n = 108$ ) non-systematically

throughout each patch of habitat (ca. three to eight sheets/ha). In 1999, I placed sheets ( $n = 79$ ) along transect lines within each patch (ca. five to nine sheets/ha). In 1998, I sampled five patches from July through September, and in 1999, I sampled three patches from May through mid-August. In both years, all sheets were checked a total of six times: three times during morning hours (between sunrise and 09:00) and three times in the evenings (between 16:00 and sunset). I restricted checks to these cooler hours because midday temperatures under a plastic sheet occasionally exceeded 40°C, and periodic checks between noon and 14:00 indicated that snakes seemed to avoid sheets during these hot periods.

Sheet checks involved lifting up one-half of a sheet at a time and collecting all snakes found underneath. Initially, sheets were checked by two observers simultaneously to compensate for inexperience in capturing snakes. For the majority of the 1998 and all of the 1999 season, however, sheets were checked by an individual observer. Captured snakes were handled in the same manner as those captured in traps, and in 1999, sheet-caught snakes were marked by clipping two ventral scutes. Snakes that were observed but not captured were not included in the analyses.

### Data Analysis

Because there was no way to effectively standardize the sampling effort of these two methods, I did not attempt to compare the number of captures per method. I restricted comparisons to the number of species caught, indices of species diversity and community evenness, and size-class distributions by method of capture. For each method of capture, indices of species diversity (Shannon-Wiener [Shannon and Weaver 1949], Simpson [1949]) and community evenness (Simpson 1949) were calculated for each method using the software associated with Krebs (1999; *Ecological Methodology*, Exeter

Software Company, Setauket, New York). I restricted comparisons of size-class distributions to common garter snakes (*Thamnophis sirtalis*) because I collected too few individuals of other species in traps. Garter snakes were partitioned by method of capture and placed into five SVL classes (<20, 20-30, 31-40, 41-50, and >50 cm). The number of recaptures in 1999 was low ( $n = 23$ ), and proportions of recaptures were approximately the same for each method of capture (sheets = 0.12; traps = 0.11); therefore, I included all captures in the analyses. Within a method, size distributions of garter snakes were compared between years using a  $\chi^2$  test of independence (Zar 1999). Similar comparisons were made between methods, and results were considered significant at  $\alpha = 0.05$ .

### Results

I captured 332 individuals of four species under cover sheets, compared to 168 individuals of six species captured with trap-fence arrays (Table 1); thus, traps yielded a higher estimate of species richness. Smooth green snakes (*Liochlorophis vernalis*) were only captured in traps. Additionally, the only ribbon snake (*T. sauritus*) captured during this evaluation was in a trap. Although more species were caught in traps, indices of species diversity were consistently higher in the sheet-caught samples as a result of consistently higher evenness measures (Table 2).

**Table 1.** Snakes captured using plastic cover sheets and trap-drift fence arrays in southern New Hampshire, 1998 and 1999.

Method	Common Garter	Brown	Redbelly	Milk	Smooth Green	Ribbon
Sheets	220	75	34	3		
Traps	153	2	2	5	5	1

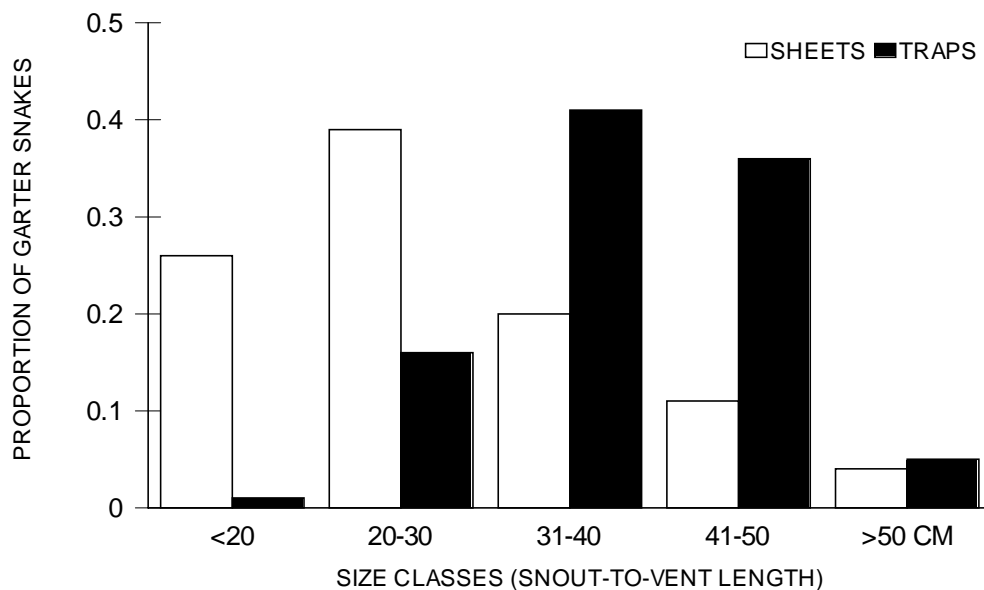
There were no between-year differences in size classes of snakes caught using traps ( $\chi^2 = 7.08$ , 4 df,  $P = 0.131$ ). There were between-year differences in size classes of snakes caught using cover sheets ( $\chi^2 = 25.0$ , 4 df,  $P < 0.001$ ). However, this was a consequence of the large number of neonatal garter snakes caught during the end of the 1998 field season. When the first size class (SVL <20 cm) was removed from the analysis, there were no between-year differences among snakes caught with cover sheets ( $\chi^2 = 0.22$ , 3 df,  $P = 0.974$ ). Therefore, I pooled the data by method of capture. Size-class distributions differed substantially by method of capture ( $\chi^2 = 91.3$ , 4 df,  $P < 0.0001$ ). The size distribution of sheet-caught snakes followed an expected distribution dominated by juveniles, whereas traps captured a higher proportion of larger snakes (Fig. 1).

Cover sheets apparently sampled a wider range of individual sizes than traps did. The two largest individuals (milk snakes, *Lampropeltis triangulum*) captured in traps and under sheets were approximately the same size (~200 g, 90 cm SVL). However, the smallest snake found in a trap was one of only two neonatal garter snakes (5 g, 18 cm

**Table 2.** Indices of species diversity and community evenness of snakes captured using plastic cover sheets and trap-drift fence arrays in southern New Hampshire, 1998 and 1999.

Year/Method	Simpson's index	Shannon-Weaver index	Simpson's evenness
1998/Traps	0.16	0.54	0.24
1998/Sheets	0.58	1.42	0.59
1999/Traps	0.17	0.60	0.24
1999/Sheets	0.43	1.14	0.44
Both years/Traps	0.16	0.59	0.20
Both years/Sheets	0.50	1.28	0.50

SVL), whereas the smallest individual caught under a sheet was a neonatal redbelly snake (*Storeria occipitomaculata*; 0.5 g, 6 cm SVL). Neonates accounted for 26% of common garter snakes found under sheets, but only 0.01% of garter snakes caught in traps. Thus, neonates and juveniles were likely underrepresented in the trap-caught sample.



**Fig. 1.** Size distribution of common garter snakes caught using plastic cover sheets ( $n_{\text{snakes}} = 220$ ) and trap-drift fence arrays ( $n_{\text{snakes}} = 153$ ) in southern New Hampshire, 1998 and 1999.

### Discussion

I was unable to compare the samples obtained by these two methods to the actual composition of resident communities; however, of the 11 snake species reported for New Hampshire (Taylor 1993), I captured six species. Two of the other species (timber rattlesnake [*Crotalus horridus*], eastern hognose [*Heterodon platirhinos*]) lacked confirmed sightings in my study area (Taylor 1993), and two other species (ringneck [*Diadophis punctatus*], water snake [*Nerodia sipedon*]) were not considered very

common in upland early-successional habitats like the ones I sampled (Conant and Collins 1991, DeGraaf et al. 1992). All species captured in traps as well as one additional species (racer [*Coluber constrictor*]) were eventually captured under cover sheets when I expanded the study to other patches in which I used cover sheets exclusively (Chapter 3).

In this study, although sheets resulted in higher evenness measures, traps sampled higher species richness. This may have been a function of sampling intensity. Whereas each sheet was visited only six times during a season, each trap was checked at least every other day during the same period. Thus, the chance of encountering a rare species in a trap may have been increased simply as a function of checking frequency.

Previous studies have compared the efficiency of traps and artificial cover (Fitch 1992, Sutton et al. 1999), but these researchers did not consider differences in size class distributions of study animals by method of capture. However, for studies in demographics, it may be necessary for researchers to be aware of size distributions to infer age structure of a population. Because passive sampling with artificial cover does not rely on activity by snakes, this method may provide a more accurate representation of the proportions of each size (and, by inference, age) class within a population (Bonnet et al. 1999). In my study, relying only on traps would have resulted in an adult-biased sample of common garter snakes. Moreover, unlike sheets, traps did not yield captures of neonatal redbelly or brown snakes.

Cover sheets may have been more effective for several reasons. First, cover sheets were distributed throughout a patch of habitat, and probably sampled a larger proportion of the habitat than drift fences did. Additionally, the temperature and

moisture differences under sheets may have attracted snakes, or their prey. Invertebrates (especially gastropods, spiders, and various insects), amphibians, and small mammals were frequently observed on or under cover sheets. Invertebrates are important prey of small snakes (Wright and Wright 1957). Large snakes (e.g., racers, milk snakes, and large garter snakes) are known to prey on small mammals, amphibians, smaller snakes, and even young conspecifics (racers: Fitch 1963; milk snakes: Dyrkacz 1977; garter snakes: Rossman et al. 1996); therefore, the presence of smaller snakes could have attracted larger snakes to the sheets as well. Furthermore, an individual snake could “condition” the substrate beneath a sheet, making it more attractive to conspecifics following scent trails (Ford and Burghardt 1993, Fitch 1999).

Cover sheets offered several other advantages over drift fence-trap arrays. First, sheets were less expensive (US\$4-6 per roll of plastic that yielded five sheets versus approximately \$50 for 60 m of fencing and \$40 for six associated traps) and required much less time and effort to deploy and dismantle than traps did. Unlike traps, cover sheets did not require constant attention and could be left in the field for several days without checking. Moreover, plastic sheets are less cumbersome to distribute than sheets of plywood (Durner and Gates 1993) or slabs of concrete (Bonnet et al. 1999) used by other researchers. Second, with one exception, no non-target vertebrates were injured or killed as a result of contact with cover sheets. The only vertebrate mortalities associated with cover sheets were six neonatal garter snakes and one meadow jumping mouse (*Zapus hudsonius*) that had evidently drowned in small pools of water that accumulated on the sheets during rainstorms. In contrast, I captured 15 small or medium-sized mammals (as large as a juvenile opossum, *Didelphis virginianus*, in a funnel trap), seven

birds, and a number of amphibians in traps. Several of these animals were incidentally injured or killed. Also, 17 garter snakes were injured or killed while attempting to escape from traps.

Cover sheets may not be effective under all conditions. During the hottest periods of summer, daytime temperatures were high (often  $>27^{\circ}\text{C}$ ) and snakes apparently avoided cover sheets. Additionally, when air temperatures were cool ( $<17^{\circ}\text{C}$ ), few snakes were captured under cover sheets because they apparently retreated beneath the matted vegetation under the sheets where they could not be captured. Diurnal differences in capture success also may have been related to ambient temperatures. For example, in 1999, I caught more garter snakes  $>20$  cm SVL ( $n = 134$ ) during evening checks than during morning checks ( $n = 32$ ) despite equal effort. Cover sheets are probably most effective in open-canopy habitats similar to those that I sampled. In closed-canopy forests, the thermal attraction is likely reduced or eliminated and other forms of concealment cover (e.g., fallen logs and rocks, leaf litter) are usually abundant.

In summary, plastic cover sheets seemed to be an effective method to sample snake populations in open habitats. They sampled a greater range of individual sizes of snakes, were less expensive and required less time to monitor, and resulted in fewer injuries and deaths than did drift fence-trap arrays. However, in varied landscapes it may be necessary to rely on a variety of capture methods to obtain representative samples (e.g., Jones 1986).

## CHAPTER 3

### COMMUNITY STRUCTURE OF SNAKES IN FRAGMENTED LANDSCAPES OF NEW ENGLAND

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 fragmentation has been implicated in affecting a number of demographic and community parameters among animal populations (e.g., Mühlenberg and Werres 1983, Mader 1984, Sarre 1998). Although small patches are typically species impoverished (e.g., Klein 1989), they may have a higher density of individuals than larger patches of similar habitat (Barbour and Litvaitis 1993). Populations on smaller fragments may show differences in body sizes (Klein 1989), analogous to the “island syndrome” observed in many taxa in response to resource limitations on oceanic islands (Case 1978). Pressures of intraguild predation (*sensu* Polis et al. 1989, Soulé et al. 1988) and competition may be relaxed with the removal of larger guild members from small patches. Resource limitation and increased competition or reduced predation may result in species on small fragments exploiting a wider range of microhabitats or otherwise displaying shifts in niche parameters (e.g., Barbour and Litvaitis 1993).

Responses by avian (e.g., Bayne and Hobson 1997, Burke and Nol 1998) and mammalian (e.g., Barbour and Litvaitis 1993, Crooks and Soulé 1999) populations to habitat fragmentation have received considerable attention. However, the effects of fragmentation on reptiles remain largely uninvestigated; exceptions include Cunningham

and Moritz (1997) and Sarre (1998). Snakes in particular may be appropriate organisms with which to examine the possible effects of habitat fragmentation (Shine and Fitzgerald 1996) because of their specific habitat requirements (Reinert 1993), thermal constraints (Peterson et al. 1993), and relatively limited mobility (Fitch and Shirer 1971) compared to many other vertebrates.

I examined how populations of snakes responded to fragmentation by comparing species diversity, abundance, size distributions within and among species, microhabitat use, 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, I predicted the following outcomes. 1. On small patches, species diversity of snakes would be less, there would be a higher proportion of small-bodied snakes, and the abundance of snakes would be greater than on large patches. 2. On small patches, small snakes would use a greater range of microhabitats than comparable sized snakes on large patches. 3. On large patches, where large snakes (potential predators of small snakes) were present, the abundance of small snakes (potential prey) would be lower in areas where large snakes concentrated their activity than in other portions of these patches.

### **Study Area**

I conducted my study within ca. 700-km<sup>2</sup> of Strafford County, New Hampshire (ca. 43°07' N, 71°00' W). Like many developing areas in southern New England, Strafford County is presently characterized by a mosaic of forests, farmland, and residential or industrial areas. At the turn of the century, large-scale clearings for farming had reduced forest coverage in New Hampshire to <50%, and ensuing abandonment of these farms in the late 1800s and early 1900s increased the availability of early-successional habitats to ca. 195,000 ha (summarized in Litvaitis 1993, Litvaitis et al.

1999). By 1960, however, most of these old-field habitats had matured into second-growth forests (Litvaitis 1993). Between 1953 and 1983, the area covered by developed lands in this county increased from 12 to 27% (Befort et al. 1987). Remaining areas of early-successional habitats are now patchily distributed within the landscape, and specific shrub and open-canopy communities (e.g., pitch pine [*Pinus rigida*]) that are associated with dry soils have been degraded (Weymouth and Ammann 1998).

I restricted my comparisons to patches of early-successional habitats because these habitats are among the most productive for the majority of species I was likely to encounter (Fitch 1999). Early-seral or disturbed habitats are dominated by forbs, grasses, and shrubs, and secondary succession has typically progressed less than 25 years (Kricher and Morrison 1988, Litvaitis 1993). I sampled patches of early-successional habitat that ranged from ca. 0.2-120 ha, including idle agricultural land, edges of industrial sites, and powerline corridors. All small patches were traffic islands because I was unable to locate other accessible patches in this size class. 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 shrubby species included *Rubus* spp., *Spiraea* spp., multiflora rose (*Rosa multiflora*), barberry (*Berberis* spp.), autumn olive (*Elaeagnus umbellata*), blueberry (*Vaccinium* spp.), and common juniper (*Juniperus communis*).

## **Methods**

### **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 the study area. Two other species (ringneck snakes [*Diadophis punctatus*], water snakes [*Nerodia sipedon*]) were not considered very common in upland early-successional habitats like the ones I sampled (Conant and Collins 1991, DeGraaf et al. 1992). Therefore, I based patch-size classes (small, intermediate, large) on home-range estimates of the species I was most likely to encounter. The two largest species, racers (*Coluber constrictor*) and milk snakes (*Lampropeltis triangulum*), have estimated home ranges of 10-20 ha (Fitch 1963, Fitch and Fleet 1970, Plummer and Congdon 1994). Therefore, I considered all patches >10 ha to be large. Home ranges of other snakes in the study area (brown snakes [*Storeria dekayi*], redbelly snakes [*S. occipitamaculata*]) are typically <1.5 ha (Freedman and Catling 1979, Semlitsch and Moran 1984), so I considered patches <1.5 ha to be small. Those patches 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. Patches used in this study were integrated within a mosaic of different habitats. Although patches were distinct from their surroundings, snakes encountered on them are known to use a wide range of habitats (e.g., common garter snakes [*Thamnophis sirtalis*]; Wright and Wright 1957). A forest used to delineate a patch would therefore not necessarily represent a barrier to the snakes. Thus, effective patch size for a snake may have been larger than the sizes of patches that I measured.

I used sheets of black plastic (1.5 m x 3 m x 0.1 mm) to sample snakes on all patches because this method was efficient and less biased towards larger snakes than known alternative approaches to capturing snakes (Chapter 2). Sheets ( $n \approx 350$ ) were

distributed non-systematically among suitable locations in 1998 and sampled from July through September. In 1999, sheets ( $n \approx 400$ ) were placed 20-40 m apart along transects and were sampled from May through mid-August. On small and intermediate-sized patches, transects ran the lengths of the patches. On large patches, transects were placed within pockets of habitat roughly equivalent in size to small and intermediate-sized patches. Density varied from 0.75-10 sheets/ha, with highest densities on small patches. Each sheet was checked a total of six times in both field seasons: three times during morning hours (between sunrise and 09:00) and three times in the evenings (between 16:00 and sunset). 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.

#### Patch Size vs. Species Diversity, Abundance, and Size Distributions

Unless noted otherwise, all analyses were performed in SYSTAT 7.0 for Windows<sup>®</sup> (SPSS, Inc. 1997), and results of all comparisons were considered significant at  $\alpha = 0.05$ . I used non-parametric statistics to circumvent problems associated with heteroscedasticity and non-normally distributed data. In many cases, I also applied parametric statistics for comparison, and results were essentially identical. Thus, because Mann-Whitney and Kruskal-Wallis tests remain valid under a wider range of conditions than their parametric equivalents (Hamilton 1996:269), I report results of non-parametric tests.

To compare species diversity among large, intermediate, and small patches, I calculated two indices of diversity (Simpson [1949] and Shannon-Wiener [Shannon and Weaver 1949]); the former is most sensitive to differences in rare species, whereas the

latter is most sensitive to differences in abundant species (Krebs 1999). I also compared an index of evenness (Simpson 1949) among patches. All indices were calculated using software associated with Krebs (1999; Ecological Software Company, Setauket, New York). I calculated these indices by first combining data for each patch-size class; therefore, I did not make any statistical comparisons. All captured snakes (adults, subadults, and neonates) were included in this comparison.

To estimate abundance of snakes (not including neonates) on a patch, I initially used a mark-recapture estimator (Schnabel [1938] method; Krebs 1999); however, recapture rates were low (<10%), with some patches having recapture rates of 0%. This resulted in very imprecise estimates of population sizes. Therefore, I compared abundance using a standardized catch-per-effort measure. I 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 multiplied by 100 to effectively yield captures per 100 sheet checks. To test my prediction that snakes on small patches would be more abundant, I used a Kruskal-Wallis test (Zar 1999) to compare capture indices among large, intermediate, and small patches. I then compared the capture index to patch size and effort using Pearson pairwise correlations (Zar 1999) to determine if effort influenced the estimate of abundance.

To test the prediction that there would be a higher proportion of smaller snakes on small patches, I tallied the number of individuals per SVL-size class ( $\leq 20$ , 21-30, 31-40, 41-50, >50 cm) on each patch. I then performed a  $\chi^2$  test of independence (Zar 1999) to compare size distributions of snakes among size classes of patches. I made similar

comparisons with the most abundant species in my samples, garter snakes. Prior to analyses of abundance, I excluded all brown and redbelly snakes <10 cm SVL and all garter snakes <20 cm SVL because I 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 affected any comparisons.

### Microhabitat Sampling

I compared habitat use by small snakes ( $\leq 30$  cm SVL ) to test the prediction that small-bodied snakes would show shifts in microhabitat use on small patches of habitat. Ten habitat features (modified from Reinert 1984) were sampled on all patches in 1999, where each cover sheet was considered a sampling point (Table 3). Percentage of ground cover was visually estimated within a 3-m radius around and including each sheet. Classes of ground-cover types included grasses (as well as sedges and rushes), forbs, and woody vegetation. I measured the height of lowest and highest vegetation layers. Woody stem density was estimated by counting all stems <7.5 cm diameter within two perpendicular 10-m<sup>2</sup> transects running through the area occupied by each cover sheet. At 1-m intervals along each transect, I estimated canopy closure by ocular tube sighting. Each point (maximum = 20) was given a “+” (indicating closed canopy) or a “-” (open canopy); the total number of +s was converted to percent canopy closure. At each sheet, I paced distances (up to 30 m) to the nearest road and nearest forest/woodlot edge. I chose 30 m as the maximum distance because I did not believe that habitat features beyond this distance influenced immediate site selection by snakes. I also measured the distance (up to 30 m) to the nearest neighboring sheet to determine if there were more snakes in areas where cover sheets were closer together, potentially resulting in higher

**Table 3.** Habitat characteristics measured on small, intermediate, and large patches of early-successional habitat in southern New Hampshire, 1999.

Mnemonic	Variable measured
% Grass	% ground cover by grasses, sedges, and rushes within a 3-m radius of a sheet
% Forb	same as above for tall and low forbs
% Wood	same as above for non-herbaceous, woody species
% Other	same as above for bare ground, sand, rocks, moss, litter
Lowveg	height of average lowest vegetation tier within 3-m radius of sheet
Highveg	height of average highest vegetation tier within 3-m radius of sheet
NSheet	distance (m) to nearest neighboring sheet within 30 m
NRoad	distance (m) to nearest paved or dirt road within 30 m
NForeedge	distance (m) to nearest forest or woodlot edge (with trees >7.5 cm dbh) within 30 m
CanClos	% canopy closure within two perpendicular 10-m <sup>2</sup> transects running through sheet
Stem/m <sup>2</sup>	density of woody stems <7.5 cm diameter, approximated by counting all stems within two perpendicular 10-m <sup>2</sup> transects running through sheet

concentrations of prey or pheromonal attractants (Fitch 1992). I completed habitat sampling within a three-week period to minimize differences in estimated ground cover caused by seasonal shifts in dominant vegetation. To avoid redundancy of habitat variables, I used a Pearson correlation matrix (Zar 1999) to identify variables with a correlation coefficient  $|r| \geq 0.8$  (deMaynadier and Hunter 1998). The variable considered biologically less influential was discarded.

#### Implications of Intraguild Predation

I restricted my evaluation of intraguild predation to a single large patch (ca. 35 ha) where I used radio telemetry to monitor racers. Five adult racers (four males and one female, 91-130 cm SVL) were captured opportunistically or under cover sheets between May and July 1999 (Appendix 3). Transmitters (Model SM1, 15-cm antennae, 150 MHz frequency range; AVM Instrument Company, Ltd., Livermore, California) were

implanted by J. Means, DVM (North Hampton Animal Hospital), following the procedures outlined by Reinert and Cundall (1982). Developing eggs in the female prevented peritoneal implantation of the transmitter; it was therefore implanted subcutaneously. Transmitters weighed between 4 and 8 g, representing <2% of the total body mass of each animal. Each snake was released at its point of capture after a minimum 24- hour observation period following surgery. Snakes were monitored for five to 18 weeks, and their locations (obtained visually or by triangulation) were recorded up to two times a day through mid-August, after which time snakes were tracked only sporadically through 26 September. I was unable to recapture the animals to remove the transmitters.

Latitude and longitude of each location were obtained with a global positioning system receiver (GPS; Garmin 75 Personal Navigator™, Garmin International, Lenexa, Kansas). Because of inherent error associated with the receiver, I recorded each location 20 times, and the average of those coordinates was used to designate the location. Locations were considered unique if they were >5 m apart (Weatherhead and Prior 1992, Plummer and Congdon 1994); for locations closer together, I recorded coordinates of the center. Individual home ranges were calculated by the minimum convex polygon method (Mohr 1947) with the program CALHOME (Kie et al. 1996). Slip and Shine (1988) suggested that sample sizes of <20 locations per animal were too small for the minimum convex polygon method to reliably estimate home range in reptiles; however, the least number of relocations for an individual in my study was 25. I performed a Spearman rank correlation (Zar 1999) to determine if home range sizes of racers were related to the number of locations recorded.

I considered the 75% isopleth of each home range to be an area of intensive activity, and areas outside of these regions were considered areas of limited activity. Choosing the 75% isopleth as an area of intensive activity may have over- (or under-) estimated the size of the actual core activity area of the racers. However, I required a method of designating more intensively used areas to draw comparisons among sympatric snake populations. Next, I compared the location of each cover sheet ( $n = 63$ ) on this patch to the home ranges of racers to determine which sheets fell within 75% isopleths. I then compared species composition of snakes captured within limited and intensive activity areas. I also used a Mann-Whitney test (Zar 1999) to compare size differences in garter snakes between areas of intensive activity and areas of limited activity.

I measured and evaluated habitat variables at each sheet on this patch as described above and then compared microhabitats between areas of intensive and limited activity with a Mann-Whitney test. I then compared microhabitat variables between sheets where small snakes (potential prey,  $\leq 30$  cm SVL) were present or absent within the areas of intensive activity.

## **Results**

### **Patch Size vs. Species Diversity, Abundance, and Size Distribution**

In 1998, I sampled 38 patches (27 small, seven intermediate, four large) of early-successional habitat, and in 1999, I sampled 22 patches (11 small, eight intermediate, three large). In both years, large patches had a higher percent occupancy (both years: 100%) than intermediate (1998: 87.5%; 1999: 75%) or small (1998: 11%; 1999: 64%) patches. For all following analyses, I considered only occupied patches that were sampled in both years. Large patches sampled in both years ( $n = 3$ ) contained more

species ( $\bar{x} = 4.2$  [range = 3-5]) than intermediate ( $n = 5$ ;  $\bar{x} = 2.1$  [range = 1-4]) or small patches ( $n = 7$ ; only one species) sampled in both years. In both years, I found only one species (garter snakes) on small patches, so I was unable to generate diversity indices for these patches. Large patches consistently had greater indices of species diversity and evenness than intermediate-sized patches (Table 4). I recorded 675 captures (small patches:  $n = 19$ ; intermediate:  $n = 95$ ; large:  $n = 561$ ), not including neonates, on the 15 occupied patches that were sampled in both years (Appendix 1).

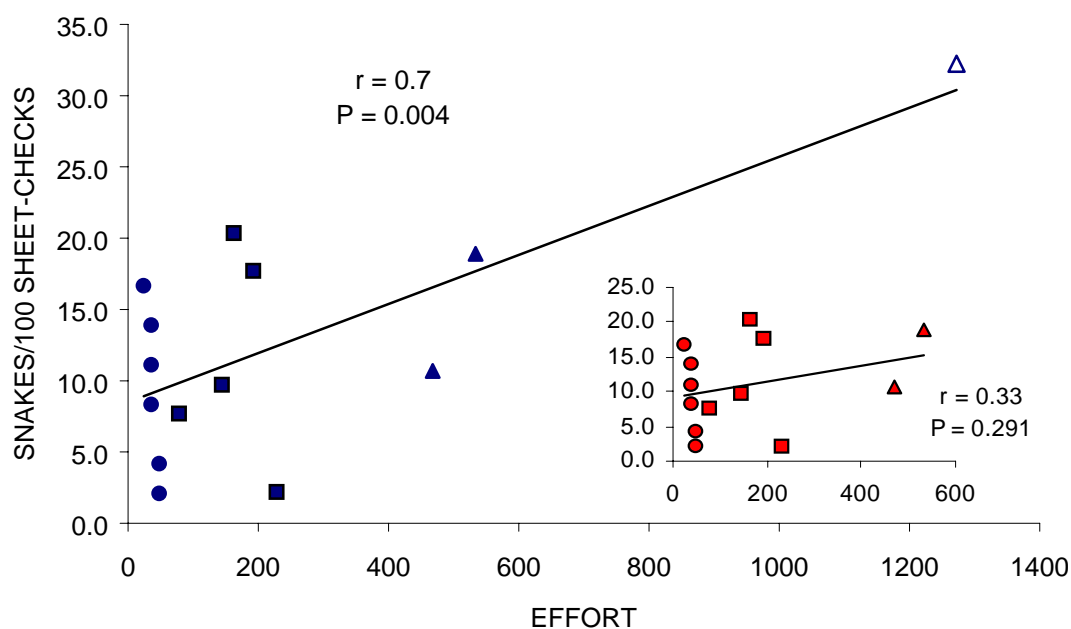
The abundance of garter snakes only did not differ among large ( $\bar{x}$  capture index = 11.0 garter snakes/100 sheet checks [range = 4.3-18.8]), intermediate ( $\bar{x} = 10.3$  garter snakes/100 sheet checks [range = 2.1-22.4]), or small patches ( $\bar{x} = 9.4$  garter snakes/100 sheet checks [range = 2.1-16.7]; Kruskal-Wallis test statistic: 0.305, 2 df,  $P = 0.859$ ). The abundance of all species combined also did not differ among large ( $\bar{x} = 20.6$  snakes/100 sheet checks, range = 10.7-32.2), intermediate ( $\bar{x} = 12.3$ , range = 2.2-20.4), and small patches ( $\bar{x} = 9.4$ , range = 2.1-16.7; Kruskal-Wallis test statistic: 2.90,  $P = 0.235$ ). Initially, capture indices of all snakes combined were correlated with effort

**Table 4.** Indices of species diversity and community evenness of snakes captured on large ( $n = 3$ ) and intermediate-sized ( $n = 5$ ) patches of early-successional habitat in southern New Hampshire, 1998 and 1999. Neonates of all species were included.

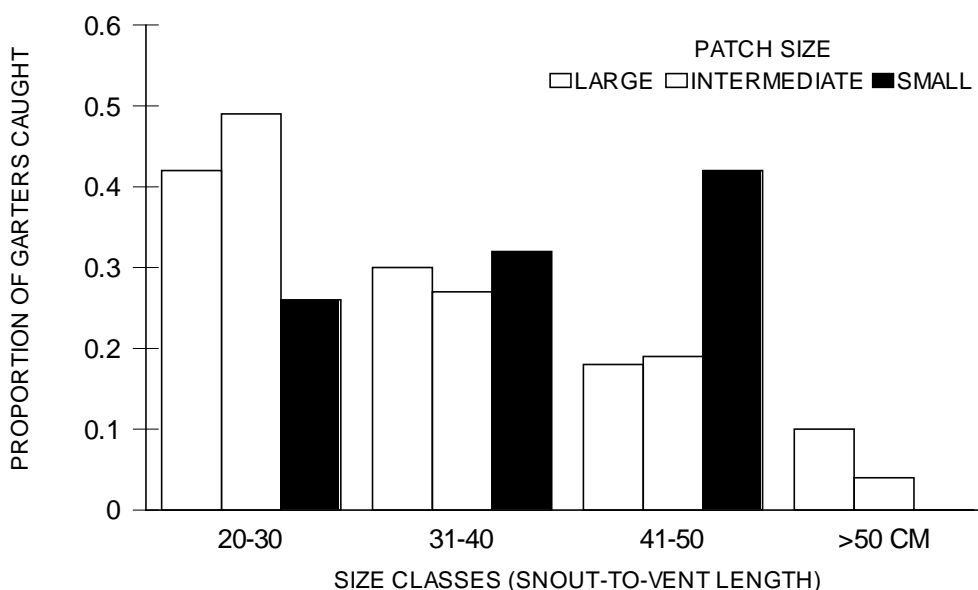
Year/Patch size	Simpson's index	Shannon-Wiener index	Simpson's evenness
<b>1998/Large</b>	<b>0.63</b>	<b>1.52</b>	<b>0.67</b>
1998/Intermediate	0.16	0.54	0.30
<b>1999/Large</b>	<b>0.51</b>	<b>1.40</b>	<b>0.34</b>
1999/Intermediate	0.31	0.97	0.29
<b>Both years/Large</b>	<b>0.57</b>	<b>1.50</b>	<b>0.39</b>
Both years/Intermediate	0.29	0.83	0.27

expended ( $r = 0.7$ ,  $P = 0.004$ ); however, this relationship did not persist after I removed the largest patch (Bellamy Wildlife Management Area) from the data set ( $r = 0.33$ ,  $P = 0.291$ ; Fig. 2). A  $\chi^2$ -goodness-of-fit test (Zar 1999) of all snakes captured by patch-size class revealed that the distribution of snakes deviated from expected values given the effort expended by patch size (all species:  $\chi^2 = 8.29$ , 2 df,  $P < 0.001$ ; garter snakes only:  $\chi^2 = 56.9$ , 2 df,  $P = 0.016$ ). Based on the relative contributions to the overall  $\chi^2$  statistics, more snakes than expected were found on large patches whereas fewer snakes than expected were found on intermediate and small patches.

I found a greater proportion of larger garter snakes on small patches. This difference in size class distributions among large, intermediate, and small patches approached significance ( $\chi^2 = 11.9$ , 6 df,  $P = 0.064$ ; Fig. 3). This trend was reinforced



**Fig. 2.** Correlation of capture index (snakes/100 sheet-checks) to effort expended (number of sheets on a patch x number of times sheets were checked) on large (triangles), intermediate (squares), and small patches (circles) sampled in southern New Hampshire in 1998 and 1999. The largest patch, Bellamy Wildlife Management Area, is identified by the large open triangle to the upper right. Inset depicts the same correlation following the removal of this patch from the analysis.



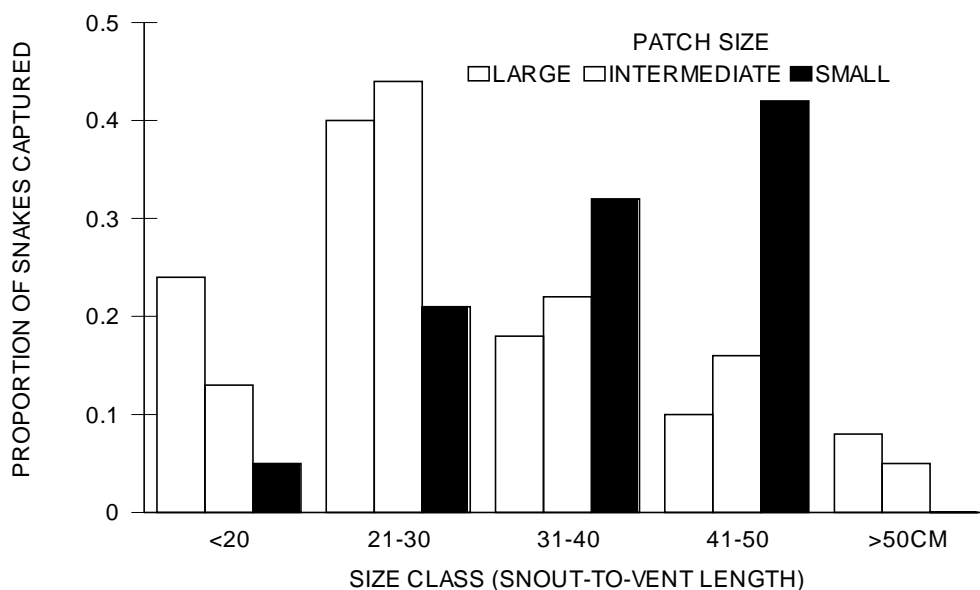
**Fig. 3.** Size distributions of common garter snakes captured on three large, five intermediate, and seven small patches of early-successional habitats in southern New Hampshire in 1998 and 1999. Neonates (<20 cm SVL) were not included.

when I considered all snakes. Because I found small-bodied species (primarily brown and redbelly snakes) only on intermediate and large patches, size-class distributions of all snakes on these patches were skewed towards smaller individuals ( $\chi^2 = 32.5$ , 8 df,  $P < 0.001$ ; Fig. 4). Almost half (44%) of the  $\chi^2$  statistic was derived from the cell for 41-50 cm SVL snakes on small patches, providing inference to reject the prediction of equal size distributions among patch size classes (after Hamilton 1996:227). This was counter to my expectation that smaller-bodied individuals would represent a greater proportion of snakes on small patches of habitat.

#### Microhabitat Use

Following disturbance of patches by mowing prior to vegetation sampling, I was able to assess habitats on only three of the occupied intermediate-sized patches.

Furthermore, limited sample size ( $n = 5$ ) of snakes  $\leq 30$  cm SVL on small patches



**Fig. 4.** Size distributions of all 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 southern New Hampshire in 1998 and 1999. Neonates were not included.

prevented any comparison of microhabitat use by small snakes among the three patch-size classes. The lack of small garter snakes and other small-bodied species (brown and redbelly snakes) on small patches was unexpected. As a result, I compared habitat features among the intermediate and large patches ( $n = 6$ ) on which I had captured brown and redbelly snakes to all small patches (occupied and unoccupied) sampled in 1999 ( $n = 11$ ). Not surprisingly, sheets on small patches were closer to roads ( $\bar{x} = 13.6$  m,  $SD = 7.1$  m) than sheets in areas where brown and redbelly snakes were found ( $\bar{x} > 30$  m,  $SD = 3.5$  m; Mann-Whitney U test statistic: 1.0,  $P = 0.001$ ). I also found that sheets on small patches were closer to forest edges ( $\bar{x} = 10.7$  m,  $SD = 11.2$  m) than sheets on larger patches ( $\bar{x} = 23.5$  m,  $SD = 2.7$  m; Mann-Whitney U test statistic: 12.0,  $P = 0.035$ ). Lastly, I found that small patches were characterized by lower vegetation (lowest vegetation tier on small patches  $\bar{x} = 11.0$  cm,  $SD = 2.4$  cm versus on intermediate and

large patches  $\bar{x} = 17.7$  cm, SD = 7.4 cm; Mann-Whitney U test statistic: 6.5,  $P = 0.008$ ; highest vegetation tier:  $\bar{x}$  on small patches = 87.8 cm, SD = 16.7 cm versus  $\bar{x}$  on intermediate and large patches = 110.3 cm, SD = 14.6 cm; Mann-Whitney U test statistic: 9.0,  $P = 0.016$ ).

### Implications of Intraguild Predation

The 100%-isopleth home ranges averaged 14.7 ha (range = 9.0-31.4 ha) and were not correlated with number of locations (Spearman  $r = -0.1$ ,  $P = 0.873$ ) or with time (number of days) that snakes were monitored (Spearman  $r = 0.7$ ,  $P = 0.188$ ). The 75%-isopleth home ranges averaged 5.6 ha (range = 1.5-12.2 ha) and were not correlated with number of locations (Spearman  $r = 0.7$ ,  $P = 0.188$ ), but were correlated with the monitoring period (Spearman  $r = 0.9$ ,  $P = 0.037$ ). Seasonal shifts in areas of concentrated activity by racers due to differential availability of prey may have caused an enlargement of core areas over time. Thus core areas of individuals tracked later in the season may have been underestimated; however, I had no means of evaluating the consequences of possible underestimations.

Thirty-two sheets were within areas of intensive activity, and 31 sheets were in areas of limited activity (Appendix 4). Garter snakes collected in areas of intensive activity ( $n = 7$ ) were larger ( $\bar{x}$  SVL = 61.4 cm, SD = 11.0 cm) than those found in areas of limited activity ( $n = 14$ ,  $\bar{x}$  SVL = 44.6 cm, SD = 14.2 cm; Mann-Whitney U test statistic: 81.0,  $P = 0.017$ ). Additionally, garter snakes had lower capture indices in areas of intensive activity (Table 5). Milk snakes were found only in areas of intensive racer activity, whereas the only brown snake caught on this patch was in an area of limited activity (Table 5). Thus, I captured a higher proportion of larger-bodied individuals of all

**Table 5.** Number, capture indices, and snout-to-vent lengths (SVL) of snakes caught in areas of intensive and limited activity by racers in southern New Hampshire, 1999. Neonates were not included.

Activity	Number caught	Capture Index (snakes/100 sheet-checks)	Mean SVL (cm)	SD
Intensive				
Brown	0	0.0		
Garter	7	3.6	61.4	11.0
Milk	3	1.6	63.7	2.3
Redbelly	4	2.1	19.3	1.9
Limited				
Brown	1	0.5		
Garter	14	7.5	44.6	14.2
Milk	0	0.0		
Redbelly	4	2.2	18.0	0.4

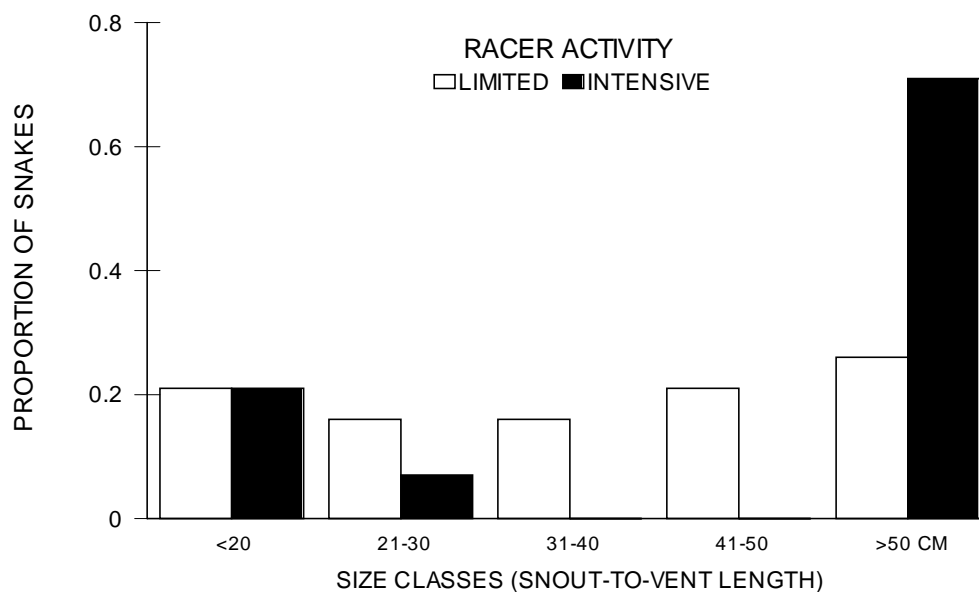
species in areas of intensive activity by racers (Fig. 5).

Percent coverage by woody vegetation and stem density were found to be redundant ( $r = 0.89$ ; Appendix 2). Therefore, I eliminated stem density from the data set. I found that areas of intensive use had a greater coverage by forbs (intensive use  $\bar{x} = 55.5\%$ ,  $SD = 23.6\%$ ; limited use  $\bar{x} = 28.1\%$ ,  $SD = 20.2\%$ ; Mann-Whitney U test statistic: 811,  $P < 0.0001$ ) and a lower coverage by woody vegetation (intensive use  $\bar{x} = 11.6\%$ ,  $SD = 13.0\%$ ; limited use  $\bar{x} = 39.2\%$ ,  $SD = 27.8\%$ ; Mann-Whitney U test statistic: 226,  $P < 0.0001$ ). Within areas of intensive activity by racers, I found no differences in habitat variables between sheets where small snakes were present or absent. However, sample size of sheets where small snakes were present was very small ( $n = 3$ ).

## Discussion

### Effects of Fragmentation

In accordance with the species-area hypothesis (MacArthur and Wilson 1967), my results supported the prediction that small patches would be species-impooverished



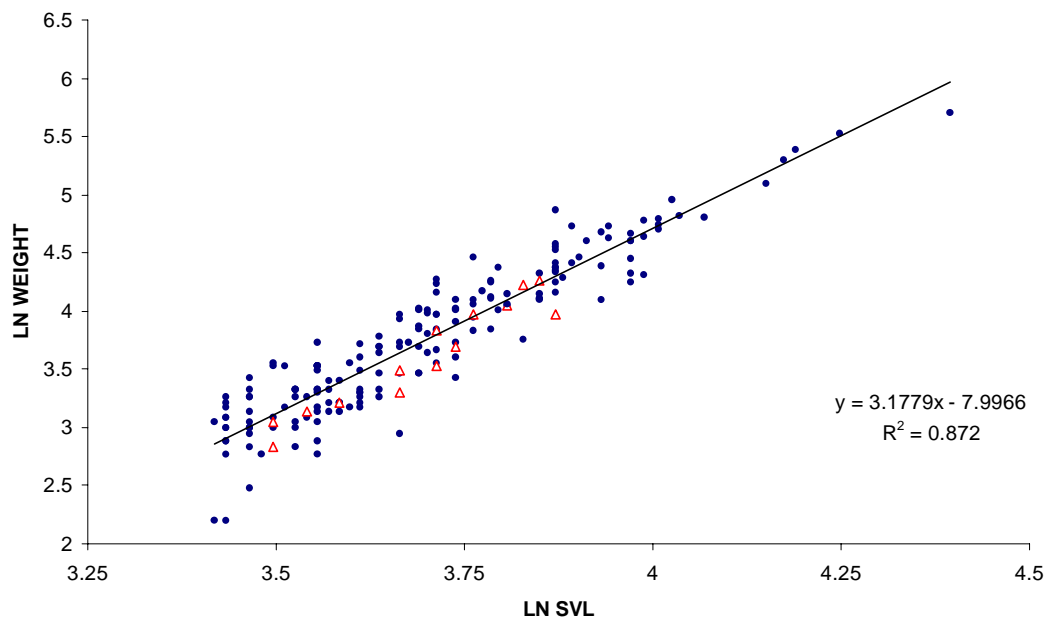
**Fig. 5.** Size distributions of all snakes captured in areas of intensive and limited activity by racers in southern New Hampshire, 1999. Neonates and racers were not included.

relative to larger patches. However, my results did not support the hypotheses that snakes would be more abundant on small patches and that there would be a higher proportion of smaller snakes on small patches. Although I had not expected to find large species (milk snakes and racers) on small patches given the area requirements of these species, the snakes found on small patches (garters) were not the smallest-bodied species encountered during the study. The absence of brown and redbelly snakes on small patches was unexpected.

It is possible that resources on small patches were too limiting to sustain larger populations of garter snakes or other species. More frequent mowing may not have allowed vegetation on these patches to develop a structure sufficiently complex to maintain diverse or abundant prey populations. In this case, garter snakes on small patches should show signs of reduced physical condition. To evaluate this hypothesis, I

compared condition index of garter snakes >30 cm SVL ( $n = 14$ ) on small patches to garter snakes >30 cm ( $n = 177$ ) on intermediate and large patches that had also contained smaller species. Positive residuals from a regression of  $\ln(\text{weight})$  on  $\ln(\text{SVL})$  characterized snakes in relatively good physical condition whereas negative residuals characterized snakes in relatively poor condition (Weatherhead and Brown 1996). I found that 71% of garter snakes on small patches were in poor condition, compared to only 44% of garter snakes on large and intermediate-sized patches (Fig. 6). This supports the notion that small patches were resource limited. Limited resources may also have restricted the duration that these sites were occupied. I did not recapture any snakes on small patches, suggesting that captured individuals may have been transients rather than residents and may have used the small patches only as stepping-stones (*sensu* MacArthur and Wilson 1967) en route to other patches. The virtual absence of neonatal garter snakes on small patches (Appendix 1) supports this hypothesis, and could also indicate low levels of recruitment into populations on small patches.

Roads are known to be effective barriers in the dispersal of amphibians (Reh and Seitz 1990) and mammals (Mader 1984). Therefore, highway islands may have been isolated enough to prevent effective immigration and dispersal of snakes, which could eventually lead to localized extinctions in these sink habitats (Fahrig and Merriam 1985). Bonnet et al. (1999) found that adult males during the mating season, adult females on egg-laying migrations, and neonates/hatchlings were the most at risk of highway mortality. Although I encountered few road-killed snakes during my study, snakes are often found dead on roads (Dodd, Jr., et al. 1989; Bonnet et al. 1999), so it is possible that mortality of small snakes was high on the traffic islands that I sampled. In addition,



**Fig. 6.** Relationship ( $P < 0.001$ ) of weight (g) to snout-to-vent length (SVL; cm) of 191 common garter snakes  $>30$  cm SVL. Residuals were used as a condition index, where positive residuals were characteristic of snakes in relatively good physical condition and negative residuals indicated snakes in relatively poor physical condition (Weatherhead and Brown 1996). Red triangles identify snakes ( $n = 14$ ) on small patches.

proximity to forest and woodlot edges on small patches may have resulted in greater exposure to generalist predators, including raccoons (*Procyon lotor*) and raptors.

Anecdotally, I found 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).

Garter snakes were the only species found on all of the occupied patches sampled in two years. Because garter snakes are generalists (Wright and Wright 1957, Rossman et al. 1996), they may not be as sensitive to alterations in their habitat and may therefore be able to persist on small fragments. Habitat generalism is considered to be an important characteristic in determining ability of a species to remain in an area following

fragmentation (Sarre et al. 1995, Sarre 1998). Blaesing (1979) found garter snakes inhabiting a semi-disturbed area to be at least as successful as those inhabiting relatively undisturbed areas. He attributed this success either to decreases in populations of raptors in disturbed areas or to the ability of garter snakes to adjust to the habitat disturbance. Ironically, brown snakes have been described as “city snakes”, because of their propensity to be found in urban cemeteries and parking lots (Conant and Collins 1991, Mazurkiewicz 1999) suggesting that they, too, are able to adjust to disturbances. However, Freedman and Catling (1979) concluded that the ability of brown snakes to persist in isolated parks and vacant lots surrounded by urban development suggested that habitat discontinuities (roads, woodlands) restricted the movements of a large proportion of the populations of this species. Another explanation for the absence of brown and redbelly snakes may lie in their feeding preferences. The primary prey of both species are gastropods, predominantly slugs (Wright and Wright 1957, Semlitsch and Moran 1984). Because the vegetation on small patches was lower than elsewhere, it is possible that the habitat became too dry to sustain sufficient populations of gastropods.

My results supported the hypothesis that intraguild predation by racers influenced snake communities. Intraguild predation (predation on potential competitors) is thought to occur in many ecological systems (Polis et al. 1989). Size differences in garter snakes between areas of intensive racer activity and areas of limited activity suggested that the presence of racers may have influenced other snakes, either through competition for shared resources, predation, or both. Rosen (1991) found that garter snakes were the third most common food item in the stomachs of 28 Michigan racers. I found more garter and milk snakes >50 cm SVL in areas of intensive racer activity, suggesting that

these individuals may have “escaped” predation by racers (Fig. 5). Common garter snakes in laboratory experiments reacted more strongly to odors from racers than to odors from control (non-ophiophagous) snakes (Weldon 1982). This indicates that garter snakes exhibit some degree of predator recognition that could lead to behavioral avoidance of areas frequented by racers and other predatory snakes (Gregory et al. 1987). Support for this conjecture comes from a comparison of neonatal garter snakes. In areas of intensive activity, I found 0.5 neonatal garter snakes/100 sheet-checks, whereas in areas of limited activity, I found 4.8 neonates/100 sheet-checks, suggesting that larger garter snakes found within areas of intensive activity may move out of these ranges to give birth. Potentially reduced populations of the generalist garter snake in areas of intensive racer activity could favor a more diverse prey base (including worms, gastropods, arthropods) for other snake species; however, I did not evaluate this relationship.

Observed differences in garter snakes between areas of intensive activity and areas of limited activity may have been a result of simple resource depletion by racers and other predators. In a long-term study, Fitch (1999) observed racers to be the most eurytrophic species in his study area. Thus, depletion of small garter snakes would not necessitate movement by racers outside of their core ranges if other prey (e.g., small mammals) were likely still available.

#### Implications for Conservation of Snakes

In a review of literature, Dodd (1987) identified habitat destruction as the principle cause of the decline of North American snake populations. In addition, he identified species on the periphery of their geographic range as warranting additional

protection (Dodd 1987, 1993). Populations of racers may be declining at the northern edge of their range (Klemens 1993; Vickery 1999; P. Mirick, Massachusetts Division of Inland Fisheries and Wildlife, personal communication); one reason for this may be the loss of early-successional habitats (Vickery 1999). Racers in other portions of their range are associated with open habitats (Kansas: Fitch 1963, 1999; Michigan: Rosen 1991; South Carolina: Plummer and Congdon 1994). The only study of racers in New England prior to my investigation concluded that racers required open areas and forest/field ecotones (Zappalorti and Brown 1988). In a 50-year study in Kansas, Fitch (1999) found that populations of racers initially increased as shrub cover increased on old fields, but numbers declined with advanced succession, as trees encroached on these areas. Moreover, three of 18 species studied by Fitch (1999) became locally extinct as succession progressed, four species (including racers) became much more scarce, and none gained appreciably in population size. It is possible that predation by raptors increased as more perch trees became available in these areas. In my study, habitat differences between areas of intensive activity and areas of limited activity indicated that racers may have selected open areas with less woody vegetation. Fewer than 4% of telemetry locations were in wooded areas. In addition, racers in my study required large areas.

Because conservation efforts in the Northeast have concentrated on wetlands and mature forests, the importance of early-successional habitats in maintaining biodiversity in the region has been largely ignored (Askins 1998). However, efforts to create, maintain, or restore large tracts of early-successional habitats in the Northeast have been recommended (Litvaitis et al. 1999). One of the proposed means of creating more of

these habitats is through clustering of clearcuts or other forms of disturbance. However, wildlife communities in regenerating forest stands may differ substantially from those communities found in old field habitats, partly because dense herbaceous cover lasts longer in old fields (DeGraaf et al. 1992). Therefore, an effective approach to enhancing habitat for early-successional species (including a number of songbirds [Askins 1994] and racers [Fitch 1999]) would be the restoration of shrub-dominated habitats or the acquisition of abandoned farmland. The New Hampshire Fish and Game Department recently acquired ca. 160 ha of land (Bellamy Wildlife Management Area) that is managed primarily for early-seral stages (J. Lanier, New Hampshire Fish and Game Department, personal communication). This area encompassed the largest of my study sites and had the highest capture index of snakes (Fig. 2).

Powerline corridors are another source of stable shrublands (Askins 1998). Racers have been observed on powerline corridors in Massachusetts and New Hampshire (S. Jackson, University of Massachusetts Cooperative Extension Service, personal communication; F. Mitchell, University of New Hampshire Cooperative Extension Service, personal communication; J. Taylor, University of New Hampshire, personal communication). Such areas may be most valuable when they occur in conjunction with other land uses that expand the area of suitable habitat (Askins 1998). By themselves, the linear configuration of corridors may facilitate intense predation, especially by raptors (Denoncour 1982).

The debate over whether to preserve single large or several small reserves to maintain species diversity has generated much discussion (e.g., Higgs and Usher 1980, Higgs 1981). Some researchers (e.g., McCoy and Mushinsky 1994) have suggested that

a number of smaller patches may harbor more species than a single patch of the equivalent area. In some instances, however, increases in species on small patches may be attributed to the encroachment of invasive species from surrounding areas (Mader 1981). My results lend support to the notion that large areas of early-successional habitat would be most beneficial to maintaining a diverse assemblage of snakes in New Hampshire.

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**Appendix 1.** Snakes collected under plastic cover sheets and in traps in southern New Hampshire, 1998 and 1999. Recaptures are included. “Adult” category includes subadults and adults.

SITE	YEAR SAMPLED	SPECIES								
		COMMON GARTER		BROWN		REDBELLY		MILK	OTHER	TOTAL ADULTS
		Adult	Neonate	Adult	Neonate	Adult	Neonate	Adult	Adult	
<i><b>SHEETS</b></i>										
Bellamy	1998, 1999	241	53	117	11	49	6	3	0	410
Channel 11	1998, 1999	4	7	0	0	1	0	1	0	6
Dudley Lot	1998, 1999	9	3	2	2	3	0	0	0	14
Foss Farm	1998, 1999	53	21	26	1	15	0	5	2 ribbon	101
Horti Farm	1998, 1999	28	13	5	0	0	0	1	0	34
Hoyt Pond	1998	6	3	0	0	0	0	1	0	7
Gables	1998	1	0	0	0	0	0	0	0	1
Moore Flds	1998, 1999	34	15	0	0	0	0	0	0	34
Pease	1998	20	8	1	0	4	0	0	0	25
Powerln-Dov	1998, 1999	3	5	0	0	2	2	1	1 green	7
Powerln-Lee	1999	0	0	0	0	0	0	0	0	0
Powerln-108	1999	0	1	0	0	1	1	0	0	1
Route 9	1998, 1999	19	11	2	0	21	1	3	5 racer	50
Route 155-1	1998, 1999	5	1	0	0	0	0	0	0	5
Route 155-2	1998, 1999	4	2	0	0	0	0	0	0	4
Route 155-3	1998, 1999	4	0	0	0	0	0	0	0	4
Route 155-4	1999	0	0	0	0	0	0	0	0	0
Route 155-5	1998, 1999	0	1	0	0	0	0	0	0	0
Route 155-6	1999	0	0	0	0	0	0	0	0	0
Route 155-7	1998, 1999	1	0	0	0	0	0	0	0	0

**Appendix 1. Continued**

Route 155-8	1998, 1999	3	0	0	0	0	0	0	0	3
Route 155-9	1998, 1999	2	0	0	0	0	0	0	0	2
Route 155-10	1999	0	0	0	0	0	0	0	0	0
Rt. 16 (x 15)	1998	0	0	0	0	0	0	0	0	0
Rt.16/New'tn	1999	0	0	0	0	0	0	0	0	0
Rt.4 (x 4)	1998	0	0	0	0	0	0	0	0	0
<b>TOTALS</b>		<b>437</b>	<b>144</b>	<b>153</b>	<b>14</b>	<b>96</b>	<b>10</b>	<b>15</b>	<b>8</b>	<b>709</b>
<b><i>TRAPS</i></b>										
Bellamy	1998, 1999	23	1	1	0	1	0	1	0	27
Channel 11	1998	4	1	0	0	0	0	0	0	5
Foss Farm	1998, 1999	26	0	1	0	0	0	2	1 ribbon	30
Horti Farm	1998, 1999	66	0	0	0	0	0	1	0	67
Pease	1998	32	0	0	0	1	0	0	5 green	38
<b>TOTALS</b>		<b>151</b>	<b>2</b>	<b>2</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>4</b>	<b>6</b>	<b>167</b>
<b>GRAND</b>										
<b>TOTALS</b>		<b>588</b>	<b>146</b>	<b>155</b>	<b>14</b>	<b>98</b>	<b>10</b>	<b>19</b>	<b>14</b>	<b>876</b>

**Appendix 2.** Pearson pairwise correlation matrix of habitat variables measured in areas of intensive and limited racer activity, southern New Hampshire, 1999. (Mnemonics as in Table 3.)

	%Grass	%Forb	%Wood	%Other	Lowveg	Hiveg	Nsheet	Nroad	Nforest	Canclos	Stems
%Grass	1.0										
%Forb	-0.2826	1.0									
%Wood	-0.3413	-0.6285	1.0								
%Other	-0.1517	-0.2818	-0.2096	1.0							
Lowveg	0.4846	-0.2994	-0.0712	0.0431	1.0						
Hiveg	-0.1979	-0.0563	0.1846	0.0297	0.0125	1.0					
Nsheet	-0.1133	0.1492	-0.1072	0.0700	-0.0372	0.1243	1.0				
Nroad	-0.0194	-0.0062	-0.0313	0.0886	0.0709	-0.1011	0.1501	1.0			
Nforest	0.0126	-0.1496	0.1496	-0.0172	-0.1765	0.0747	0.0568	-0.0675	1.0		
Canclos	-0.1482	-0.2205	0.1089	0.3590	-0.0640	0.0186	-0.0849	0.1021	-0.2257	1.0	
Stems	-0.1461	-0.6811	<b>0.8914</b>	-0.1712	0.0356	0.0912	-0.1401	-0.1091	0.1013	0.1104	1.0

**Appendix 3.** Racers monitored in southern New Hampshire, 1999.

<b>RACER #</b>	<b>SEX</b>	<b>SVL (cm)</b>	<b>WEIGHT (g)</b>	<b>DATE CAPTURED</b>	<b>DATE RELEASED</b>	<b>DATE OF LAST LOCATION</b>	<b># OF LOCATIONS</b>	<b>HOME RANGE (75%/ 100% ISOPLETH) -ha</b>
1	M	91	400	12 MAY 99	17 MAY 99	2 SEPT 99	72	12.2 / 31.4
2	M	102	435	4 JUN 99	8 JUN 99	13 AUG 99*	84	5.9 / 11.1
3	M	119	650	6 JUN 99	8 JUN 99	6 AUG 99	77	5.5 / 9.5
4	M	130	750	18 JUN 99	19 JUN 99	17 JULY 99	25	1.5 / 12.5
5	**F	97	430	21 JUL 99	22 JUL 99	13 AUG 99*	28	3.0 / 9.0
MEAN	-	109	533	-	-	-	57	5.6 / 14.7

\* SIGNALS RECEIVED THROUGH 2 SEPT 99, BUT NOT CONSISTENTLY ENOUGH FOR POSITIVE LOCATIONS.

\*\* GRAVID (EGGS PRESENT); TRANSMITTER IMPLANTED SUBCUTANEOUSLY.

Appendix 4. Home ranges of five racers monitored in southern New Hampshire, 1999.

