# MICROHABITAT FACTORS INFLUENCING SHREW DIVERSITY IN A SOUTHERN APPALACHIAN DECIDUOUS FOREST

A Thesis

by

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# ABSTRACT

## MICROHABITAT FACTORS INFLUENCING SHREW DIVERSITY IN A SOUTHERN APPALACHIAN DECIDUOUS FOREST

(December 1997)

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Shrews are important, keystone predators in many forest communities. Because of their extremely high metabolism, they feed voraciously and almost continuously on a wide variety of terrestrial invertebrates and small vertebrates. While previous studies suggest a relationship between shrew abundance and environmental moisture, relatively little is known about how other environmental factors influence microgeographic distribution and abundance of individual shrew species. To examine this problem, twelve 50x50 m plots were established in the Pisgah National Forest, Burke County, N.C., which consisted of three replicates in each combination of north and south slope (N/S) with and without a nearby stream (+ / -). A Y-shaped drift fence array with four pitfalls was placed in the center of each plot and opened monthly from August - November 1996, and from March - August 1997. Environmental factors such as temperature and rainfall, leaf litter moisture and depth, vegetative composition and cover, and volume and decay class of logs were measured to examine correlations with shrew diversity.

Five species of shrews (41 *Sorex cinereus,* 1 *S. dispar,* 105 *S. fumeus,* 15 *S. hoyi,* and 14 *Blarina brevicauda* ) were captured. Pitfalls also collected representatives of prey including invertebrates, salamanders, and small rodents. Results were consistent with those of other investigators that environmental moisture was most important in determining shrew species abundances and distributions. Shrews were more numerous and species diversity greatest in wetter sites (N+, N-, S+), and surface activity was increased during rainfall .

Resource partitioning was observed between *Sorex fumeus* and *S. cinereus.* Backwards-elimination, stepwise multiple regression analyses found *Sorex fumeus* abundance to be related to litter moisture, usable volume of very decomposed logs, and number of invertebrates ($R^2$=86.6%); while *S. cinereus* abundance was related to litter moisture, litter depth, and invertebrate size ($R^2$=54.9%). A strong relationship was also found between litter moisture, litter depth, and invertebrate size and overall shrew abundance ($R^2$=73.4%). Linear discriminant function analyses verified a significant separation of microhabitat between these two shrew species; with the microhabitat niche breadth of *S. cinereus* (1.33) narrower than than that of the larger *S. fumeus* (1.43). These species appear to follow the assembly rules of Fox and Kirkland (1992), that the structure of soricid communities is a result of competition between species of dissimilar size, mediated through the differential use of microhabitat.

# ACKNOWLEDGEMENTS

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Thanks also to Dr. Bob Murray for his helpful comments and for allowing me to use his drying ovens. He also supplied his 1996 Communities and Ecosystems class to help with vegetation analysis at my study sites. Special thanks to Dr. Ed Greene for his invaluable assistance with my statistical analyses, Judy Williamson for her clerical assistance, and to Bonnie Amaral of the USDA Forest Service for her cooperation with this project. Thanks also to the Graduate School, the Graduate Student Association Senate, and the Biology Graduate Student Association for providing me with necessary funding for my research.

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# DEDICATION

This paper is dedicated to my wife Janis for all of her patience while I completed my Master's degree. She has sacrificed a lot, and was willing to work in sometimes not-so-pleasant places in order to help earn money to let me go to school. Without her help in the field and her love and support, this research would not have been possible.

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# INTRODUCTION

One of the keys to balanced land management is an understanding of the ecological processes which support diverse forms of life (Dunson *et al.,* 1992; Sharitz *et al.,* 1992). Previous research into the management of small mammal communities has been prompted by the deleterious impact of many species on forest regeneration through the consumption of seeds and the destruction of seedings (Kirkland, 1977). Insectivorous mammals may be economically important in controlling insect pests which can defoliate trees or reduce seed germination (Anderson and Folk, 1993; Buckner, 1964, 1969; Churchfield, 1990; Holling, 1959). Where several species of shrews coexist, they may clear as much as 1.1 $m^2$ of insects per day (Churchfield and Brown, 1987), and can potentially promote regrowth of oak populations through their consumption of acorn predators such as weevils (Andersen and Folk, 1993).

Shrews (Family Soricidae) are very small, insectivorous mammals with extremely high metabolic rates (Buckner, 1964; Genoud, 1988; Morrison *et al.,* 1957). They prefer moist, cool forests with abundant leaf litter and fallen logs for nesting sites and for cover while foraging (e.g. Aitchison, 1987a; Churchfield, 1990; French, 1980; Hamilton, 1940; Jackson, 1928). Prey are primarily epigean (soil surface and litter-dwelling) and hypogean (soil-living) invertebrates (e.g. Bellocq *et al.,* 1994; French, 1984; Hamilton, 1930; Martin, 1981b; Ryan, 1986; Whitaker and French, 1984; Whitaker and Mumford, 1972) , although shrews have been known to feed also on seeds (Criddle, 1973), fungi (Whitaker, 1962), and small vertebrates such as salamanders (Brodie *et al.,* 1979; Hamilton, 1930) and rodents (Getz *et al.,* 1992; Martin, 1981a).

Shrews are important as secondary or tertiary consumers in litter-detritus food webs. They cull dominant, large-sized invertebrates and allow greater species diversity and increased trophic complexity (e.g. Aitchison, 1987a; Churchfield, 1990). In a variety of terrestrial ecosystems, shrews may be keystone predators (Aitchison, 1987a; Churchfield, 1990; Platt and Blakley, 1973). Shrews serve as prey to tertiary or quaternary predators such as owls, hawks, snakes, foxes, and mustelids (Aitchison, 1987a; French, 1980; Hamilton, 1940; Jackson, 1928; Pearson and Pearson, 1947).

Although primarily nocturnal (Teferi and Herman, 1995), shrews must forage regularly because of their high metabolism, and often consume more than their body weight per day (Buckner, 1964; Morrison *et al.,* 1957). Shrews usually eat any organism they encounter of energy value (Barnard and Hurst, 1987; Getz, 1961a; Pierce, 1987; Ryan, 1986). Foraging is followed by short periods of sleep (Saarikko and Hanski, 1990). In winter, shrews forage in underground burrows (Aitchison, 1987a; Merritt, 1986), but over 80% of their time is spent inactive at low, resting metabolism (Aitchison, 1987b; Churchfield, 1982a; Martinsen, 1969).

Habitat utilization by small mammals is dependent upon a wide range of environmental factors (e.g. Buckner and Shure, 1985; Dueser and Shugart, 1979; Getz, 1961a, 1961b). Since the quality of small mammal habitat often relates to the composition of the vegetation (Fox and Fox, 1981), species diversity may differ significantly between different successional stages of forest (Kirkland, 1977; Petranka *et al.,* 1994). Likewise, compositions of small mammal faunas may vary greatly within same-age forest stands due to environmental differences between adjacent north- and south-facing slopes (Vaughan, 1954, 1986). In the northern hemisphere, north-facing slopes receive less direct-beam radiation than south-facing slopes and thus tend to be cooler and moister (Matlack, 1993, 1994; Wales, 1972).

Previous studies have demonstrated that environmental moisture may be the ultimate determinant of within-habitat diversity and relative abundances of soricids (Feldhamer *et al.*, 1993; Wrigley *et al.*, 1979; Getz, 1961a) because it affects the amounts of prey (e.g. Getz, 1961a) and the water balance of shrews (Chew, 1951). More shrews are captured in hydric and mesic communities than in xeric ones (Wrigley *et al.,* 1979). In addition, shrews may reside under logs or rocks, beneath litter, or beneath dense foliage because prey are abundant in these places, and because temperature and humidity are moderated by such cover (Ash, 1995; Maser *et al.,* 1979; Petranka *et al.,* 1994; Tallmon and Mills, 1994; Vaughan, 1986; Yahner, 1986).

I hypothesize that variations in moisture, cover, and food should produce significant differences in the richness and evenness of shrew species within same-age forests. Areas of high moisture, cover, and prey availability should produce more shrew captures than those without. In addition, competition between sympatric species should be minimized by differential use of these resources (Dickman, 1988; Fox and Kirkland, 1992; Terry, 1981; Yashino and Abe, 1984). Examinination of how microhabitat affects shrew diversity will provide a greater understanding of how the physical environment contributes to community structure, how biological diversity controls ecological processes, and how ecological processes can be sustained through improved management strategies (Lubchenko *et al.*, 1991).

## LITERATURE REVIEW

Shrews are of greatest importance to small mammal communities in terms of diversity in northern third of the United States and the higher elevations of the Appalachian Mountains, where they comprise over 25 percent of the species richness (Kirkland, 1991). Common shrew species in the southern Appalachians include *Sorex cinereus,* the masked shrew; *S. fumeus,* the smoky shrew; and *Blarina brevicauda,* the northern short-tailed shrew. *Sorex (Microsorex) hoyi,* the pygmy shrew; *S. dispar,* the long-tailed or rock shrew; and *S. palustris,* the water shrew, are also present but are rare. At lower elevations, species include *S. longirostris,* the southeastern shrew; *B. carolinensis,* the southern short-tailed shrew; and *Cryptotis parva,* the least shrew (Webster *et al.,* 1985).

Assemblages tend to consist of four to five shrew species (e.g. Buckner, 1966; Caldwell and Bryan, 1982; Kirkland, 1991; Spencer and Pettus, 1966; Wrigley *et al.,* 1979), each of which is dissimilar in size. This dissimilarity in species' sizes results in partitioning of resources (Feldhamer *et al.,* 1993), because according to the assembly rule for soricid communities (Fox and Kirkland, 1992), larger body size conveys a competitive advantage by improving access to higher-quality microhabitats. Larger species forage more extensively in dense or structurally complex microhabitats that contain larger, more energetically profitable prey (Dickman, 1988), usually require more food than small species to sustain their body mass, and may have longer durations of diurnal foraging activity (Dickman, 1988). Thus large shrews utilize the very best food patches to minimize both energy expenditure and the risk of predation (Barnard and Brown, 1987; Barnard and Hurst, 1987; Hanksi, 1989).

Larger species also dig more extensively in topsoil and litter than do smaller species (Dickman, 1988; Terry, 1981; Yashino and Abe, 1984). While no shrew species is adapted for a truly fossorial lifestyle (Churchfield, 1980a; 1990; Hamilton, 1940), larger species are typically thick-bodied and robust , enabling them to push their way through soil and leaf litter using their snout, teeth, and fore feet to excavate passages

(Churchfield, 1980a, 1990; Dueser and Shugart, 1979; Jackson, 1928). Earthworms and soil-dwelling insect larvae are often important prey items for hypogeal shrews, which distinguishes them from the more epigeal species (Churchfield, 1990).

Ecological separation based on prey size has been demonstrated for lizard communities (Asplund, 1974; Pianka, 1986). Although diminutive shrews are more capable than large shrews of utilizing small invertebrate prey (Getz, 1961a), shrews do not restrict their diets to a particular size range of prey (Churchfield, 1990). Smaller shrews are quite capable of consuming large prey when it is present in the available food spectrum (Churchfield, 1990; Dickman, 1988). Although Getz (1961a) discounted interspecific competition as an important factor in determining shrew distributions, removal experiments have demonstrated that in the absence of larger congeners, smaller shrew species switched to more productive microhabitats and ate larger prey (Churchfield, 1990; Dickman, 1988; Neet and Hausser, 1990). Therefore, shrew community diversity should depend primarily upon the availability of different foraging microhabitats (Fox and Kirkland, 1992; Hawes, 1977; Terry, 1981; Yashino and Abe, 1984).

Microhabitat selection is strongly influenced by environmental moisture (Ash, 1995; Doyle, 1987; Getz, 1961a; Jaeger, 1980; Maser *et al.,* 1979; Tallmon and Mills, 1994), availability of prey (Bellocq *et al.,* 1994; Buckner, 1964; Getz, 1961a; Hanksi, 1989); and protection from predators (Churchfield, 1990; Doyle, 1987; Seagle, 1985). Shrews prefer mesic habitats not only because food is more abundant (Churchfield, 1990; Feldhamer *et al.,* 1993; Wrigley *et al.,* 1979), but also because shrews are unable to regulate their evaporative water loss in low humidities (Chew, 1951; Getz, 1961a). Some species such as *Blarina brevicauda* can only maintain a water balance if the air in their burrows is saturated (Chew, 1951; Getz, 1961a). Environmental moisture is perhaps the most important factor in determining the distributions and diversity of shrews (Feldhamer *et al.,* 1993; Getz, 1961a; Spencer and Pettus, 1966; Wrigley *et al.,* 1979).

Surface activity of shrews is greatly influenced by rainfall (Doucet and Bider, 1974; McKay, 1996; Vickery and Bider, 1978). Nocturnal rainfall can cause a 50% increase in activity (Vickery and Bider, 1978). Amount of precipitation is also important.

Shrews are more active during moderate levels of rainfall and less active during heavy rain (Vickery and Bider, 1978). Rainfall may increase surface activity of shrews because it either provides conditions necessary for the maintenance of proper water balance, or increases the availability of invertebrate prey (Fraser, 1976; Jaeger, 1980; McKay, 1996).

Moisture is mediated during dry periods by the amount of available cover (Ash, 1995; Getz, 1961a; Jaeger, 1980; Maser *et al.,* 1979; Morris, 1979; Yahner, 1986). This cover may be in the form of leaf litter (Ash, 1995; Petranka *et al.,* 1994); herbs (Yahner, 1986), or downed logs (Jaeger, 1980; Maser *et al.,* 1979; Petranka *et al.,* 1994; Tallmon and Mills, 1994). Cover in these forms is also important for protection against predation while foraging (Doyle, 1987; Maser *et al.,* 1979; Seagle, 1985; Yahner, 1986).

Leaf litter acts as sponge to retain moisture following rains (Petranka *et al.,* 1994). Litter moisture and depth is lower in areas with xeric conditions (Ash, 1995; Buckner and Shure, 1985). Moisture content and decomposition rates of leaf litter are also related to its vegetative composition (Dix, 1984; Elliott *et al.,* 1993), as is the size of invertebrate prey living within (Aitchison, 1987a). If the litter becomes dry, patchy, or thin, then shrews may be deprived of the moisture necessary for maintenance of their water balance (Chew, 1951), and adequate prey populations may no longer be present (Ash, 1995). Likewise, a dense layer of herbaceous cover produces suitable mesic conditions in the soil and litter (Yahner, 1986). Shading by vegetation minimizes evaporative drying of leaf litter during dry periods (Petranka *et al.,* 1994). Adequate vegetative cover also ensures appropriate microenvironments for litter-dwelling arthropods (Yahner, 1986).

The importance of logs as wildlife habitat is often overlooked (Maser *et al.,* 1979). Because of their persistence, logs provide a long-term stable structure on which many animals depend for survival (Maser *et al.,* 1979). Logs are used for hiding cover and as foraging or nesting sites (e.g. Doyle, 1987; Hamilton, 1940; Jaeger, 1980; Kitchings and Levy, 1981; Maser *et al.,* 1979; Tallmon and Mills, 1994). Logs decompose more slowly under xeric conditions (Abbott and Crossley, 1982), but logs in the later stages of decay serve as reservoirs of moisture (Jaeger, 1980; Maser *et al.,* 1979).

Much of a shrew's water intake comes directly from its food. In feeding primarily on invertebrates, it gets food of high (60-90%) water content (Chew, 1951). While shrews do demonstrate some prey preferences (Churchfield, 1990), they usually have a very generalized diet (e.g. Aitchison, 1987a; Hamilton, 1930), eating almost any organism that they encounter (Barnard and Hurst, 1987; Getz, 1961a; Martinsen, 1969; Pierce, 1987; Ryan, 1986). Size of available invertebrate prey may be more important to shrews than the taxonomic category (Ryan, 1986; Whitaker and French, 1984; Yalden, 1981). Getz (1961a) surmised that within areas having favorable moisture conditions, food availability was the most important factor in the distribution of shrews.

Although they feed almost exclusively on invertebrates, shrews will also occasionally eat vegetable matter, fungus, and other small vertebrates (Hamilton, 1930). When invertebrate food supplies are low or inaccessible, as in winter, shrews also eat seeds (Criddle, 1973) or the subterranean fungus *Endogone* (Whitaker, 1962). Larger shrews such as *Blarina brevicauda* and *Sorex fumeus* are known to eat nestling voles (Getz *et al.,* 1992) and salamanders (Hamilton, 1930, 1940; Brodie *et al.,* 1979; Robinson and Brodie, 1982). In laboratory experiments, shrews prefer the mountain dusky salamander, *Desmognathus ochrophaeus* (Brodie *et al.,* 1979; Orr, 1967), presumably because it lacks the noxious skin secretions found in many other salamander species (Brodie, 1983; Brodie *et al.,* 1979; DiGiovanni and Brodie, 1981).

Species respond to components of their environment on a scale of resolution much finer than gross habitat differences (Dueser and Shugart, 1978; Seagle, 1985). Most studies of small mammal diversity and distributions have examined differences between grossly dissimilar habitat types (e.g. Feldhamer *et al.,* 1993; Getz, 1961a,b; Innes *et al.,* 1990; Kirkland, 1977; Wrigley *et al.,* 1979). Fewer studies have examined small mammal species distributions within the same habitat (Doyle, 1987; Kitchings and Levy, 1981; Hawes, 1977; Seagle, 1985; Yahner, 1986). To my knowledge, only one of these (Ford *et al.,* 1996) has closely examined shrew communities in the southern Appalachian Mountains, despite being an area of very high soricid species richness (Kirkland, 1991). Here, I present one of the first studies on the relationship between microhabitat and shrew diversity within an even-aged, southern Appalachian deciduous forest.

## MATERIALS AND METHODS

The study area was located within a one-mile radius of the Gingercake Creek drainage of the Pisgah National Forest, Burke County, North Carolina (Fig. 1). This area is characterized by steep slopes (range 20 to 38°) with numerous streams and seepages. Vegetation consists primarily of mixed deciduous hardwoods with an understory of *Rhododendron maximum* and *Kalmia latifolia.* Stand age is approximately 55 years old according to a USDA Forest Service CISC database used by Petranka *et al.* (1994), and elevations average approximately 787 m (2600 feet) (range 757 to 818 m) Sites were selected according to two classification variables: aspect (North- or South-facing) and the presence (+) or absence (-) of a permanent water source, as these variables contribute greatly to environmental moisture (Doyle, 1987; Getz, 1961a; Matlack, 1993, 1994; Petranka *et al.,* 1994; Wales, 1972). Three replicates were assigned for each of the four site classes (N+, N-, S+, S-). At each of these twelve sites a 50 m x 50 m plot was established, positioned with boundary lines parallel and perpendicular to prevailing contours. Slope steepness was measured for each plot. Those sites with permanent water sources had a stream or seepage located within the perimeter of the plot, and were located at the bottom of slopes. By contrast, sites without water sources were located high on ridges.

In the center of each plot I constructed a Y-shaped drift fence array with four pitfall traps; one at the end of each 3.0 m arm and one at the intersection (Fig. 2). Pitfall-trapping has been shown to be more effective at capturing shrews than snap- or live-trapping (e.g. Brown, 1967; MacLeod and Lethiecq, 1963; Mengak and Guynn, 1987), especially for the smaller species of *Sorex* (Brown, 1967; Wolfe and Esher, 1981), which often have been considered rare in many locales simply due to ineffective trapping methods (Gibbons and Semlitsch, 1981).

As suggested by Gibbons and Semlitsch (1981), drift fence arrays were constructed of 50 cm high aluminum flashing, of which 10 cm was placed below the

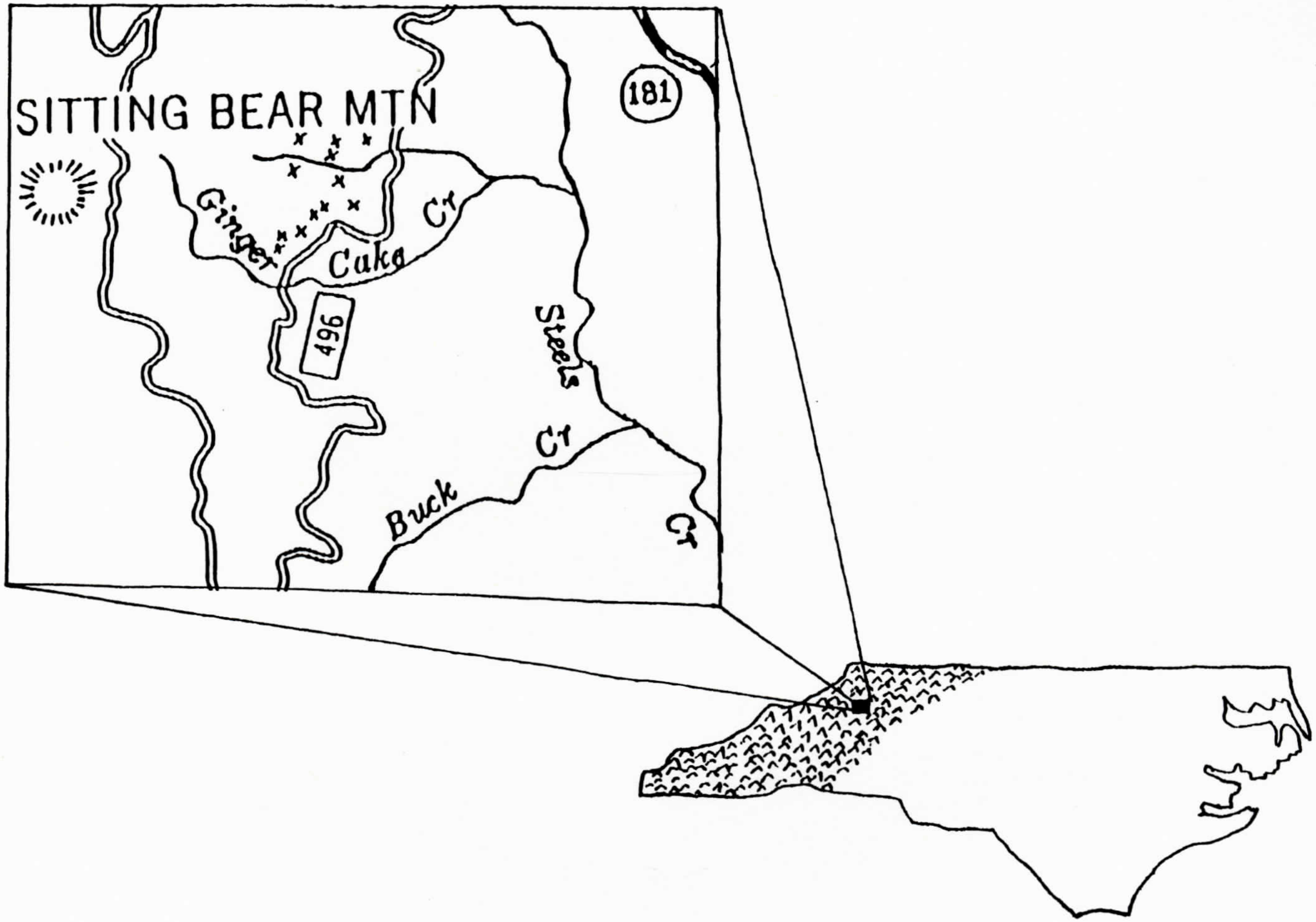

Figure 1. Location of study sites (x) within the Pisgah National Forest, Burke County, N.C.

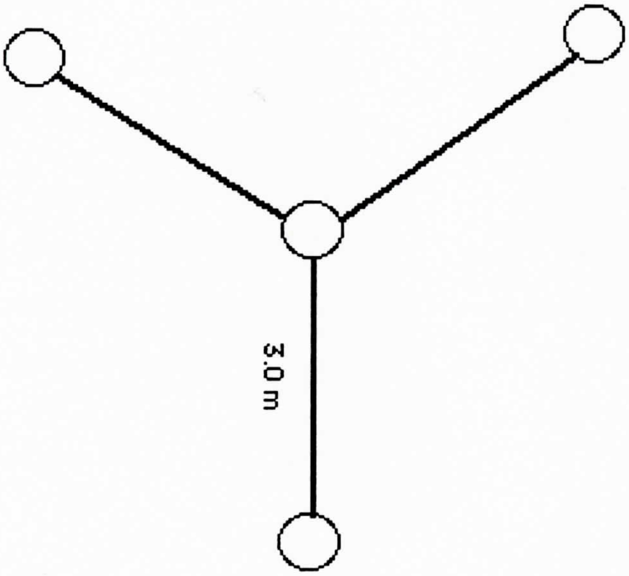

Figure 2. Drift fence array with four pitfalls.

surface of the ground to prevent animals from passing underneath. Twenty-liter (5 gallon) plastic buckets served as pitfalls, to permit the capture of species that could easily escape from shallow containers. To prevent accumulation of rain and leaves and to exclude larger animals, a 50 x 50 cm board was placed over each pitfall, elevated approximately 10 cm with nails (Fig. 3).

Humane methods of kill-trapping are those that kill animals swiftly and avoid damaging the body parts required for research (Rudran and Kunz, 1996). Each pitfall contained approximately 10 cm of 10% formalin (Ryan, 1986), so animals quickly drowned upon entering. The use of a preservative in pitfalls prevents escape, predation within traps, and decomposition of the individual and its stomach contents (e.g. Bellocq *et al.*, 1994; Howard and Brock, 1961; Ryan, 1986). Besides their effectiveness, the use of pitfalls with formalin is advantageous because they can be left continuously set, each trap can catch more than one animal, and they can be examined with one visit convenient to the investigator (Howard and Brock, 1961).

Although drift fences with pitfalls require extensive time and effort put into construction, maintenance, and operation (Gibbons and Semlitsch, 1981), the amount of data obtained is often far superior to other forms of collecting for a wide array of terrestrial animals (e.g. Gibbons and Semlitsch, 1981; Mengak and Guynn, 1987; Ryan, 1986). In addition to shrews, pitfalls capture invertebrates (insects, spiders, centipedes, annelids, and molluscs, among others) and salamanders, which serve as representatives of prey availability for each plot. Pitfalls also capture many species of rodents.

Data collection occurred for a period of six consecutive days each month from August 1996 through November 1996, and from March 1997 through August 1997. No collection was done during the winter months due to site inaccessibility, and the relative inactivity of shrews during this period (Aitchison, 1987a; Churchfield, 1980b, 1982a; Merritt, 1986). Vertebrates were removed from traps daily, and invertebrates were strained from pitfalls on the last day of each trapping period. Pitfalls were closed with tight-fitting plastic lids when not in use.

Vertebrate specimens were immediately taken back to the lab where they were

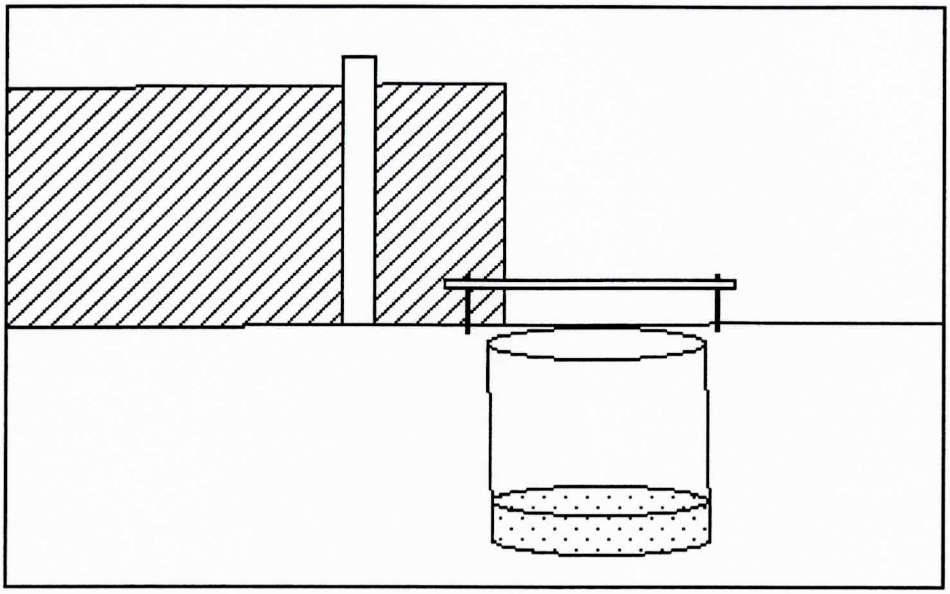

Figure 3. Detail of drift fence with 20 L pitfall containing 10% formalin. Boards covered pitfalls to exclude rain, leaves, and larger animals.

measured, identified, and cataloged. Shrews were identified using the key of Caldwell and Bryan (1982) (Appendix A), and the species descriptions in Webster *et al.* (1985). As a precaution, approximately 1 cc of 20% formalin into the abdomen of each mammal to prevent further degradation of the stomach contents. Specimens were fixed in 10% formalin and later transferred to 70% ethanol.

For each plot, invertebrates were identified to order. For each order, the number of individuals was counted and collectively weighed to obtain a total biomass. These figures were then used to calculate the average prey size (mass in grams) for each individual invertebrate order. In addition, the total number of invertebrates and biomass per plot were calculated, as well as the overall average invertebrate prey size.

Shrew stomach contents were analyzed for comparisons with prey availability (Bellocq *et al.,* 1994; French, 1984; Ryan, 1986). Stomachs were removed from shrews, and the contents emptied into a shallow petri dish and examined under a binocular dissecting microscope. Contents were identified to order, if possible, and visually estimated as a percent of the total volume.

In addition to an examination of the items collected in pitfalls, other components of the microhabitat were measured. Microhabitat variables (Table 1) were selected based upon their importance to shrews in providing environmental moisture, prey abundance, and protective cover (Doyle, 1987; Dueser and Shugart, 1978; Getz, 1961a; Kitchings and Levy, 1981; Seagle, 1985; Yahner, 1986). These included vegetation (composition and % herbaceous cover); cover (number and volume of logs, and leaf litter depth); litter moisture; and temperature. Some of these variables required sampling only once (trees and logs), while others vary temporally and required multiple sampling.

Trees and shrubs were examined using the point-quarter method (Cox, 1996). Three 50 m transects were located across contours within each plot; one along the midline and one 12.5 m to the inside of each of the two parallel sides. Trees and shrubs were considered to be significant if they were ≥ 4 cm in stem diameter. Measurements were used to obtain importance values for each species per plot, as well as species richness.

The same transects were used to determine the relative amounts of logs (coarse

Table 1. Summary of 35 measured habitat variables.

| Mnemonic | Description |
|---|---|
| INVERTN | Number of invertebrates |
| INVERTBM | Invertebrate biomass (g) |
| INVERTG | Average invertebrate size (mass in grams) |
| BETULA | Importance value of Betula lenta |
| CHOAK | Importance value of Quercus montanus |
| PINUS | Importance value of Pinus strobus |
| POPLAR | Importance value of Liriodendron tulipifera |
| RHODO | Importance value of Rhododendron maximum |
| TSUGA | Importance value of Tsuga canadensis |
| EVRGRN | % of evergreen vegetation |
| TREEN | Number of tree and shrub species |
| HERBN | Number of herbaceous species |
| HERBCVR | % herbaceous cover |
| CWDN | Number of downed logs ( ≥ 10 cm in diameter) |
| USEVOL | Total usable volume of logs (m3) |
| USEVOL3 | Usable volume of CWD Class 3 |
| USEVOL4 | Usable volume of CWD 4 |
| USEVOL5 | Usable volume of CWD 5 |
| LITDEPTH | Leaf litter depth (cm) |
| LITMOIST | % moisture content of leaf litter |
| AVGTEMP | Average temperature (° F) |
| TEMPFLX | Average daily temperature fluctuation |
| SLOPE | Steepness of site ( ° from 0) |
| SLMNDRS | Number of salamanders |
| DOCHR | Number of Desmognathus ochrophaeus |
| EURYCEA | Number of Eurycea wilderae |
| PCINER | Number of Plethodon cinereus |
| PCYLIND | Number of Plethodon cylindraceus |
| PYONAH | Number of Plethodon yonahlossee |
| RODENTS | Number of rodents |
| CLETHR | Number of Clethrionomys gapperi |
| PEROMYS | Number of Peromyscus leucopus |
| NAPOZAP | Number of Napaeozapus insignis |
| RAINDAYS | Number of rainy days per trapping period |
| INRAIN | Amount of rain per trapping period in inches |

woody debris, or CWD) within plots, using a line-intercept method (Howard and Ward, 1972; Petranka *et al.*, 1994). The diameter and length of any fallen log ≥10 cm in diameter at the point of intersection along the transect were recorded. If the log had any branches ≥10 cm in diameter, they were treated as separate logs.

Additionally, the log's decomposition class was ranked using the system described by Maser *et al.* (1979). This scale ranges from Class 1 CWD for recently fallen trees with support points intact and little evidence of decay; to Class 5 CWD for extremely decomposed, soft, moist logs which are mostly buried by soil and forest litter (Fig. 4, Table 2). Shrews do not utilize all decay classes (Maser *et al.*, 1979). Class 1 and 2 logs were considered "unusable" for shrews because they provide little cover since they are suspended above ground and have not undergone significant decay (Petranka *et al.*, 1994).

The volume of logs which is usable by shrews as refugia while foraging or as nesting sites was calculated based upon the log's dimensions and decay class (Fig. 5). Since a Class 3 log is completely on the ground, but has a texture that is too hard for burrowing, the amount of cover it provides is limited to the shelter space alongside and underneath the edges of the log (Maser *et al.*, 1979). This cover is calculated as the half the volume of the imaginary rectangular box minus half the volume of the cylindrical log, or $(0.5d^2 l) - (0.5\pi r^2 l)$, where d is the diameter, l is the length, and r is the radius. In contrast, Class 5 logs are very soft, and shrews can therefore penetrate the interior (Maser *et al.*, 1979). However, they are embedded in the soil and have no shelter underneath their edges. The usable volume of Class 5 logs then is calculated simply as the volume of the log, or $(\pi r^2 l)$. A Class 4 log provides both interior space and edge shelter (Maser *et al.*, 1979), and so its usable volume may be calculated as $(0.5d^2 l) + (0.5\pi r^2 l)$.

Components of the herbaceous layer were measured for each trapping period. At every 5 meters along the midline transect, a 1 $m^2$ quadrat was established, for a total of ten quadrats per plot. For each quadrat, the percent cover of each plant species < 0.5 m high (Doyle, 1987; Nudds, 1977) was visually estimated. These values were used to calculate

Table 2. A 5-class system of log decomposition (after Maser *et al.*, 1979).

| Log characteristics | CWD Class 1 | Class 2 | Class 3 | Class 4 | Class 5 |
|---|---|---|---|---|---|
| Bark | intact | intact | trace | absent | absent |
| Twigs <3 cm | present | absent | absent | absent | absent |
| Texture | intact | intact to partly soft | hard, large pieces | small, soft blocky pieces | soft and powdery |
| Shape | round | round | round | round to oval | oval |
| Color of wood | original color | original color | original color to faded | light brown to faded brown or yellowish | faded to light yellow or grey |
| Portion of log on ground | log elevated on support points | log elevated on supports but sags slightly | log is sagging near ground | completely on ground | completely on ground or embedded |

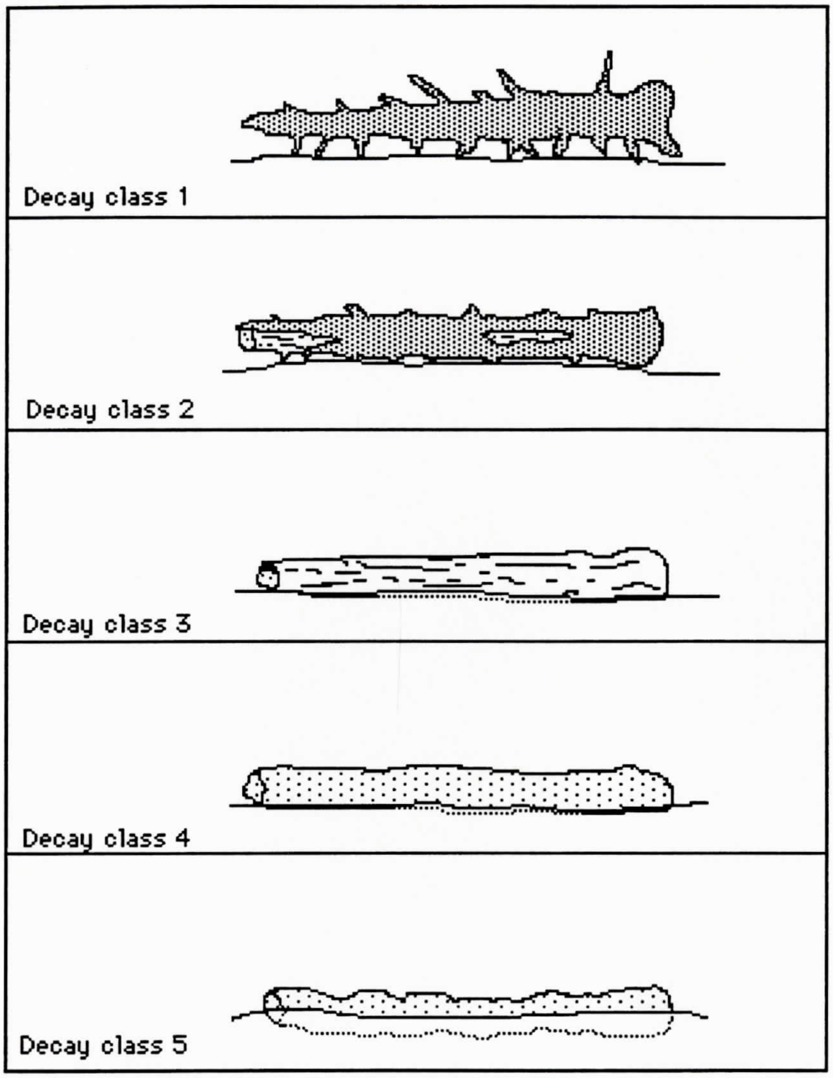

Figure 4. The appearance of logs in each of the five decomposition classes (after Maser *et al.,* 1979).

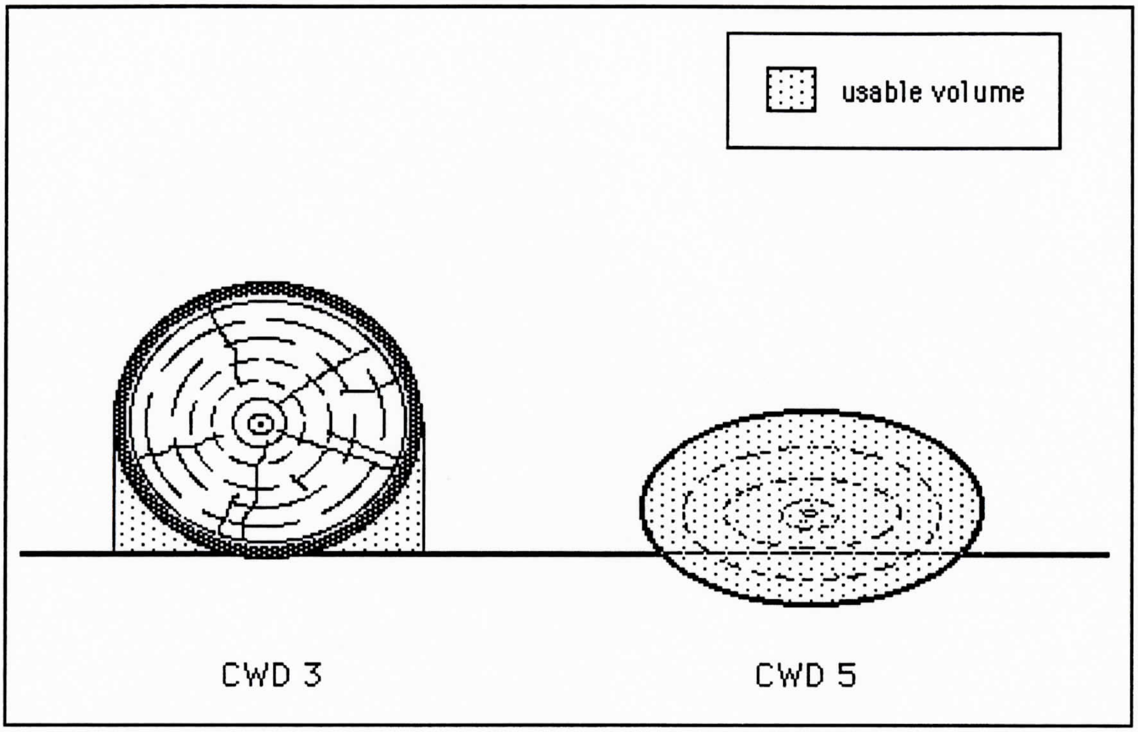

Figure 5. The amount of cover provided by logs (CWD) for small vertebrates is directly related to the size of the log and its decomposition class. Larger logs provide more cover than do smaller logs. A Decay Class 3 log is round and is too hard in texture for animals to burrow into, so the amount of usable volume it provides is limited to the shelter space underneath and alongside the edges. A Decay Class 5 log is flattened and very soft for burrowing, allowing animals such as shrews to utilize its interior. Decay Class 4 logs provide a combination of these usable spaces.

average species richness and percent cover of herbs for each plot.

Leaf litter depths were measured by simply pressing a cm ruler through the litter to the A-horizon of the soil. These measurements were also taken at each quadrat, for a total of ten measurements per plot (Ash, 1995). Litter depth was measured for each trapping period and was averaged per plot.

Litter moisture measurements were obtained using the procedure described by Ash (1995). Litter was defined as non-woody material and woody stems <10 mm in diameter. A 0.25 $m^2$ sample was randomly collected from each plot on three days during each trapping period. Samples were transported in plastic bags and weighed immediately upon return to the lab (wet mass). They were then transferred into paper bags, dried at 100° C for 24 hours, and reweighed (dry mass). Litter moisture content was calculated as wet mass - dry mass, and expressed as a percent of wet mass.

Measurements of ground temperatures were obtained by placing a Max-Min thermometer on a tree approximately 0.5 m above the ground (Getz, 1961a; Matlack, 1993). Thermometers were oriented parallel with the aspect of the plot slope, to simulate the effect of sunlight on the ground surface temperatures (Wales, 1972). Maximum and minimum temperatures were recorded daily during each trapping period to obtain average temperatures per plot, and the degree of temperature fluctuation (thermal stability).

Daily precipitation data were collected approximately 14.5 km (9 miles) from the study site at the Morganton, Burke County, NC weather station (National Climatic Data Center, 1997). For each sampling period, the number of rainy days and the total amount of precipitation was recorded. Rainy days were defined as those during which 2.5 mm (0.1 in) of rain was recorded (McKay, 1996).

For each of the 35 variables in Table 1, a one-way analysis of variance was performed on the twelve plots by their respective site classifications. Possible significant interactions between site classification variables (aspect and proximity to water) were analyzed using a two-way ANOVA. In addition, mean values for percent litter moisture were used to designate site classes as either hydric (wet), mesic (moderate), or xeric (dry), (after Wrigley *et al.,* 1979).

Abundances of shrews were pooled by site class, and subjected to a Chi-square goodness-of fit test between moisture regimes. The Shannon-Weiner index was used to calculate species diversity (H') for each regime. In addition, a two-way ANOVA was performed for shrew abundances to examine within-site variance created by differences in microhabitat. Species with small sample sizes were excluded from individual analyses.

Regression analysis was performed for shrew abundances on each of the 35 variables in Table 1. Although univariate tests may not demonstrate significant relationships, variables may become significant in combination with other variables (Seagle, 1985). The best three predictors of shrew abundances were determined by entering the entire set of habitat variables into a stepwise multiple regression with a value of 2.0 for both "F-to-enter" and "F-to-remove". This procedure first selects the predictor with the highest correlation coefficient. Then at each step, an F-statistic was calculated for each remaining predictor. If the partial correlation coefficient for any of these variables was less than the value of "F-to-remove" it was eliminated from the model, and if any value was greater than the "F-to-enter" it was added. Steps were repeated until no variables met the criteria for addition or removal (Minitab Incorporated, 1996).

Additionally, a separate analysis was performed to examine niche partitioning between shrew species. This analysis used only the forest-floor microhabitat variables (Dueser and Shugart, 1978) and primary prey variables (Brodie *et al.,* 1979; Ryan, 1986; Yalden, 1981) previously determined to be important to shrews. Because many of these variables are conceptually similar or are significantly correlated, some had to be eliminated from consideration (Draper and Smith, 1966; Dueser and Shugart, 1979). For example, INVERTBM was excluded because it relates to both INVERTN and INVERTG, which could be partitioned separately by shrews. Similarly, AVGTEMP was excluded because it directly influences LITMOIST. By eliminating redundancy, the entire set of variables was reduced to the eleven most ecologically important or meaningful (Table 3).

The importance of each of these 11 variables to individual shrew species was determined by regressing the number of shrews captured per plot (dependent variable) on these predictors (independent variables), using backwards-elimination, stepwise multiple

Table 3. Correlation coefficients (r) for the subset of 11 habitat variables used for backwards-elimination, stepwise multiple regression and discriminant function analyses.

| **Mneumonic** | DOCHR | EVRGRN | HERBCVR | HERBN | INVERTG | INVERTN | LITDEPTH | LITMOIST | USEVOL3 | USEVOL4 | USEVOL5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| DOCHR | — | 0.764 | -0.016 | -0.366 | -0.155 | -0.486 | 0.047 | 0.557 | -0.236 | 0.533 | 0.184 |
| EVRGRN | 0.764 | — | -0.346 | -0.573 | -0.524 | -0.266 | 0.006 | 0.752 | -0.35 | 0.463 | 0.568 |
| HERBCVR | -0.016 | -0.346 | — | 0.634 | 0.361 | -0.092 | -0.281 | -0.11 | 0.025 | -0.019 | -0.142 |
| HERBN | -0.366 | -0.573 | 0.634 | — | 0.453 | -0.055 | -0.296 | -0.309 | 0.028 | -0.036 | -0.396 |
| INVERTG | -0.155 | -0.524 | 0.361 | 0.453 | — | -0.225 | -0.338 | -0.657 | 0.203 | 0.174 | -0.61 |
| INVERTN | -0.486 | -0.266 | -0.092 | -0.055 | -0.225 | — | 0.023 | -0.373 | 0.443 | -0.602 | -0.098 |
| LITDEPTH | 0.047 | 0.006 | -0.281 | -0.296 | -0.338 | 0.023 | — | -0.024 | -0.526 | -0.061 | -0.073 |
| LITMOIST | 0.557 | 0.752 | -0.11 | -0.309 | -0.657 | -0.373 | -0.024 | — | -0.368 | 0.405 | 0.791 |
| USEVOL3 | -0.236 | -0.35 | 0.025 | 0.028 | 0.203 | 0.443 | -0.526 | -0.368 | — | -0.403 | -0.276 |
| USEVOL4 | 0.533 | 0.463 | -0.019 | -0.036 | 0.174 | -0.602 | -0.061 | 0.405 | -0.403 | — | 0.322 |
| USEVOL5 | 0.184 | 0.568 | -0.142 | -0.396 | -0.61 | -0.098 | -0.073 | 0.791 | -0.276 | 0.322 | — |

regression (Yahner, 1986). Unlike normal stepwise multiple regression, the backwards-elimination method has the advantage of being unaffected by the order in which predictors are entered, but is more limited in the amount of variables it can accommodate conveniently (Minitab Incorporated, 1996). This method begins with a model containing a combination of all possible predictors, and systematically removes those variables which contribute the least to the overall regression equation (Draper and Smith, 1966; Minitab Incorporated, 1996). This procedure was continued until the three most powerful predictors of shrew species abundances remained. Those species with small sample sizes were not included in the analyses. When the number of predictors approaches the number of data points in a sample, it is probable that any observed patterns are fortuitous and of no ecological consequence (Williams, 1983).

To verify ecological separation between shrew species, the same eleven predictor variables were entered into a linear discriminant function analysis (Minitab Incorporated, 1996). This procedure predicts species membership based on a set of continuous variables, with g= number of groups (species), and p= number of predictors (Dueser and Shugart, 1978, 1979; Williams, 1983). Stepwise models sequentially extract those orthogonal variables most capable of separating species by maximizing the among- to within-groups sums of squares (Morris, 1979); and provide the Mahalanobis distances ($D^2$), or sample squared distances between group means (Johnson and Wichern, 1992). Mahalanobis distances may be used to test if the population means of two groups show significant separation by referring Fisher's equation:

$$[(n_1+n_2-p-1) / ((n_1+n_2-2)p)] * [(n_1 n_2) / (n_1+n_2)] D^2$$

to an F-distribution with $\nu_1 = p$ and $\nu_2 = n_1+n_2-p-1$ degrees of freedom, and with $n_1$ and $n_2$ representing the sample size of each of the two species, respectively (Johnson and Wichern, 1992). Breadth of microhabitat use (MB) for each of these species was determined using the modification of Levins' equation:

$$MB = -\sum_j P_{ij} \log P_{ij}$$

where $P_{ij}$ is the proportion of the total number of captures for species $_i$ captured at plot $_j$ (Yahner, 1986).

# RESULTS

During 2544 trap-nights (TN), a total of 776 vertebrates were collected. Of this total, 176 shrews (105 *Sorex fumeus,* 41 *S. cinereus,* 15 *S. hoyi,* 1 *S. dispar,* 14 *Blarina brevicauda*) were captured. Pitfalls also captured 336 rodents, 259 salamanders, 3 frogs, 1 toad, and 1 snake. Numbers of vertebrate species collected for each of the four site classes are given in Table 4.

One-way analysis of variance showed that shrew species differed significantly in both mass (F= 421.94; d.f.= 3,119; P <.001) and body length (F=334.49; d.f.=3,119; P <.001). Mean mass (g) (± SE) was 23.27 ± 3.89 for *Blarina brevicauda,* 10.47 ± 1.52 for *Sorex fumeus,* 5.92 ± 0.80 for *S. cinereus,* and 4.04 ± 0.56 for *S. hoyi.* Mean body length (mm) was 76.29 ± 5.37 for *B. brevicauda,* 55.36 ± 3.86 for *S. fumeus,* 46.51 ± 2.50 for *S. cinereus,* and 40.27 ± 1.44 for *S. hoyi. Sorex dispar* was not included in the ANOVA due to the small sample size (N=1), but had a mass (6.7 g) and body length (60.0 mm) similar to that of *S. fumeus.*

Overall number of shrews per sampling period was relatively constant from August to November, but was highly variable from March through August (Fig. 6). Months with little or no rain had few shrew captures, and those with many rainy days had the greatest capture success. Overall shrew abundances were significantly correlated with the number of rainy days per trapping period ($y= 3.96 + 7.18x$; $r^2= 62\%$; F= 12.85; d.f.= 1,8; P <.01) (Fig. 8). Shrew capture rate was nearly five times greater on rainy days (6.79) compared to nonrainy days (1.38). I captured 129 shrews during 19 rainy days, whereas only 47 shrews were captured during 34 nonrainy days. Shrew abundances were not significantly correlated with total amount of rain (mm) received per trapping period (F=.73; d.f.= 1,8; P=.42).

Monthly variability in capture success was also observed for individual species (Fig. 7). *Sorex fumeus* abundance was significantly correlated with the number of rainy days per trapping period ($y= 0.56 + 5.23x$; $r^2= 71\%$; F= 19.45; d.f.=1,8; P <.01). *Sorex*

Table 4. Summary of vertebrate captures per site class. Numbers in parentheses are captures for each of the three replicates.

| **Species** | **N (+)** | **N (-)** | **S (+)** | **S (-)** | **Total** |
|---|---|---|---|---|---|
| Class Mammalia | | | | | |
| Order Insectivora | | | | | |
| *Blarina brevicauda* | **2** (1, 0, 1) | **4** (3, 0, 1) | **7** (3, 3, 1) | **1** (1, 0, 0) | **14** |
| *Sorex cinereus* * | **9** (2, 5, 2) | **17** (4, 12, 1) | **11** (1, 5, 5) | **4** (0, 3, 1) | **41** |
| *S. dispar* * † | **0** | **1** (1, 0, 0) | **0** | **0** | **1** |
| *S. fumeus* | **30** (9, 17, 2) | **31** (8, 14, 9) | **34** (20, 8, 6) | **10** (4, 6, 0) | **105** |
| *S. hoyi* * | **6** (4, 1, 1) | **2** (2, 0, 0) | **2** (0, 1, 1) | **5** (2, 3, 0) | **15** |
| Order Rodentia | | | | | |
| *Clethrionomys gapperi* * | **12** (2, 8, 2) | **1** (1, 0, 0) | **1** (1, 0, 0) | **2** (1, 0, 1) | **16** |
| *Napaeozapus insignis* * | **71** (34, 22, 15) | **23** (11, 9, 3) | **14** (8, 3, 3) | **7** (4, 1, 2) | **115** |
| *Ochrotomys nuttalli* * | **5** (3, 0, 2) | **4** (2, 2, 0) | **1** (1, 0, 0) | **1** (0, 1, 0) | **11** |
| *Peromyscus leucopus* | **48** (23, 15, 10) | **49** (18, 17, 14) | **39** (10, 7, 22) | **56** (19, 23, 14) | **192** |
| *Tamias striatus* * | **0** | **1** (1, 0, 0) | **1** (1, 0, 0) | **0** | **2** |
| Class Amphibia | | | | | |
| Order Caudata | | | | | |
| *Desmognathus monticola* | **9** (0, 9, 0) | **1** (0, 0, 1) | **2** (2, 0, 0) | **0** | **12** |
| *D. ochrophaeus* | **37** (6, 25, 6) | **14** (14, 0, 0) | **14** (5, 7, 2) | **0** | **65** |
| *D. quadramaculatus* | **4** (0, 4, 0) | **0** | **0** | **0** | **4** |
| *Eurycea wilderae* | **9** (5, 1, 3) | **4** (2, 0, 2) | **8** (5, 2, 1) | **7** (5, 2, 0) | **28** |
| *Gyrinophilus porphyriticus* | **5** (3, 1, 1) | **2** (1, 0, 1) | **6** (1, 3, 2) | **1** (1, 0, 0) | **14** |
| *Plethodon cinereus* | **4** (3, 0, 1) | **6** (1, 3, 2) | **5** (2, 1, 2) | **30** (7, 9, 14) | **45** |
| *P. cylindraceus* | **11** (5, 0, 6) | **13** (5, 3, 5) | **14** (3, 5, 6) | **18** (5, 6, 7) | **56** |
| *P. yonahlossee* | **7** (3, 0, 4) | **10** (7, 3, 0) | **14** (2, 4, 8) | **4** (3, 1, 0) | **35** |
| Order Anura | | | | | |
| *Bufo americanus* | **0** | **0** | **0** | **1** (0, 1, 0) | **1** |
| *Rana sylvatica* | **1** (0, 0, 1) | **0** | **2** (2, 0, 0) | **0** | **3** |
| Class Reptilia | | | | | |
| Order Serpentes | | | | | |
| *Carphophis amoenus* | **0** | **1** (0, 0, 1) | **0** | **0** | **1** |
| **Totals:** | **270** | **184** | **175** | **147** | **776** |

* new record for Burke County, NC

† NC species of special concern

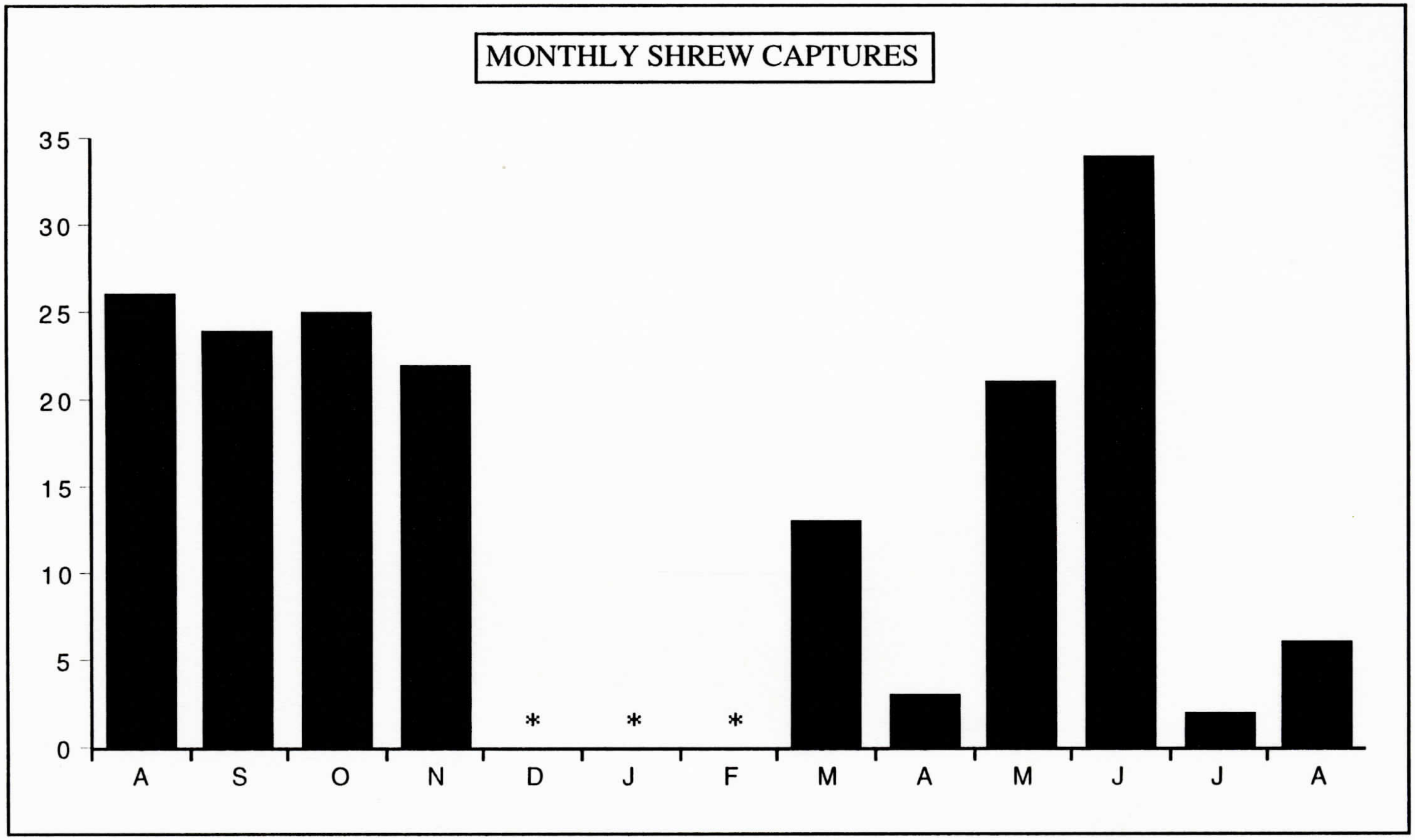

Figure 6. Total number of shrews captured per monthly trapping period. * No collecting was performed in winter (December, January, February) due to site inaccessibilty and reduced activity of shrews during this period.

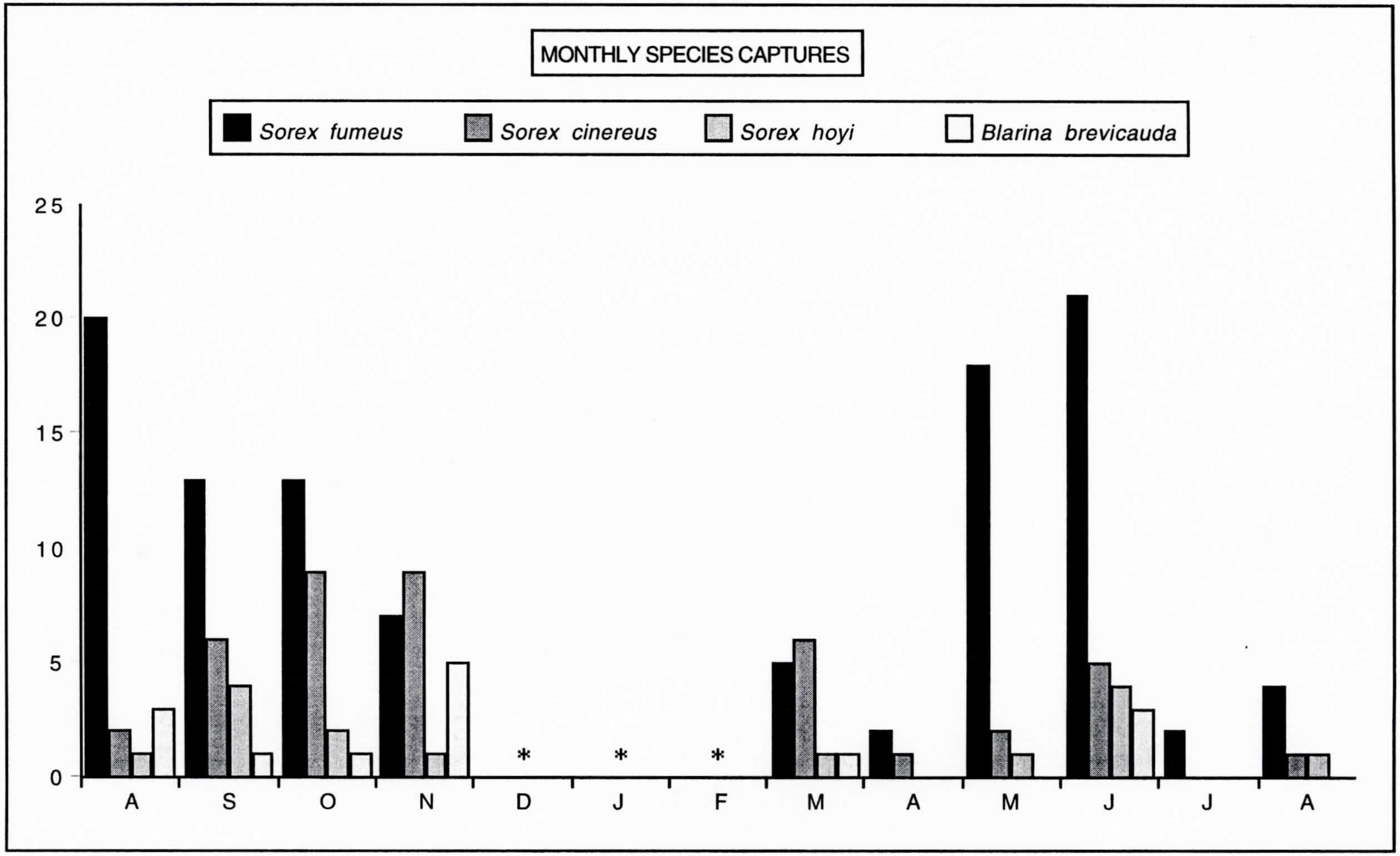

Figure 7. Numbers of individual shrew species collected per monthly trapping period.

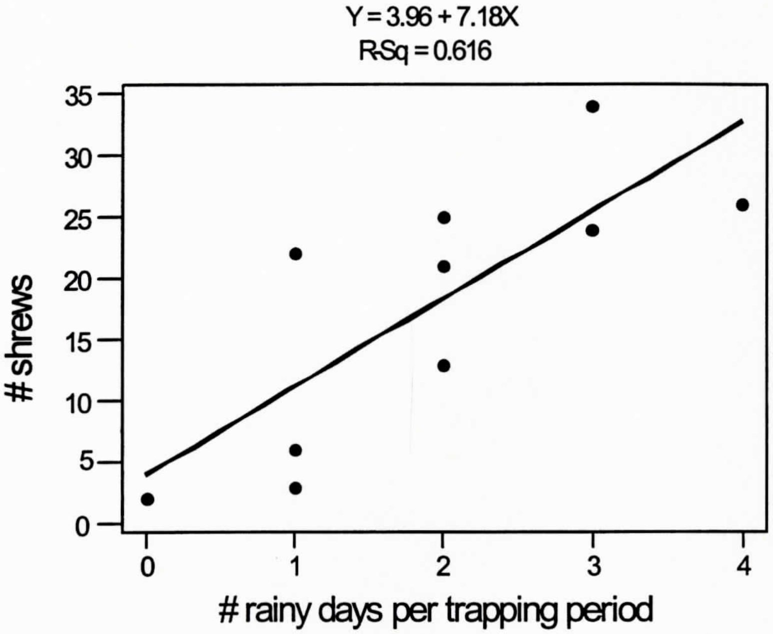

Figure 8. The effect of rainfall on the capture rate of shrews per trapping period.

*cinereus* also showed a positive relationship with the number of rainy days, but it was nonsignificant (F= .42; d.f.=1,8; P= .53). Numbers of *Sorex cinereus* demonstrated a significant curvilinear relationship with *S. fumeus* abundance during periods of rainfall ($y= -2.24 + 1.68x - 0.07x^2$; $r^2 = 58\%$; F= 4.79; d.f.= 2,7; P <.05) (Fig 9). Captures of neither species were correlated with amount of rain. Due to the small sample sizes of *S. hoyi, S. dispar,* and *Blarina brevicauda,* they were excluded from individual analyses.

Rainfall had no significant effect on prey abundances. Capture success of both invertebrates (F= .33; d.f.= 1,8; P=.58) and salamanders (F= .77; d.f.= 1,8; P=.19) was similar on rainy and nonrainy days. Amount of rainfall also had no effect on prey numbers (F=.80; d.f.=1,8; P=.40 for invertebrates; F=1.06; d.f.=1,8; P=,33 for salamanders).

A total of 9486 invertebrates were captured in pitfalls. These consisted primarily of 3764 Orthopterans, 1569 Coleopterans, 431 Hymenopterans, 171 Lepidopteran larvae, 163 Thysanurans, 1783 spiders, 863 millipedes, 398 centipedes, 143 annelids, and 48 snails; with each plot yielding relatively identical taxa. Mean values for invertebrate abundance and biomass per site class are given in Table 5. Due either to the high metabolic rate (Buckner, 1964; Genoud, 1988; Morrison *et al.,* 1957) and highly masticatory teeth (Carroway *et al.,* 1996) of shrews, or rapid spoilage in the field before preservation (Stewart *et al.,* 1989), determination of stomach contents was difficult. Contents of all stomachs examined consisted only of very masticated, unidentifiable fragments of chitin, and thus prevented comparisons between diet and prey availability.

Twenty of the measured habitat variables had no significant differences between site classes (Table 5), and there was no significant interaction between aspect and proximity to water. Number and biomass of invertebrate prey did not differ significantly, but prey size (mass in grams) did (P<.05), with smaller prey occurring at north-facing sites. Salamander abundances did not differ significantly, with the exception of *Plethodon cinereus* (P<.01) which was more numerous at S- sites. Site classes produced significant differences in the numbers of overall rodents (P<.05). Overall rodent abundance was less variable at sites without streams, and most numerous at N+ sites. Of the individual rodent

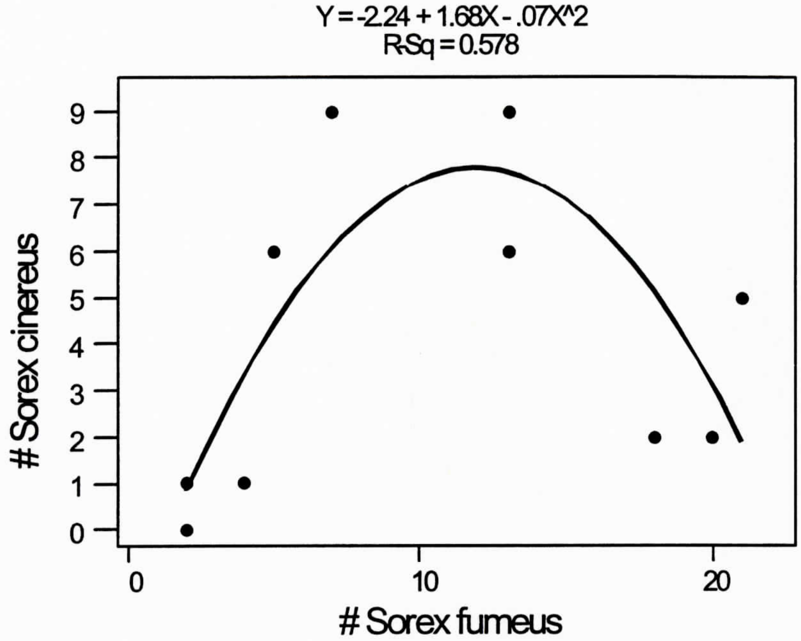

Figure 9. The relationship between surface activity of *Sorex fumeus* and *S. cinereus* during periods of rainfall.

Table 5. Results of one-way ANOVA for habitat variables between site classes. Mean values (± SE) of variables for each site class, F- values (d.f. =3,8), and P- values are given. Significance is denoted by asterisks (* P ≤ .05; ** P ≤ .01).

| **Variable** | **N+** | **N-** | **S+** | **S-** | ***F*** | ***P*** |
|---|---|---|---|---|---|---|
| INVERTN | 661.7 ± 273.2 | 904.7 ± 192.9 | 673.3 ± 296.6 | 922.3 ± 265.3 | 0.9 | 0.48 |
| INVERTBM | 184.60 ± 71.41 | 237.41 ± 41.56 | 230.98 ± 105.92 | 313.68 ± 73.16 | 1.47 | 0.3 |
| INVERTG | 0.28 ± 0.01 | 0.26 ± 0.04 | 0.34 ± 0.04 | 0.34 ± 0.04 | 4.32 | 0.04 * |
| BETULA | 13.54 ± 8.15 | 6.83 ± 6.09 | 8.20 ± 1.35 | 0.00 ± 0.00 | 3.54 | 0.06 |
| CHOAK | 3.37 ± 1.36 | 12.45 ± 8.22 | 6.03 ± 4.61 | 21.71 ± 2.15 | 8.38 | 0.01 * |
| PINUS | 7.00 ± 6.52 | 12.53 ± 7.69 | 6.03 ± 2.88 | 14.34 ± 8.58 | 1.09 | 0.41 |
| POPLAR | 5.87 ± 1.32 | 4.27 ± 2.35 | 13.60 ± 11.10 | 1.18 ± 1.13 | 2.54 | 0.13 |
| RHODO | 19.10 ± 6.14 | 18.60 ± 7.86 | 10.43 ± 3.82 | 0.87 ± 1.03 | 7.64 | 0.01 ** |
| TSUGA | 18.38 ± 8.23 | 8.36 ± 7.12 | 11.37 ± 5.53 | 0.86 ± 1.02 | 4.21 | 0.05 * |
| EVRGRN | 50.16 ± 8.98 | 42.42 ± 12.00 | 33.87 ± 3.89 | 23.31 ± 6.29 | 5.72 | 0.02 * |
| TREEN | 15.67 ± 1.53 | 13.67 ± 1.53 | 16.00 ± 2.65 | 13.00 ± 2.65 | 1.4 | 0.31 |
| HERBN | 6.50 ± 3.92 | 6.13 ± 1.01 | 10.80 ± 1.47 | 8.27 ± 1.70 | 2.54 | 0.13 |
| HERBCVR | 17.50 ± 13.40 | 11.11 ± 4.72 | 17.24 ± 1.11 | 18.91 ± 2.57 | 0.69 | 0.59 |
| CWDN | 23.33 ± 6.81 | 22.33 ± 6.03 | 21.33 ± 9.29 | 17.00 ± 1.73 | 0.54 | 0.67 |
| USEVOL | 9.97 ± 1.47 | 4.03 ± 0.92 | 4.18 ± 2.08 | 2.06 ± 1.04 | 16.66 | 0.001 ** |
| USEVOL3 | 0.45 ± 0.49 | 0.11 ± 0.04 | 0.49 ± 0.18 | 1.05 ± 0.71 | 2.32 | 0.15 |
| USEVOL4 | 4.18 ± 1.19 | 1.51 ± 0.62 | 3.16 ± 2.49 | 0.65 ± 1.12 | 3.28 | 0.08 |
| USEVOL5 | 5.34 ± 2.16 | 2.40 ± 1.14 | 0.53 ± 0.45 | 0.36 ± 0.63 | 9.77 | 0.01 ** |
| LITDEPTH | 291.33 ± 27.02 | 331.67 ± 23.97 | 300.00 ± 32.05 | 289.67 ± 20.82 | 1.66 | 0.25 |
| LITMOIST | 63.08 ± 0.41 | 56.92 ± 1.24 | 55.57 ± 2.15 | 47.40 ± 2.55 | 39.05 | 0.001 ** |
| AVGTEMP | 59.87 ± 0.71 | 60.80 ± 0.52 | 64.53 ± 1.99 | 66.70 ± 0.44 | 25.02 | 0.001 ** |
| TEMPFLX | 17.18 ± 2.30 | 17.96 ± 2.53 | 26.68 ± 3.59 | 27.78 ± 2.13 | 12.92 | 0.002 ** |
| SLOPE | 23.67 ± 3.22 | 29.67 ± 7.64 | 31.33 ± 4.93 | 29.00 ± 3.46 | 1.26 | 0.35 |
| SLMNDRS | 28.67 ± 10.01 | 16.67 ± 11.59 | 21.00 ± 1.00 | 20.00 ± 1.73 | 1.29 | 0.34 |
| DOCHR | 12.33 ± 10.97 | 4.67 ± 8.08 | 4.67 ± 2.52 | 0.00 ± 0.00 | 1.63 | 0.26 |
| EURYCEA | 3.00 ± 2.00 | 1.33 ± 1.15 | 2.67 ± 2.08 | 2.33 ± 2.12 | 0.39 | 0.76 |
| PCINER | 1.33 ± 1.53 | 2.00 ± 1.00 | 1.67 ± 0.58 | 10.00 ± 3.61 | 12.55 | 0.002 ** |
| PCYLIND | 3.67 ± 3.22 | 4.33 ± 1.16 | 4.67 ± 1.53 | 6.00 ± 1.00 | 0.77 | 0.54 |
| PYONAH | 2.33 ± 2.08 | 3.33 ± 3.51 | 4.67 ± 3.05 | 3.33 ± 1.53 | 0.86 | 0.5 |
| RODENTS | 45.33 ± 16.50 | 26.00 ± 8.19 | 18.67 ± 7.77 | 25.33 ± 1.53 | 3.94 | 0.05 * |
| CLETHR | 4.00 ± 3.46 | 0.33 ± 0.58 | 0.33 ± 0.58 | 0.67 ± 0.58 | 2.94 | 0.1 |
| PEROMYS | 16.00 ± 6.56 | 16.33 ± 2.08 | 13.00 ± 7.94 | 18.67 ± 4.51 | 0.5 | 0.7 |
| NAPOZAP | 23.67 ± 9.61 | 7.67 ± 4.16 | 4.67 ± 2.89 | 2.33 ± 1.53 | 9.27 | 0.01 ** |

species, only *Napaeozapus insignis* was significantly different in number between site classes (P<.01), with the greatest number of captures also occurring at N+ sites (Table 5).

Important trees and shrubs (Table 6) were mainly *Tsuga canadensis, Betula lenta,* and *Rhododendron maximum* on N+ sites; *Pinus strobus, Quercus montanus,* and *R. maximum* on N- sites; *Liriodendron tulipifera, T. canadensis,* and *R. maximum* on S+ sites; and *P. strobus, Q. montanus,* and *Q. rubra* on S- sites. Of these, only *Q. montanus* (P=.01), *T. canadensis* (P=.05), and *R. maximum* (P=.01) were significantly different between site classes; as was the overall percent of evergreen vegetation (P<.05). Chestnut oak, *Q. montanus,* was less important near streams on both north- and south-facing slopes. *Rhododendron* importance was low on south-facing slopes, especially without streams. Eastern hemlock, *Tsuga canadensis,* was most important at sites with streams, and least important and variable at S- sites. Overall, the percent of trees which were evergreen was smallest and least variable on south-facing slopes. Species richness of trees, shrubs, and herbs did not differ significantly between sites (Table 5).

Percent herbaceous cover and litter depth were not significantly different between site classes. Number of logs (CWD) did not differ significantly, but the amount of usable volume of CWD did (P=.001). Total usable volume of logs was highest at N+ sites and lowest at S- sites. Of each decay class only the usable volume of Class 5 logs was significantly different between sites (P=.01), and was much higher at north-facing sites (Table 5).

Average temperatures, temperature fluctuation, and percent litter moisture differed significantly between sites (P<.001 for all). South-facing sites were hotter and had a higher degree of temperature fluctuation than north-facing ones; with those lacking streams or seepages the hottest and driest. Litter moisture, however, was dependent on both aspect and stream proximity. While N+ sites were wettest ("hydric") and S- sites were driest ("xeric"), N- and S+ sites were indistinguishable for this variable and were pooled as "mesic" for some subsequent analyses.

Pooled shrew abundances differed significantly between these moisture regimes ($\chi^2$= 13.57, P< .01 for *Sorex fumeus;* $\chi^2$= 6.71, P< .05 for *S. cinereus;* $\chi^2$= 18.30,

Table 6. Average importance values of tree and shrub species in each site classification. Species with very low importance values for all site classes are not presented.

| **Species** | **Importance Values** | | | |
|---|---|---|---|---|
| | **N+** | **N-** | **S+** | **S-** |
| *Acer rubrum* | 2.3 | 11.58 | 7.73 | 13.89 |
| *Betula lenta* | 13.54 | 6.83 | 8.2 | 0 |
| *Kalmia latifolia* | 5.25 | 2.91 | 6.03 | 6.02 |
| *Liriodendron tulipifera* | 5.87 | 2.67 | 13.6 | 0.43 |
| *Oxydendrum arboreum* | 0 | 4.3 | 4.07 | 14.11 |
| *Pinus strobus* | 7 | 12.53 | 6.03 | 14.34 |
| *Quercus alba* | 0 | 0 | 6.27 | 0 |
| *Quercus montana* | 3.37 | 12.45 | 6.03 | 21.71 |
| *Quercus rubra* | 0.97 | 0.63 | 8.83 | 14.45 |
| *Rhododendron maximum* | 19.1 | 18.6 | 10.43 | 0.87 |
| *Tsuga canadensis* | 18.38 | 8.36 | 11.37 | 0.86 |

$P < .001$ overall). Shrews were less numerous and had a lower diversity of species on xeric sites (Table 7, Fig. 10). Using the twelve individual plots, however, a two-way ANOVA showed no significant differences in shrew abundances between the original four site classifications, probably due to the high degree of within-site variance (Table 4).

Within- site class variance of shrew captures may relate to several interrelated habitat variables. Univariate regression analyses (Table 8) found eight separate variables significantly correlated with overall shrew and *S. fumeus* abundances, but only one habitat predictor for *S. cinereus.* Overall number of shrews was positively correlated with *Betula* ($r^2$=34.0%) and *Tsuga* ($r^2$=43.3%); and negatively correlated with usable volume of CWD 3 ($r^2$=46.7%), number and biomass of invertebrates ($r^2$=54.6%; 57.1% respectively), and the salamanders *Plethodon cylindraceus* ($r^2$=61.7%) and *P. cinereus* ($r^2$=42.8%). A curvilinear relationship existed between shrew abundance and total CWD usable volume ($r^2$=49.8%) (Fig. 11).

*Sorex fumeus* abundance was positively correlated with *Tsuga* ($r^2$=45.2%) and litter moisture ($r^2$=31.2%); and negatively correlated with CWD 3 usable volume ($r^2$=32.8%), invertebrate number ($r^2$=66.2%) and biomass ($r^2$=76.2%), *Plethodon cylindraceus* ($r^2$=74.7%) and *P. cinereus* ($r^2$=34.0%). A curvilinear relationship existed between *S. fumeus* numbers and CWD 5 usable volume ($r^2$=47.0%) (Table 8, Fig. 12). *Sorex cinereus* abundance was positively correlated with litter depth ($r^2$=40.0%) (Table 8, Fig. 13).

Using all variables in Table 5, stepwise multiple regression analysis (Table 9) found overall shrew abundances to be best predicted by a combination of the absence of the slimy salamander *Plethodon cylindraceus,* the red-backed vole *Clethrionomys gapperi,* and Class 3 logs ($y= 37.46 - 3.90x_1 -1.46x_2 - 5.07x_3$; $R^2$= 89.2%). The three best predictors of *Sorex fumeus* abundance were found to be an absence of *P. cylindraceus* and *C. gapperi,* and low invertebrate biomass ($y= 30.24 - 2.46x_1 - 1.15x_2 - 0.35x_3$; $R^2$= 95.8%). *Sorex cinereus* abundance was best predicted by the presence of deep leaf litter,

Table 7. Distribution of shrews in each moisture regime.

| Species | Habitat type | No. plots | No. captures | Avg. # of individuals | % captures per habitat | Avg. # species | Avg. Shannon index (H') |
|---|---|---|---|---|---|---|---|
| Overall | Hydric | 3 | 47 | 15.7 | 38.7 | 3.7 | 0.435 |
| | Mesic | 6 | 109 | 18.2 | 44.8 | 3.5 | 0.401 |
| | Xeric | 3 | 20 | 6.7 | 16.5 | 2.3 | 0.289 |
| *Sorex fumeus* | Hydric | 3 | 30 | 10 | 41.5 | | |
| | Mesic | 6 | 65 | 10.8 | 44.8 | | |
| | Xeric | 3 | 10 | 3.3 | 13.7 | | |
| *S. cinereus* | Hydric | 3 | 9 | 3 | 33.3 | | |
| | Mesic | 6 | 28 | 4.7 | 52.2 | | |
| | Xeric | 3 | 4 | 1.3 | 14.4 | | |

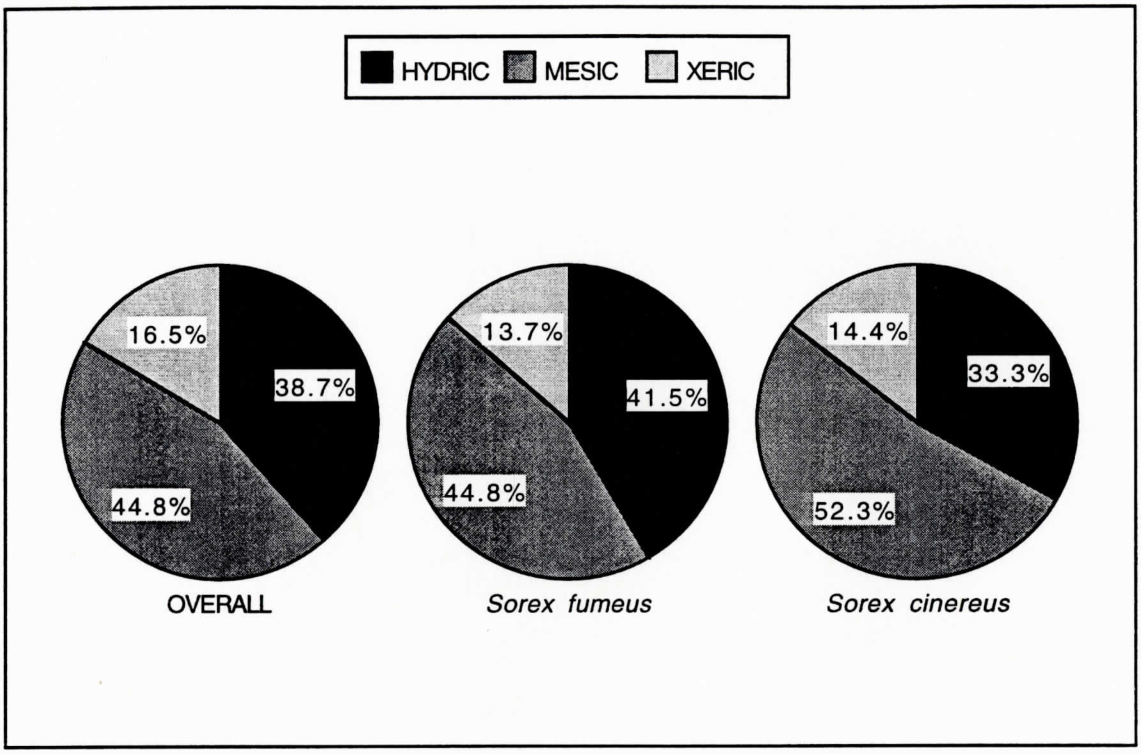

Figure 10. Capture rates of shrews for each of three moisture regimes.

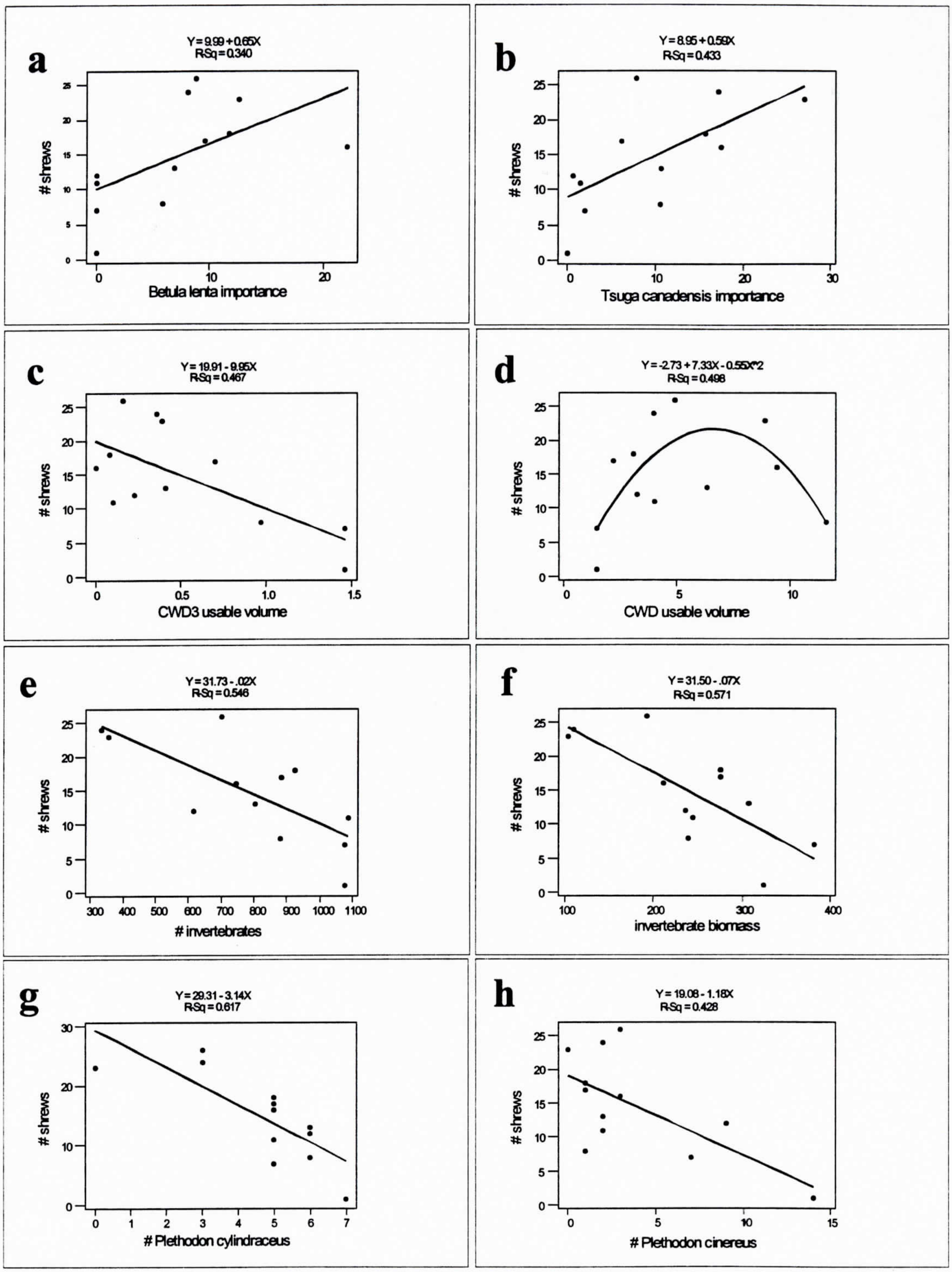

Figure 11. Significant best-fit regression lines for overall shrews: (a) *Betula* importance; (b) *Tsuga* importance; (c) CWD3 usable volume; (d) CWD total usable volume; (e) invertebrate number and (f) biomass; (g) *Plethodon cylindraceus*; (h) *P. cinereus.*

Table 8. Regression analyses for shrew captures with habitat variables. Only those with significant F values (d.f.= 1,10 for linear; 2,9 for quadratic) are presented.

| **Species** | **Variable** | **Regression equation** | **F value** | **P value** | **r-squared (%)** |
|---|---|---|---|---|---|
| Overall | BETULA | $y= 10.0 + 0.65x$ | 5.14 | 0.05 | 34 |
| | TSUGA | $y= 8.95 + 0.59x$ | 7.62 | 0.02 | 43.3 |
| | USEVOL3 | $y= 19.9 - 9.95x$ | 8.77 | 0.01 | 46.7 |
| | INVERTN | $y= 31.70 - 0.02x$ | 12.04 | 0.006 | 54.6 |
| | INVERTBM | $y= 31.50 - 0.07x$ | 13.28 | 0.005 | 57.1 |
| | PCYLIND | $y= 29.30 - 3.14x$ | 16.14 | 0.002 | 61.7 |
| | PCINER | $y= 19.1 - 1.18x$ | 7.47 | 0.02 | 42.8 |
| | USEVOL | $y= -2.73 + 7.33x - 0.55x2$ | 4.47 | 0.04 | 49.8 |
| *Sorex fumeus* | TSUGA | $y= 4.28 + 0.46x$ | 8.26 | 0.02 | 45.2 |
| | LITMOIST | $y= -18.20 + 0.49x$ | 4.54 | 0.05 | 31.2 |
| | USEVOL3 | $y= 12.1 - 6.37x$ | 4.87 | 0.05 | 32.8 |
| | INVERTN | $y= 23.1 - 0.02x$ | 19.59 | 0.001 | 66.2 |
| | INVERTBM | $y= 23.6 - 0.06x$ | 32.1 | 0.001 | 76.2 |
| | PCYLIND | $y= 21.1 - 2.64x$ | 29.51 | 0.001 | 74.7 |
| | PCINER | $y= 11.8 - 0.80x$ | 5.16 | 0.05 | 34 |
| | USEVOL5 | $y= 4.53 + 5.62x - 0.81x2$ | 3.98 | 0.05 | 47 |
| *S. cinereus* | LITDEPTH | $y= -18.3 + 0.07x$ | 6.68 | 0.03 | 40 |

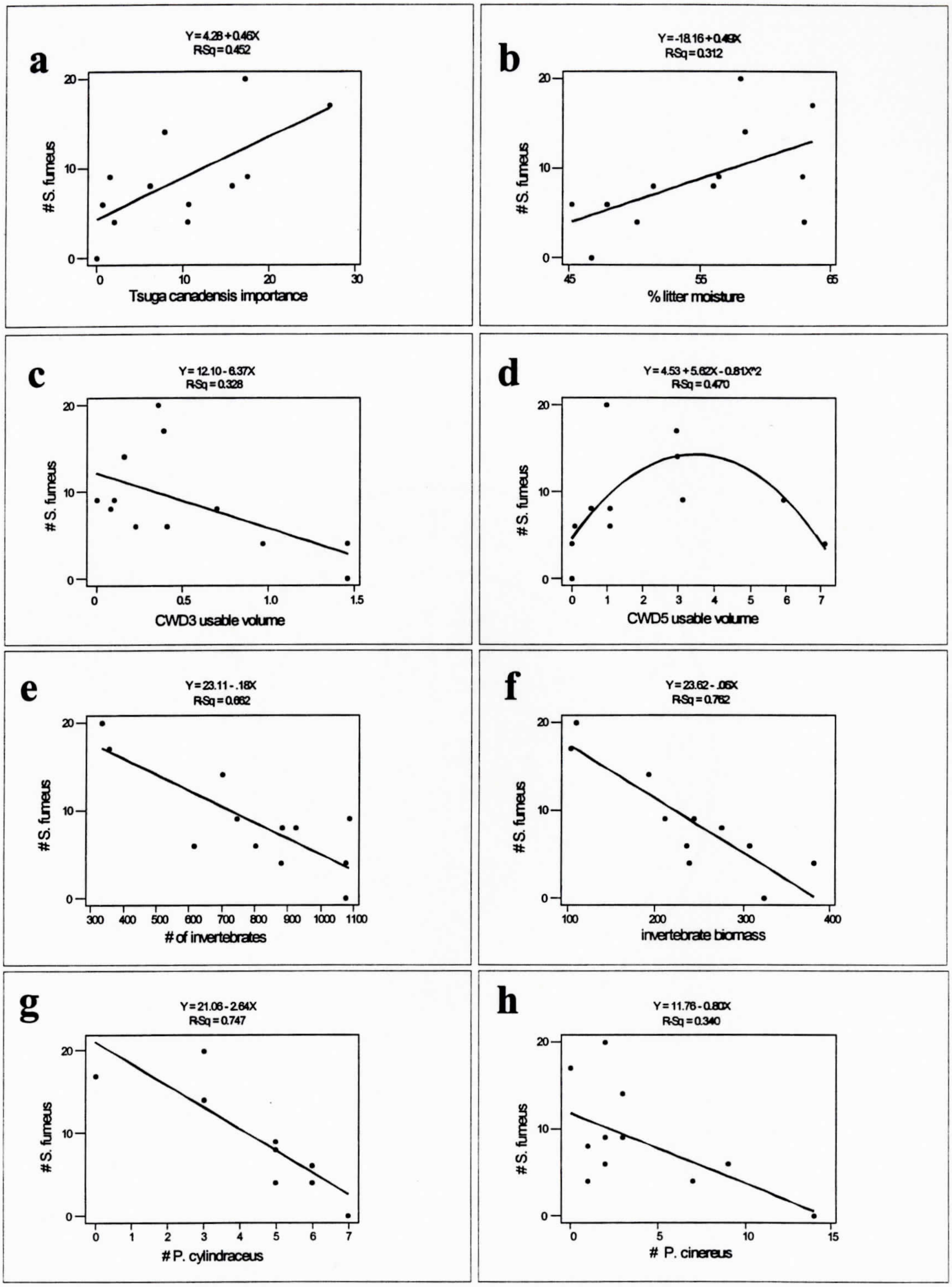

Figure 12. Significant best-fit regression lines for *Sorex fumeus:* (a) *Tsuga* importance; (b) % litter moisture; usable volume of (c) CWD3 and (d) CWD5; (e) number and (f) biomass of invertebrates; (g) *Plethodon cylindraceus*; (h) *Plethodon cinereus.*

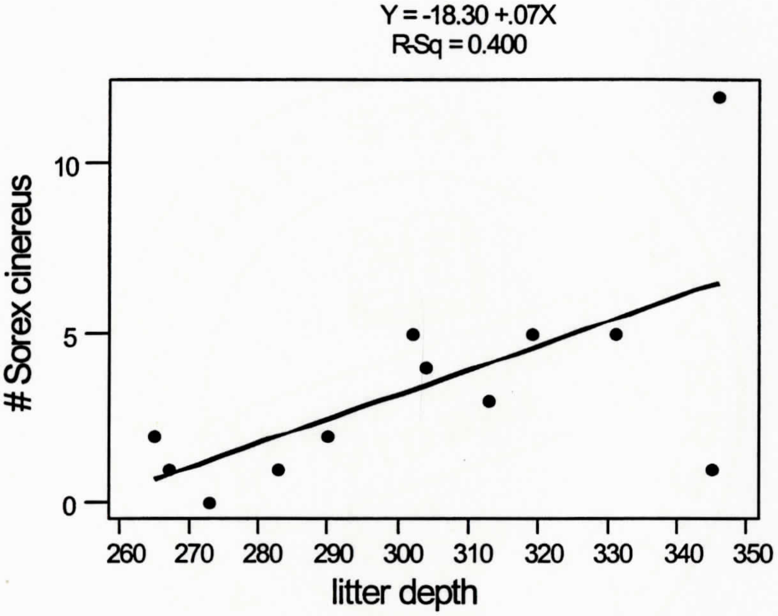

Figure 13. The relationship between *Sorex cinereus* abundance and leaf litter depth.

Table 9. Best predictors of shrew abundances as determined by stepwise multiple regression analyses. The correlation coefficients of these predictors with the species of shrew are given. T-values are equal to the square root of the F-statistic and are given as the same sign as the coefficient of each x variable in the regression equation.

| **Species** | | **Best predictors (x)** | **Correlation coefficents (r)** | **T-values** | **Constant** | **R-squared (%)** |
|---|---|---|---|---|---|---|
| Overall | 1) | PCYLIND | -0.786 | -5.16 | 37.46 | 89.22 |
| | 2) | CLETHR | 0.258 | -2.45 | | |
| | 3) | USEVOL3 | -0.683 | -2.62 | | |
| *Sorex fumeus* | 1) | PCYLIND | -0.864 | -5.99 | 30.24 | 95.81 |
| | 2) | CLETHR | 0.385 | -4.37 | | |
| | 3) | INVERTBM | -0.873 | -4.48 | | |
| *S. cinereus* | 1) | LITDEPTH | 0.633 | 3.22 | -18.36 | 63.5 |
| | 2) | PYONAH | 0.252 | 1.83 | | |
| | 3) | INVERTN | -0.271 | -1.62 | | |

the salamander *Plethodon yonahlossee,* and low numbers of invertebrates ($y = -18.36 + 0.08x_1 + 0.50x_2 - 0.01x_3$; $R^2 = 63.5\%$).

A degree of resource partitioning was observed between *Sorex fumeus* and *S. cinereus.* Using the subset of 11 variables, the backwards-elimination, stepwise multiple regression analyses (Table 10) found *Sorex fumeus* abundance to be related primarily to a combination of litter moisture, number of invertebrates, and usable volume of CWD 5 ($y = -18.69 + 0.74x_1 - 0.01x_2 - 1.51x_3$; $R^2=86.6\%$); while *S. cinereus* abundance was related to litter moisture, invertebrate size, and litter depth ($y = -49.81 + 0.25x_1 + 36.00x_2 + 0.09x_3$; $R^2=54.9\%$). A strong relationship was also found between litter moisture, invertebrate size, and litter depth and overall shrew abundance ($y = -150.30 + 1.24x_1 + 134.00x_2 + 0.18x_3$; $R^2=73.4\%$). Discriminant function analysis determined that this microhabitat niche separation between *S. fumeus* and *S. cinereus* was significant ($D^2 = 0.753$; $F=1.89$; d.f.= 11,134; $P<.05$), with 65.8% of the original observations correctly classified. Microhabitat niche breadth of *S. cinereus* (MB= 1.33) was found to be narrower than that of *S. fumeus* (MB= 1.43).

Table 10. The three most important resources for individual shrew species as determined by backwards-elimination, stepwise multiple regression analyses.

| Species | | Resource variables (x) | Correlation coefficents (r) | T-values | Constant | R-squared (%) |
|---|---|---|---|---|---|---|
| Overall | 1) | LITMOIST | 0.505 | 4.18 | -150.3 | 73.36 |
| | 2) | INVERTG | -0.099 | 3.09 | | |
| | 3) | LITDEPTH | 0.389 | 3.39 | | |
| *Sorex fumeus* | 1) | LITMOIST | 0.559 | 3.48 | -18.69 | 86.56 |
| | 2) | INVERTN | -0.814 | -3.77 | | |
| | 3) | USEVOL5 | 0.099 | -2.76 | | |
| *S. cinereus* | 1) | LITMOIST | 0.143 | 1.52 | -49.81 | 54.88 |
| | 2) | INVERTG | -0.085 | 1.48 | | |
| | 3) | LITDEPTH | 0.633 | 3.06 | | |

# DISCUSSION

One goal of shrew research is an understanding of which aspects of the environment are important determinants of shrew population density and community structure. Primary factors suggested in the past include moisture (e.g. Getz, 1961a; Wrigley *et al.,* 1979), structural complexity of the environment (e.g. Dueser and Shugart, 1978, 1979; Seagle, 1985; Yahner, 1986), food availability (e.g. Getz, 1961a; Innes *et al.,* 1990), and potential interspecific competition (Fox and Kirkland, 1992; Hawes, 1977; Terry, 1981). The present study provides data relevant to determining the importance of each of these factors to shrew distributions and diversity.

My results are consistent with those of others (e.g. Getz,1961a; Wrigley *et al.,* 1979) that moisture is the most important factor in determining the overall distribution and diversity of shrews. But while most of these studies examined very dissimilar habitat types, my study, like that of Vaughan (1954), demonstrates that similar effects can be observed between opposing slopes within the same habitat type. North-facing slopes are cooler and moister and thus are more favorable to shrews because of their high water turnover rate (Chew, 1951). These conditions also produce higher proportions of eastern hemlock *(Tsuga canadensis)* and yellow birch *(Betula lenta)* (Whittaker, 1956), and logs in the later stages of decay (Abbott and Crossley, 1982; Kirkland, 1977; Maser *et al.,* 1979). In general, south-facing slopes are hotter and drier due to greater direct-beam radiation (Matlack, 1993, 1994; Wales, 1972), but the presence of streams or seepages work to offset the evaporative effect (Doyle, 1987). Thus, moisture appears to be more important than temperature in determining shrew distributions, as more shrews were captured near water at south-facing sites.

Surface activity of shrews was greatly affected by rainfall (Doucet and Bider, 1974; McKay, 1996; Vickery and Bider, 1978). Studies on the effect of precipitation on salamander activity have demonstrated that increases are associated with enhanced mobility rather than prey abundance (Fraser, 1976; Jaeger, 1980), as they require moist conditions to avoid dessication (Ash, 1995; Petranka *et al.,* 1994). Likewise, shrews require high humidity to maintain their water balance (Chew, 1951). In my study, prey abundances were not greater during periods of rainfall while shrew abundances were. This suggests that shrews, like salamanders, increase their activity during rainfall not in response to increased prey availability, but rather to enhanced mobility associated with suitable environmental conditions for foraging.

Shrews are voracious predators in many forest-floor ecosystems (Aitchison, 1987b; Anderson and Folk, 1993; Bellocq *et al.,* 1994; Buckner, 1964, 1969; Churchfield, 1990), and have been shown to demonstrate a numerical response to prey abundance. High densities of *Blarina brevicauda* (Getz, 1961a) and *Sorex cinereus* (Holling, 1959; Stewart *et al.,* 1989) have been found to be positively correlated with invertebrate availability. Sometimes, however, potential prey items are less common in areas with high shrew densities (Innes *et al.,* 1990; Platt and Blakley, 1973). In these cases shrews may be controlling prey abundance through their voracious consumption (Churchfield, 1990; Platt and Blakley, 1973). This is certainly true in experiments utilizing small field enclosures. Although these enclosures allow free entry to invertebrates, prey numbers are significantly reduced in plots with shrews compared to those without (Anderson and Folk, 1993; Churchfield, 1990). Similarly, in my study, invertebrates were fewer and their biomass lower in areas of high shrew abundances.

Since shrews are restricted to mesic areas because of their high water turnover rates, a large population of soricids in these environments could indeed have a pronounced effect on prey abundance. Although moist habitats usually support more invertebrate prey than do dry habitats (Feldhamer *et al.,* 1993; Getz, 1961a; Churchfield, 1990; Wrigley *et al.,* 1979), numbers of invertebrates in this study did not differ significantly among site classes despite differences in environmental moisture. Greater numbers of shrews in mesic areas may be acting to maintain macroinvertebrate abundances at the level of xeric sites. Shrews forage primarily for large, more energetically profitable prey (Aitchison, 1987a; Barnard and Hurst, 1987; Fox and Kirkland, 1988). Although large, surface active invertebrates are efficiently captured in pitfall traps (Dickman, 1988; Ryan, 1986), burrowing invertebrates may be difficult to sample (Churchfield, 1982b; Dickman, 1988), and could actually be more abundant than the observed patterns indicate.

However, most shrews are not well-adapted for digging, at least not to great depths (Churchfield, 1980a,1990; Dickman, 1988), and are primarily epigeal foragers (Teferi and Herman, 1995). Although diminutive species frequently consume smaller food items due to their small teeth (Getz, 1961a) and the energy expense of handling larger prey (Barnard and Hurst, 1987), they will often eat larger, more profitable prey in the absence of larger congeners (Churchfield, 1990; Dickman, 1988; Neet and Hausser, 1990). Morphological differences of shrew species allow for exploitation of various microhabitats (Huggins and Kennedy, 1989) in search of prey. Hypogeal foragers are typically larger and more robust (Churchfield 1980b, 1990; Dickman, 1988; Terry, 1981; Yashino and Abe, 1984), and are more capable of handling larger prey (Barnard and Hurst, 1987; Martin, 1981a) and accessing dense or structurally complex microhabitats where large prey are more abundant (Dickman, 1988). Thus the larger *Sorex fumeus* inhabits areas of high log cover, exploits all sizes of prey, and is limited only by prey abundance; while the smaller *S. cinereus* is competitively excluded from such areas and is limited more by prey size. Competition for such optimal microhabitat results in partitioning of prey items based on size rather than taxonomic group (Fox and Kirkland, 1992; Ryan, 1986; Yalden, 1981), as shrews are primarily opportunistic generalists (e.g. Bellocq *et al.,* 1994; Churchfield, 1990; Criddle, 1973; Hamilton, 1930; Ryan, 1986).

Differential use of microhabitat to reduce interspecific competition is important in determining niche relationships of shrews and the structure of soricid assemblages (Fox and Kirkland, 1992; Hawes, 1977; Terry, 1981; Yashino and Abe, 1984). Shrew species occupy different size niches (small, medium, large); and according to Fox and Kirkland's (1992) species-assembly rule for soricid communities, each of these should be filled before a second species of the same size is added to the community. If there is a second species of the same body size class, it should be rare. In this study, communities consisted of three *Sorex* species *(S. fumeus, S. cinereus, S. hoyi)* and *Blarina brevicauda,* each of significantly different size (Fig. 14). *Sorex dispar* approaches the

| Species | Relative size | Body mass (g) | Body length (mm) |
|---|---|---|---|
| *Sorex hoyi* |  | 3.5 - 4.6 | 38.8 - 41.7 |
| *Sorex cinereus* |  | 5.1 - 6.7 | 44.0 - 49.0 |
| *Sorex fumeus* |  | 9.0 - 12.0 | 51.5 - 59.2 |
| *Blarina brevicauda* |  | 19.4 - 27.2 | 70.9 - 82.0 |

Figure 14. Comparison of shrew species sizes.

size of *S. fumeus* and is closely related (George, 1988) , but appears to be a rare species as only one individual was captured. In cases where species are similar in size, body shape may be an important factor in the partitioning of resources (Huggins and Kennedy, 1989). The narrow rostrum of *S. dispar* allows it to exploit food reserves in the narrow crevices of rocks which may be inaccessible to the more robust *S. fumeus* (Huggins and Kennedy, 1989; Richmond and Grimm, 1950).

Habitat generalists should be numerically dominant over specialists, with separation occurring on a localized, microhabitat scale (Churchfield, 1990; Feldhamer *et al.,* 1993; Fox and Kirkland, 1992). In multi-species soricid communities, larger species have greater access to optimal microhabitat (Dickman, 1988; Fox and Kirkland, 1992) and thus should have a greater niche breadth and be more numerous. *Blarina brevicauda,* the largest shrew species captured, is normally a very common species (Webster *et al.,* 1985). Its low numbers are likely a result of trap avoidance due to its its more fossorial habits (Aitchison, 1987a; Dueser and Shugart, 1979; Getz *et al.,* 1992; Merritt, 1986) rather than scarcity, although it is a solitary and territorial species (Martin, 1981b). Of the species of *Sorex,* however, the largest species, *S. fumeus,* was the most numerous and the smallest, *S. hoyi,* was the least numerous. *Sorex cinereus* was less abundant than the larger *Sorex fumeus* and also had a narrower microhabitat niche breadth (Fig. 15). A narrowing of niche breadth in the presence of larger congeners has also been observed for other vertebrate species (Krzysik, 1979). Potential competition with larger species limits the available resources, making smaller species less general in their use of microhabitat.

Microhabitats are conspicuously nonuniform even in deciduous forests with continuous canopies (Seagle, 1985), creating a patchy utilization of space (Barnard and Brown, 1987; Hanksi, 1989; Seagle, 1985). Environmental moisture is an important factor for all shrew species (Chew, 1951; Getz, 1961a; Wrigley *et al.,* 1979). Within mesic areas, microhabitat factors that mediate moisture and food abundance are partitioned among sympatric species. The larger *Sorex fumeus* utilizes logs in the advanced stages of decomposition. Heavily rotted logs are reservoirs of moisture (Maser *et al.,* 1979; Tallmon and Mills, 1994), and are important refuges during the day and during periods of

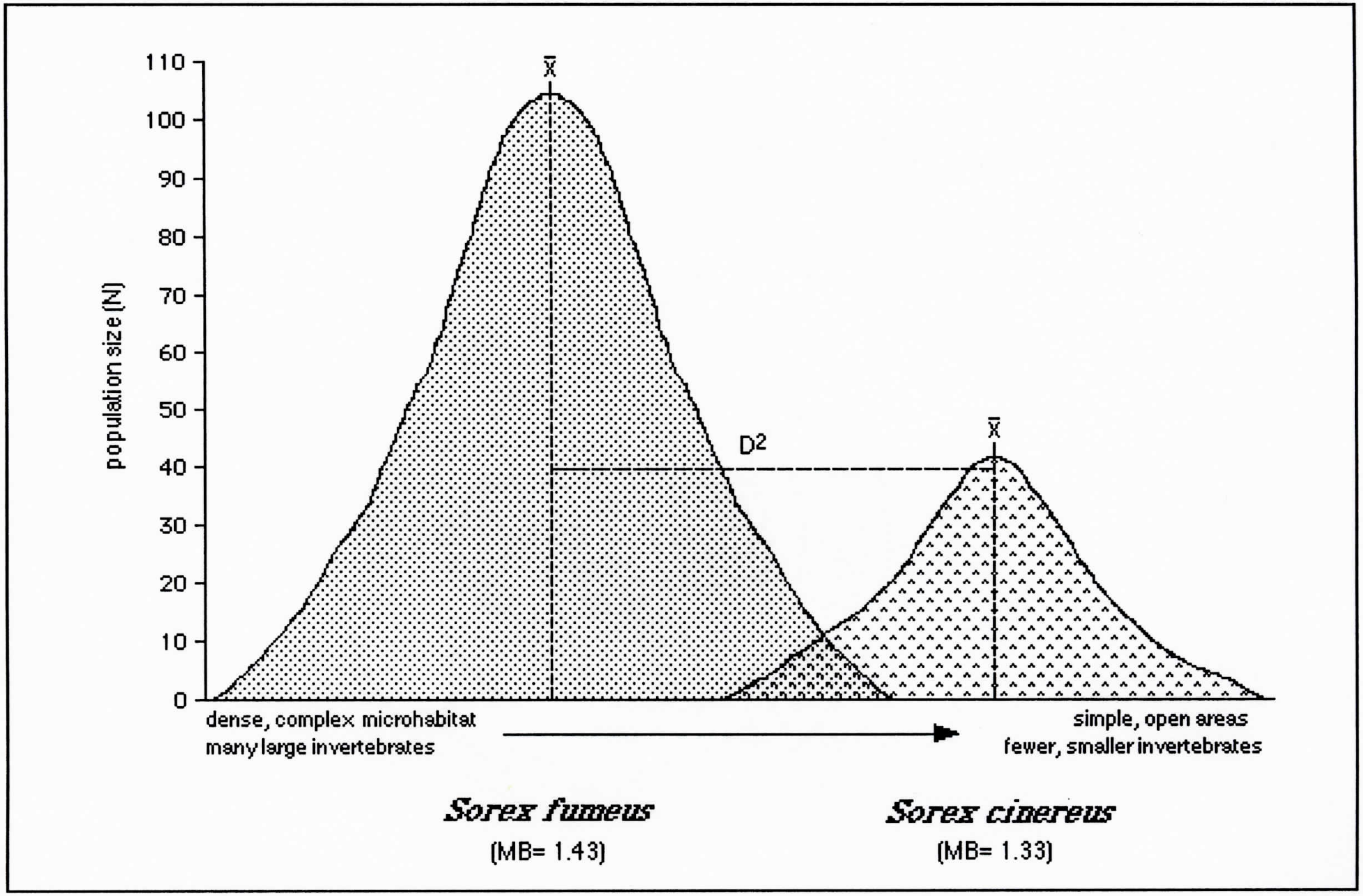

Figure 15. Resource partitioning between sympatric species of *Sorex* based upon body size. The larger *S. fumeus* is more numerous and has a greater microhabitat niche breadth (MB) than the smaller *S. cinereus,* and is also associated more with areas containing dense, structurally complex microhabitat and larger invertebrate prey size. The squared distance between species' population means ($D^2$), located along the resource gradient provided by the linear discriminant function, was found to be significant ($F=1.89$; d.f.=11,134; $P<.05$).

drought (Jaeger, 1980). The amount of usable volume for shrews for Class 4 and 5 logs is greater than for Class 3 logs of the same dimensions, as the soft texture of these decay classes permits hypogeal shrews to burrow into the log's interior spaces (Maser *et al.*, 1979). The increased moisture level of very decomposed logs leads to a greater abundance of large, soil-dwelling invertebrates (Churchfield, 1990; Getz, 1961a; Maser *et al.*, 1979), salamanders (Jaeger, 1980; Petranka *et al.*, 1994), and the subterranean fungus *Endogone* (Slankis, 1974; Tallmon and Mills, 1994), of which *S. fumeus* is sometimes a consumer (Whitaker, 1962). Cover in this form allows for an environmentally stable, productive space (Hanski, 1989; Jaeger, 1980; Maser *et al.*, 1979) to forage and nest that is safe from both diurnal and nocturnal predators (Barnard and Brown, 1987; Seagle, 1985).

While logs are an important microhabitat feature, high concentrations may have a somewhat negative effect on shrew abundance. Logs are effective microhabitat for small mammals when they are well distributed over the ground (Maser *et al.*, 1979). Too many logs, on the other hand, are ground-level obstructions which may impede foraging of shrews on the forest floor (Yahner, 1986).

The utilization of rotten logs by *Sorex fumeus* prevents *S. cinereus* from occupying this choice microhabitat. *Sorex cinereus* must forage in more open areas where larger prey is less abundant (Dickman, 1988), and the risk of dessication (Chew, 1951; Getz, 1961a) and predation greater (Seagle, 1985). In such areas, a deep layer of leaf litter is essential for maintaining moisture levels (Ash, 1995). Deep leaf litter also provides greater abundances of prey (Dickman, 1988; Petranka *et al.,* 1994 ) and greater concealment from avian, reptilian, and mammalian predators (Seagle, 1985, Yahner, 1986). The more diminutive size of *S. cinereus* allows it to hide more effectively in litter than can larger species, which may be another reason why *S. fumeus* is associated more with logs.

Salamanders and rodents also utilize these microhabitats as foraging and nesting sites (e.g. Ash, 1995; Jaeger, 1980; Petranka *et al.*, 1994; Dueser and Shugart, 1979; Seagle, 1985; Yahner, 1986; Wells, 1980), and encounters with shrews may be common

(Getz *et al.,* 1992; Jaeger, 1971). Although shrews occasionally eat other small vertebrates (Brodie *et al.,* 1979; Getz *et al.,* 1992), these food items make up only a very small percentage of their diets (Hamilton, 1930; Whitaker and Mumford, 1972). The role of salamanders and rodents as potential competitors, however, is less understood (Dueser and Shugart, 1979; Jaeger, 1971; Kitchings and Levy, 1981). Rodents are not likely competitors in most circumstances as they tend to occupy different niches than shrews (Morris, 1979). Although *Clethrionomys gapperi* and *Napaeozapus insignis* also forage frequently in rotten logs (e.g. Doyle, 1987; Maser *et al.,* 1979; Tallmon and Mills, 1994), most rodents are granivorous or herbivorous (Kirkland, 1977), whereas shrews are primarily insectivorous (e.g. Aitchison, 1987a; Hamilton, 1930). In addition, rodents can be beneficial as shrews frequently occupy the runways and burrows of other small mammals (Churchfield, 1980a, 1990; Hamilton, 1940).

Salamanders, however, are almost exclusively insectivorous (e.g. Fraser, 1976; Mitchell and Taylor, 1986) and have very similar moisture requirements to shrews (Ash, 1995; Fraser, 1976; Jaeger, 1980; Petranka *et al.,* 1994; Spotila, 1972). Shrews will eat salamanders, especially *Desmognathus ochrophaeus* (Brodie *et al.,* 1979; Orr, 1967), but avoid noxious species (Brodie, 1983; Brodie *et al.,* 1979; DiGiovanni and Brodie, 1981). Salamanders of the genus *Plethodon* exude slimy skin secretions which have been shown to be a very effective predator deterrent (Brodie, 1983). The slimy salamander, *Plethodon cylindraceus* (once *P. glutinosus* ) is one of the least palatable species (Brodie *et al.,* 1979), and is unlikely to be eaten even under periods of food scarcity. In this study, numbers of overall shrews and of *Sorex fumeus* were negatively correlated with *P. cylindraceus* abundance. The slimy salamander is one of the larger plethodontids, and can reach high densities on the forest floor (Ash, 1995; Petranka *et al.,* 1994) and under logs (Jaeger, 1980; Petranka *et al.,* 1994; Wells, 1980). This species could therefore be a potential competitor with shrews for food and cover. It is unlikely that the same ecologic situation is true of *Plethodon cinereus,* the red-backed salamander. Shrews usually take prey normally beyond the size range of this small salamander species (Jaeger, 1971). The negative relationship observed between *P. cinereus* and shrew numbers may simply reflect subtle habitat differences.

Although Getz (1961a) discounted interspecific competition as an important factor in determining shrew distributions, several aspects of the present study supports a competitive view. Competition between shrew species should be reflected in their distributions and in an inverse relationship in abundances where they coexist (Terry, 1981). In my study, there was no correlation between any species of shrews, except during rainy periods. Increased surface activity associated with rainfall leads to more frequent encounters with other species. During dry periods, *Sorex fumeus* and *S. cinereus* occupy distinct subdivisions of the microhabitat, and so competition is presumed to be low (Dickman, 1988; Fox and Kirkland, 1992; Hawes, 1977; Terry, 1981). During and shortly following a rain, however, species are freed from the risk of dessication and forage in the moist forest litter where prey are abundant (Jaeger, 1980; McKay, 1996; Vickery and Bider, 1978). In such situations, *S. cinereus* must face competition from the larger species. In this study, *S. fumeus* shows dramatic increases in activity with rainfall that is not completely demonstrated with the smaller *S. cinereus. Sorex cinereus* activity does increase a bit with rainfall, but then decreases when *S. fumeus* becomes most active (Fig. 9). This pattern suggests that *S. fumeus* does have a competitive impact on the smaller species when the two are no longer segregated. Thus, my data support the idea that larger body size conveys a competitive advantage (Dickman, 1988), and is important in structuring soricid communities (Fox and Kirkland, 1992).

Body size is believed to be an important, organizing factor in the community structure of many vertebrate species (e.g. Asplund, 1974; Bowers and Brown, 1982; Dickman, 1988; Hairston, 1986; Krzysik, 1979; M'Closkey, 1978; Pianka, 1986; Schoener, 1974; Wilson, 1975). Results of my study are consistent with this hypothesis, and provide support for Fox and Kirkland's (1992) assembly rule for North American soricid communities. Shrew diversity should therefore be dependent upon dissimilar sized species utilizing measurably different portions of their common environment, or different microhabitat niches.

The predictive and explanatory models developed in the present study should provide useful tools for evaluation and management of potential shrew habitats as part of a larger conservation effort. Governmental land management agencies play a pivotal role in protecting global biodiversity because they have stewardship over extensive tracts of land that can be managed from an ecosystem perspective (Petranka *et al.,* 1994). Historically, forest management in the Appalachian Mountains has centered on timber production at the expense of many animal species intolerant of the xeric conditions and loss of microhabitat associated with clear-cutting (Ash, 1995; Buckner and Shure, 1985; Kirkland, 1977; Petranka *et al.,* 1994; Ramirez and Hornocker, 1981). Today greater emphasis is being placed on the development of harvesting methods which support better ecosystem management including forest productivity, nutrient cycles, water quality, and the preservation of biodiversity (Sharitz *et al.,* 1992). The goals of ecosystem management are to manipulate the heterogeneity and dispersion of forest communities such that viable populations of a wide array of species can be maintained within a managed landscape, and to develop techniques that allow timber harvesting in a manner that maintains healthy levels of all key functional groups (Petranka *et al.,* 1994; Sharitz *et al.,* 1992).

My study demonstrates that shrew species respond to components of their environment on a scale of resolution much finer than gross habitat differences. The importance of such microgeographic features is often overlooked by forest managers (Ash, 1995; Maser *et al.,* 1979; Petranka *et al.,* 1994). The utilization of innovative harvest methods that preserve a variety of moist, forest -floor microhabitats would help to maintain diversity of these economically and ecologically important insectivorous mammals within managed southern Appalachian forests.

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# APPENDIX A

## KEY TO THE SORICIDAE OF KENTUCKY *

(after Caldwell and Bryan, 1982)

1a. Less than 5 unicuspids visible from the side, or if 5, the third and fifth greatly reduced; medial tine of first upper incisor present or absent ........................2
1b. Five unicuspids visible from side, fifth may be very reduced; medial tine present ......................................................................................4

2a. Three or four unicuspids visible from the side; upper incisors not possessing medial tine ..........................................................................3
2b. Unicuspids 3 and 5 greatly reduced, may not be readily apparent in side view; fifth unicuspid peglike, third unicuspid platelike; medial tine of upper incisors well developed ............................................ *Sorex (Microsorex) hoyi*

3a. Three unicuspids visible in side view; fourth unicuspid hidden from view; total number of teeth 30 .................................................. *Cryptotis parva*
3b. Four unicuspids visible in side view; first and second upper unicuspids large, third and fourth smaller and subequal; total number of teeth 32 ........*(Blarina)* 8

4a. Total length usually greater than 140 mm; fringe of hairs between toes; maxillary breadth 6.0 mm or greater ........................................... *Sorex palustris*
4b. Total length usually less than 140 mm; no fringe of hairs between toes; maxillary breadth less than 6.0 mm ...........................................................5

5a. Infraorbital foramen with posterior border lying behind space between first and second upper molars; rostrum long with uncrowded unicuspids; cranium relatively flat; tail robust and longer than 50 mm ..................... *Sorex dispar*
5b. Infraorbital foramen with posterior border lying ahead of the space; rostrum shorter and unicuspids more crowded; cranium more bulbous; tail thinner and less than 50 mm ........................................................................6

6a. Third unicuspid usually smaller than the fourth; tail relatively shorter, generally 32-38% of total length; rostrum short and wide; length of posterior palate to anterior end of first incisors usually less than twice the greatest width across outside of first large molariform tooth .......................... *Sorex longirostris*
6b. Not with above combination of characters ...........................................7

7a. Ventral color distinctly lighter than dorsal color; midventral hairs just anterior to axillary region light from midshaft to tip; maxillary breadth narrower than 4.6 mm ........................................................................ *Sorex cinereus*

7b. Ventral color not distinctly lighter than dorsal color; midventral hairs just anterior to axillary region dark tipped; maxillary breadth greater than 4.6 mm .............. ........................................................................ *Sorex fumeus*

8a. Total length greater than 105 mm, or hind foot 13 mm or longer; condylobasal length greater than 20 mm ......................................... *Blarina brevicauda*

8b. Total length 105 mm or less, and hind foot shorter than 13 mm; condylobasal length less than 20 mm ........................................... *Blarina carolinensis*

* applicable for species which occur in North Carolina

# VITA

Michael Patrick Brannon was born in Greenville, South Carolina, on March 4, 1970. He attended elementary schools in Taylors, South Carolina and in Tryon, North Carolina. He graduated salutatorian from Tryon High School in 1988. The following August he entered the University of North Carolina at Asheville, and in May 1992 received a Bachelor of Arts degree in Biology with the completion of his research, "Parasites as ecological indicators of resource partitioning in sympatric whiptail lizards *(Cnemidophorus)*". That summer he accepted a temporary position with the USDA Forest Service performing research on the effects of clear-cutting on salamander populations, which was later published in *Forest Ecology and Management* in 1994. From August 1992 to August 1994, he was employed at Penn 4-H Center in Reidsville, North Carolina as an environmental educator and ropes course facilitator. In Fall of 1994, he accepted a Teaching Assistantship at Appalachian State University and began study towards a Master of Science degree in Biology. This degree was awarded in December 1997.

The author is a member of the Association of Southeastern Biologists, the North Carolina Herpetological Society, and the ASU Biology Graduate Student Association. Mr. Brannon's address is 356 Paris Road, Boone, North Carolina. He is the son of Mr. Michael J. Brannon of Aiken, South Carolina, and Mrs. Anne C. Vassey of Six Mile, South Carolina. He is married to the former Janis K. Heller of Summerfield, North Carolina.