PREY PREFERENCES OF THE NORTHERN SAW-WHET OWL (*AEGOLIUS ACADICUS*) IN THE SOUTHERN APPALACHIAN MOUNTAINS.

A Thesis

by

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ABSTRACT

PREY PREFERENCES OF THE NORTHERN SAW-WHET OWL (*AEGOLIUS ACADICUS*) IN THE SOUTHERN APPALACHIAN MOUNTAINS.

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Saw-whet owls are common throughout much of North America, but only a small, disjunct population exists in the southern Appalachian Mountains. The diet of this owl is well known from some areas of its range, but prey preferences have not yet been addressed; moreover, little research has been done on the isolated southeastern population.

The main habitat of the disjunct southeastern population is the high elevation spruce-fir forests above 1524 m (5000 ft). These forests have declined tremendously since the 1800's due to the combined effects of fire, logging, and insect pests. This habitat decline, coupled with a lack of research on saw-whet owls from the region, has led North Carolina, Virginia, and Tennessee to list this disjunct population of saw-whet owls as a "species of special concern."

The diet of the saw-whet owl has not been determined in the southern Appalachian Mountain population, although it might be assumed to be similar to that of saw-whet owls from other areas. To determine whether this assumption is borne out, 15 saw-whet owls were fitted with radio-transmitters in 1993 and 1994. Owls were tracked to their day roosts, where pellets were collected. The diet of southern Appalachian saw-whet owls was determined from 143 pellets collected from beneath these day roosts and from two habitual roost sites. Ninety pellets were collected in 1993 and 53 in 1994. Pellets were analyzed by soaking them in water before carefully teasing out bones and other identifiable remains. Prey were keyed to species based on skull and dental characteristics. Most pellets (n = 132) were collected from the Mt. Mitchell, N.C. area (MMA); the rest were from Roan Mountain, N.C., or the Great Balsam Mountains, N.C. A total of 129 prey items representing eight species were found in these pellets. *Sorex cinereus* (n = 36), *Peromyscus maniculatus* (n = 30), *Sorex fumeus* (n = 25), and *Clethrionomys gapperi* (n = 15) comprised 82% of the diet by frequency. The diet differed greatly between the two years. In 1993 the diet was 70% shrews (*S. cinereus*, *S. fumeus*, *Blarina brevicauda* and *Sorex* spp.), 23% mice (*P. maniculatus*, *C. gapperi*, and *Napaeozapus insignis*), and 7% birds (*Junco hyemalis*). In 1994 the diet was 48% shrews, 44% mice, and 8% birds.

Prey preferences for the MMA were determined by comparing proportions of prey species in the diet with estimates of small mammal abundances in the environment. Small mammal abundance in the MMA was determined from the literature for 1993 and from trapping in 1994. The most common species trapped in 1993 was *S. cinereus* (5.1 per 100 pitfall nights), and in 1994 it was *P. maniculatus* (6.5 per 100 Sherman™ trapnights). Shrew trap rates differed little between 1993 and 1994, (5.7 vs. 5.3), while trap rates of mice increased (4.9 vs. 12.0). Three different preference tests generally found shrews to be preferred over mice. However, when mice trap rates increased, so did the proportion of mice in the diet. A concomitant drop was observed in the proportion of shrews in the diet, even though shrew abundance changed little between the years. This suggests that mice may actually be preferred, or that saw-whet owls take prey according to their availability.

The food niche breadth was higher for saw-whet owls in this study than in 14 other such studies. It is possible

that small mammal densities are lower in the southern Appalachian Mountains than elsewhere in the saw-whet owl's range. Low prey abundance may force southern Appalachian saw-whet owls to have broad diets. Dietary evenness in the present study was also among the highest found. Several prey species appear to be important saw-whet owl food items in the southern Appalachian Mountains, in contrast with one or two dominant prey species in other areas.

Profitable (i.e., larger) prey were taken more often when available; less profitable smaller prey were more common in the diet when larger prey were less abundant. This might indicate that owls are optimal foragers which select prey based on energetic considerations. Alternatively, dietary prey proportions may be a reflection of the owls' sit-and-wait foraging strategy. Diets may be determined by relative abundances of prey, and not according to optimal foraging theory. The increase of mice in both the environment and the diet in 1994, coupled with similar shrew abundances in both years, is consistent with both hypotheses.

Each of the three preference methods employed showed shrews to be the preferred prey. This may be due to inherent biases in the trapping methods used to determine small mammal abundances. Indeed, if shrews were really

preferred, the frequency of shrews in the diet should have been similar between years, since little change in their abundance was found between years. Shrews decreased greatly in the diet from 1993 to 1994. Thus, shrews are probably not preferred prey. Furthermore, the relative abundances of mice most likely determines the diet of saw-whet owls in the southern Appalachian Mountains.

ACKNOWLEDGEMENTS

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DEDICATION

I dedicate this thesis to the loving memory of my parents, Bennie L. and Joyce C. Cockerel. I am sure they would be most proud of me and the direction that my life has taken. My parents always loved the outdoors and freely encouraged me to enjoy it whenever possible. They would remember a wild-eyed little boy bringing home frogs and snails and would be happy to know that I put that love of the outdoors to good use with the research presented herein. I will always be grateful to them. I love you Mom and Dad!

TABLE OF CONTENTS

Page

LIST OF TABLES

Page

Page

LIST OF FIGURES

INTRODUCTION

The northern saw-whet owl (*Aegolius acadicus*) is a small owl found throughout much of the contiguous United States (Figure 1). The range of this owl extends from southeastern Alaska, southward throughout the Rocky Mountains to the southwestern United States, east to the Great Lakes region, southeastern Canada, and the northeastern U.S. A disjunct population in the southern Appalachian Mountains of North Carolina, Tennessee and Virginia is restricted primarily to high elevation spruce-fir forests above 5,000 ft (1524 m) (Simpson 1972; Crutchfield 1990).

In the last century, the spruce-fir component of the southern Appalachian Mountains has decreased in area by as much as 90% due to the combined effects of logging, fire, balsam woolly adelgid (*Adelges piceae*) infestations and acid rain (Crutchfield 1990). Fraser fir (*Abies fraseri*) has been especially devastated by the adelgid. Adams and Hammond (1991) noted that greater than 95% of fir canopy trees had died between 1962 and 1985 on Mt. Mitchell, N.C. Many areas now are either devoid of mature fir or will be

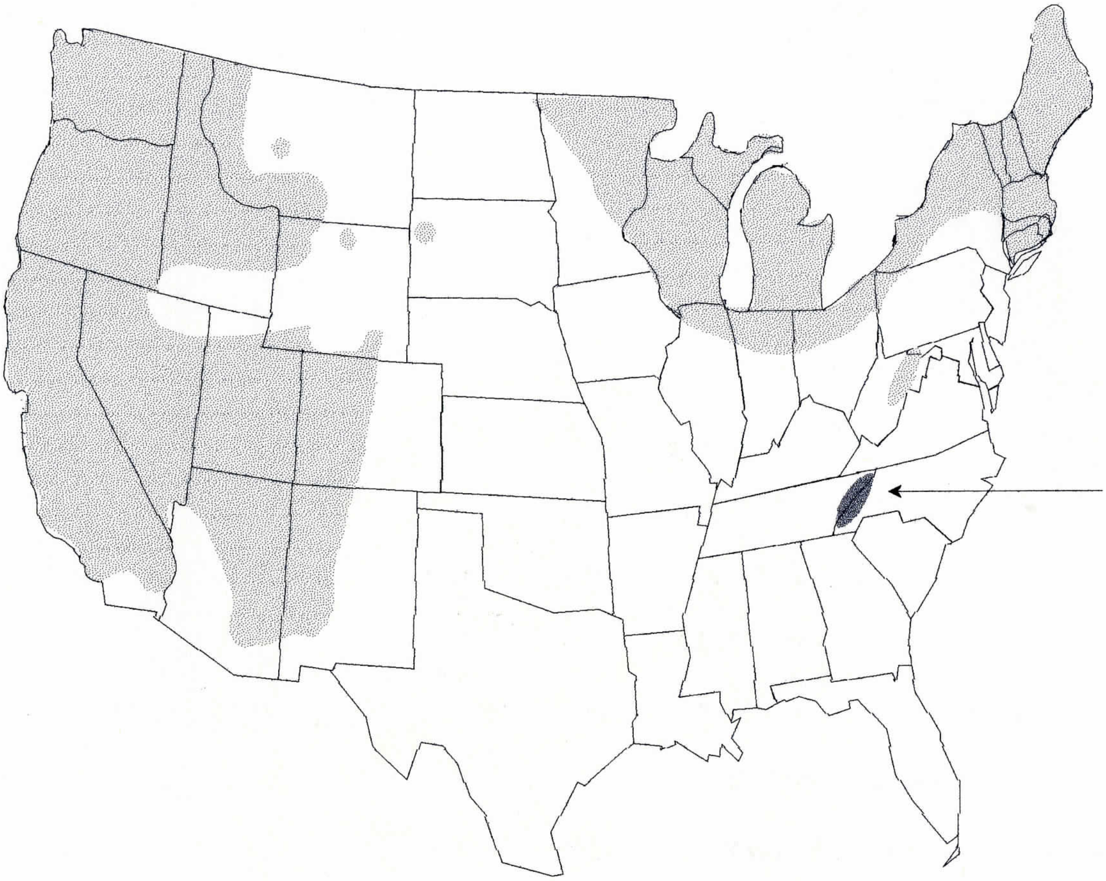


Figure 1. Distribution of the Northern Saw-whet Owl in the contiguous United States (adapted from Johnsgard 1988). Arrow designates southern Appalachian disjunct population.

soon (Witter and Ragenovich 1986; Busing et al. 1988). Some authors believe the spruce-fir forests of the southern Appalachian Mountains will continue to shrink and face possible extinction (Boyce and Martin 1993).

What then will be the fate of the flora and fauna associated with the spruce-fir? Some of these species are already on the U.S. Fish and Wildlife Service endangered species list (e.g. northern flying squirrel, *Glaucomys sabrinus coloratus;* spruce-fir moss spider, *Microhexura montivaga;* and rock gnome lichen, *Gymnoderma lineare*) (Payne et al. 1989; USFWS 1994). Although it is not federally endangered, the saw-whet owl is listed as a "species of special concern" by the states of North Carolina, Tennessee, and Virginia. This status is due in part to a lack of knowledge of the basic biology of this owl in these states (Crutchfield 1990). Tamashiro (1996) postulates that the southern Appalachian saw-whet owl population may be a genetic reservoir and deserves management attention.

Although few studies of the saw-whet owl have been performed in the southern Appalachian Mountains, many ecological studies of these owls have been conducted in the northern and western parts of their range. These include studies on feeding biology (Catling 1972; Boula 1982; Smith and Devine 1982; Hayward 1983; Toland 1984; Grove 1985; Hayward and Garton 1988; Marks and Doremus 1988; Dinsmore and Clark 1991; Hobson and Sealy 1991; Holt et al. 1991; Parker 1991; Dancey 1992; Swengel and Swengel 1987, 1992a; Holt and Leroux 1996), breeding biology (Cannings 1987), metabolism (Graber 1962; Collins 1963), roost site locations (Swengel and Swengel 1992b), radio-telemetry (Forbes and Warner 1974), migration (Catling 1971; Holroyd and Woods 1975; Carpenter and Carpenter 1993), parasites (Woods 1971; Cannings 1986), vocalizations (Hill 1995; Otter 1996), and general ecology (Bent 1938; Scott 1938; Randle and Austing 1952; Mumford and Zusi 1958; Palmer 1986). Few studies deal with saw-whet owls in Tennessee and/or North Carolina (Stupka 1963; Simpson 1968, 1972; Parmalee and Klippel 1987; Mayfield and Alsop 1992; Barb 1995; Tamashiro 1996). Of these, only Parmalee and Klippel (1987) examine the diet of saw-whet owls. These data were from middle Tennessee and represent only a single owl.

Early dietary studies of owls and other raptors consist mainly of stomach analyses of shot birds (see Marti 1987). Since this type of collection is illegal today, the technique is of limited value and can provide data only for legally salvaged dead raptors, usually road kills. Other techniques used to determine dietary habits of raptors include direct observation of prey captures, photographic recording of prey brought into nests, identification of prey remains at nests, and pellet analysis.

Direct observation involves watching the species in question and identifying its prey. This technique has proven useful for bald eagles (*Haliaeetus leucocephalus*), golden eagles (*Aquila chrysaetos*), and some other diurnal raptors (Collopy 1983; Stalmaster and Plettner 1992). It is, however, much more difficult to observe the feeding of nocturnal raptors.

Two kinds of nest site studies provide diet data. Photographic studies require the use of cameras and suitable locations to take quality pictures. This type of research has been useful in determining diets of nesting diurnal raptors (see Marti 1987), although Powers et al. (1996) used this technique for nocturnal flammulated owls (*Otus flammeolus*). Prey remains found at nest sites have been used to assess diets of bald eagles (Stalmaster and Plettner 1992), boreal owls (*Aegolius funereus*) (Korpimäki 1988), and other raptors. This technique works only for active nests. Also, this technique is biased against soft bodied prey due to quick consumption or rapid decay (Collopy 1983; Simmons et al. 1991).

Cached prey provide additional evidence on the diet of many raptors, including owls. Caches are prey stored for future use (Vander Wall 1990). Cached prey are normally found on a branch near the owl (Cannings 1993). Several species of owls cache prey, including barn owls, *Tyto alba* (Kaufman 1973), screech owls, *Otus asio* (Phelan 1977; Cope and Barber 1978), great horned owls, *Bubo virginianus* (Collins 1976), boreal and saw-whet owls, (Bondrup-Nielsen 1977). Compared to studies of remains at nests or pellets, caches typically provide less dietary information, due to the small sample sizes commonly achieved with this method (Simmons et al. 1991). Caches provide useful corroborational data in conjunction with other methods to determine the diet of raptors.

The most common technique used to determine diets of raptors is pellet analysis. All raptors produce pellets of the less digestible remains of prey (bones, hair, feathers, etc.). These pellets are regurgitated periodically, usually daily (Marti 1987). Pellets can be used to assess raptor diets qualitatively and quantitatively. Prey remains in owl pellets are more representative of the actual diet than are those of other raptors (Errington 1930). Hawks, for example, tend to digest more bone than do owls, so identification of prey species is more difficult. The good quantitative aspects of prey in owl pellets, especially for smaller owls, have been noted. Pellets of small owls contain a greater proportion of bone than those of larger owls, because large owls crush more bones (Duke et al. 1976). Not surprisingly, most dietary studies of owls, including saw-whet owls, are based on pellet analysis (Short and Drew 1962; Maser and Brodie 1966; Catling 1972; Clark 1972; Marti 1974; Boula 1982; Tilley 1982; Colvin and Spaulding 1983; Marks 1984; Grove 1985; Kotler 1985; Bull et al. 1989; Smith and Cole 1989; Ganey 1992; Swengel and Swengel 1992a; Galeotti and Canova 1994; Tome 1994; Vassallo et al. 1994; Zalewski 1994).

Owl pellet analyses are used in various ways. The primary goal of most research is to identify the diet of owls in particular locations and/or times. Diets of owls can be compared among local sites, states, and countries (e.g. Jaksic and Marti 1981; Jaksic et al. 1982; Marti 1988). Owl pellet data are also used to update small mammal ranges, to estimate density of small mammals, and to study taphonomy of fossilized bone assemblages (e.g.

Pearson and Pearson 1947; Osborn and Hoagstrom 1989; Kusmer 1990).

Many pellet analysis studies are done in conjunction with small mammal trapping so owl prey selection can be compared with actual small mammal abundances (Voight and Glenn-Lewin 1978; Jaksic and Yañez 1979; Jaksic et al. 1982; Colvin and Spaulding 1983). A prey species is said to be "preferred" or "selectively preyed upon" if consumption of a prey species is greater than its abundance in the area (Jaksic and Yañez 1979). Such prey preferences must be assessed cautiously. Unequal "catchability" of different prey by predators may yield misleading results (Rapport and Turner 1970). Prey species may be very abundant (as shown by trapping), yet remain under-utilized if the owls are unable to capture them, regardless of preference. For example, mammal trapping in a dense forest may lead to high estimates of small mammals. However, owls may not be able to fly well in these dense forests, so their access to that particular prey base would be restricted. Complex habitat structure alters the prey choices of belted kingfishers (*Ceryle alcyon*). In simple habitats, kingfishers prefer large fish (11-13 cm), but in structurally complex habitats, they took prey in accordance to availability and not size (Kelly 1996).

Another potential problem in determining owl prey preferences is the differential trappability of small mammal species by researchers. Since estimates of prey abundance directly impact preference analyses, a biased trap design in favor of shrews, for example, would make shrews seem more abundant than other small mammals. To reduce this bias, several different trap types are used to capture small mammals. Usual techniques include live traps, pitfalls, and snap traps. There are drawbacks to each of these techniques. Live traps are more effective at capturing voles and mice than are pitfall traps, but pitfalls capture more shrews than do live traps (Andrzejewski and Rajska 1972; Briese and Smith 1974; Williams and Braun 1983; Walters 1989). Snap traps are unreliable for shrews (Brown 1967) and sacrifices each animal captured. A mixture of trap types is often used to provide a less biased estimate of small mammals (Briese and Smith 1974). In many areas, however, it is impractical or unacceptable to use destructive sampling methods, so trapping options are limited. For example, destructive trapping may be prohibited in protected areas, such as wildlife preserves and state or national parks, or if rare species are involved.

More than 27 species of small mammals are known prey for saw-whet owls (Cannings 1993). Although small mammals are the main prey of saw-whet owls, birds, insects, and amphibians are also eaten (see reviews in: Catling 1972; Cannings 1993). Mice, especially *Peromyscus*, are frequently the dominant prey (Scott 1938; Boula 1982; Cannings 1987; Swengel and Swengel 1987; Holt et al. 1991; Swengel and Swengel 1992a), but voles of the Genus *Microtus* are also taken in large numbers (Randle and Austing 1952; Catling 1972; Toland 1984; Grove 1985; Marks and Doremus 1988; Smith and Devine 1982). However, invertebrates make up a substantial portion of the diet in the disjunct population of saw-whet owls in the Queen Charlotte Islands (Hobson and Sealy 1991).

Food niche breadths (FNB) have been reported for saw-whet owls from northern and western North America (Marks and Doremus 1988; Holt et al. 1991; Swengel and Swengel 1992a). FNB's measure richness and evenness of prey species in the diet and provides a measure of dietary diversity (Marti 1987). Richness is the number of prey species and evenness is the measure of how uniformly each species is represented in the diet. Comparisons of FNB's among locations can provide clues about the relative prey base of an area. Smaller values of FNB's may result from a narrower assemblage of prey (i.e., fewer species) and from skewed distributions of individuals among species. For example, Holt et al. (1991) state that their small FNB was indicative of the limited faunal diversity of the study area. Dietary evenness is also a part of the FNB, but it is often calculated separately to measure the equitability of species abundances (Alatalo 1981).

Optimal foraging theory predicts that predators should take prey that maximizes food intake for any level of energy output (Schoener 1971). Several additional variables may also be involved in prey selection. One is the "cost" associated with catching and eating of prey. If large prey are difficult or dangerous to catch, predators may choose smaller prey that are relatively easy and/or less dangerous to catch, regardless of their abundances. In this way, the owl uses less energy and reduces its chance of injury. Search time, handling costs, and relative abundances of prey items all may affect diet choice (Schoener 1971).

Hunger level or related incentives can also affect prey choices. Barn owls (*Tyto alba*) chose neither the smallest nor the largest prey available (Ille 1991). Large prey are unattractive if handling (subduing, carrying, or tearing) involves much effort, and small prey were often overlooked. Screech owls, however, choose small prey over large prey almost exclusively, even after fasting for 36 hours (Marti and Hogue 1979). Another factor involved in prey selection is conspicuousness of the prey. Resident mice familiar with the local environment are captured significantly less often than are transients, which are unfamiliar with the local environment (Metzgar 1967). Higher activity of transient mice probably makes them more conspicuous to owls (Kaufman 1974).

Saw-whet owls are sit-and-wait predators (Hayward and Garton 1988) that do not waste energy on flight while searching for prey. Such sit-and-wait predators are probably number maximizers; i.e., they take prey as they are encountered instead of according to optimal foraging predictions (Griffiths 1975). Thus, saw-whet owls should take prey species randomly as encountered. If prey visibility to owls is equal across prey species, saw-whet owls should take prey in proportion to actual prey abundances. Owls foraging in habitats with markedly different prey spectra should have diets reflecting these differences. For example, most shrew species are uncommon in open fields. Owls foraging mainly in fields should have few shrews in their diet.

The brief review above suggests that many factors may affect dietary preferences. Prey preference studies are useful whenever endangered or threatened species are involved. Management plans for owls must include consideration of diets (species and numbers of prey) in order to determine appropriate sizes and types of habitats to protect (e.g., Wesemann and Rowe 1987; Murphy and Noon 1992). Used cautiously, preference data, along with food niche breadth and evenness data, can aid the wildlife manager in determining the correct direction for management of raptors (Brown 1974).

The present study will try to answer several questions concerning the diet of northern saw-whet owls in the southern Appalachian Mountains: 1. What do saw-whet owls eat? 2. Do they show preferences for particular species? 3. Do diets vary seasonally and/or between owls? 4. Do diets differ among years, and if so, do these differences mirror changes in small mammal abundance? 5.

How does the food niche breadth of northern saw-whet owls in the southern Appalachian disjunct population compare with other saw-whet owl studies? Answers to these questions will be invaluable for future management decisions regarding the northern saw-whet owl in the southern Appalachian Mountains.

This study is the first documented dietary analysis of the northern saw-whet owl in the southern Appalachian Mountains, and is also the first attempt at identifying prey preferences for this strigid. This research is a necessary first step towards understanding the basic biology of the smallest owl in the southeast.

MATERIALS AND METHODS

Pellet Collection Sites

Pellets were collected in 1993 and 1994 from roost sites of radio-telemetered owls and from two habitual roosts. Owls were captured and pellets collected from the following sites: Mount Mitchell State Park, Yancey County, NC, and surrounding area (MMA); Roan Mountain, Mitchell County, NC; and the Southern Great Balsam Mountains, Haywood and Jackson counties, NC. Sites were chosen because they were accessible by vehicle and contained relatively large populations of saw-whet owls (Simpson 1972; Crutchfield 1990; Milling et al. in press). Elevation at these sites ranged from approximately 1585 m at Bald Knob Ridge Trail (along the Blue Ridge Parkway) to greater than 2000 m on Mt. Mitchell.

Data Collection

Preliminary auditory census work began in the winter of 1993. This involved surveying suitable habitat using recorded advertisement calls ("tooting"; see Hill 1995) of saw-whet owls played through a portable tape player with an external, amplified speaker. For two minutes prior to broadcast of recorded calls, any unsolicited, singing owls were noted. The tape was then played intermittently for five minutes. After playbacks had ceased, another two minute period was spent listening for owl responses before moving to the next location. The tape was broadcast every 0.5 to 0.8 km, depending on topography (see Milling et al. in press).

From May 1993 to June 1994, saw-whet owls were captured using mist-nets and taped playback calls. A mounted specimen of either *A. acadicus* or *Asio otus*, the eastern screech owl, was often used to provide a visual target for an incoming owl. Playback tapes consisted of advertising calls and/or whines (Cannings 1993; Hill 1995; Otter 1996).

After an owl was captured and removed from the net, standard biological measurements were taken: wing length, weight, and culmen length. All owls were banded with U.S. Fish and Wildlife Service aluminum leg bands. The owl was visually inspected for signs of parasites and ill health. If the owl was determined to be healthy, a small (< 3 g) radio-transmitter (SOPB-2070, Wildlife Materials Inc. (WMI), Carbondale, Illinois) was attached.

Two styles of harness were used. Style A utilized braided nylon cord set in a figure 8 style with the transmitter in the center of the owls' back. Style B was similar to A except elastic cord was used and the method of securing the harness was different. Style A used knots covered with glue, while B used a metal crimp covered with a plastic sheath. Style A was used in 1993, while style B was used in 1994.

The entire process of capture to release varied from approximately one hour to roughly three hours. This interval depended on the weather, the temperament of the owl, and the skill of the researcher. Each owl was released as close to the original site of capture as was possible. Each owl was observed after release for abnormal reactions.

Once tagged, the owl was located the next day to determine how the bird was adjusting to the radio package. Thereafter, owls were located as many times as was feasible throughout the study. Intensive searches for radio-tagged owls were conducted the first few weeks after release to ensure that no harm came to the owl as a result of a poorly installed harness. Each owl was found at least once every two weeks after it had adjusted to the harness. Owls were located by using a WMI (model 1000) or a Telonics (model TR-2) receiver attached to a WMI three element Yagi directional antenna.

Once an owl was found, the area directly beneath the roosting owl was searched for pellets (in expanding concentric circles around the base of the tree). Leaf/needle litter was frequently scraped away to ensure fewer pellets were overlooked. When the ground under the roost tree had been searched, adjacent trees were also checked in case the owl had shifted from one tree to a nearby one. Branches of roosts and nearby trees were searched for cached prey items. Often more than one researcher participated in these searches.

In addition to roost sites of radio-tagged owls, two habitual roost sites were found. These were roost sites where pellets were found in the same area at different times over a period of several months.

Pellet Analysis

Each pellet was collected, placed in a crushproof container for transport to the laboratory, air dried for a minimum of three days, and measured for length and width with calipers. Pellets were then water softened to facilitate sorting the remains within. Measurements were only performed on intact pellets, however all pellets and pellet fragments were examined for remains. Prior to dissection, each pellet was searched for intact feathers and other identifiable parts. Most pellets were soaked in water for 2-5 minutes and teased apart with forceps and probe. Ten pellets were soaked in a 2M NaOH solution for two to four hours (Marti 1987). This method dissolves fur and feathers leaving bones and chitin of insects unharmed. However, this method proved more time consuming due to the clean-up required, and was abandoned.

Mammalian prey species were identified by skulls, dentaries, and/or teeth. Birds were identified by beaks and/or feathers. Prey in pellets were identified using keys (Burt 1987; Glass 1973) and museum specimens (ASU collection).

Minimum number of individuals of small mammal prey was established conservatively based on skull and/or mandible identifications (Marti 1987). Thus, if one skull and three mandibles were found in a pellet, it was considered to contain two prey items. Birds and insects were so infrequently found that they were enumerated directly since no pellets contained more than one individual.

Small Mammal Trapping

Small mammals were trapped from April to July, 1994 at two sites on Mt. Mitchell. Site 1 was above Alice Camp road and below the Mt. Mitchell restaurant at an elevation of 1847 m (6060 ft). Site 2 was below the Buncombe horse trail at an elevation of 1675 m (5496 ft). These sites were chosen because owls were captured in the vicinity of these areas, and it was felt that these sites would be within the owls' foraging areas. Vegetation and physical characteristics were recorded at each site. Vegetation was identified using Radford et al. (1983). Each site was trapped for a minimum of four nights each month except April, when only one night of trapping was accomplished. Additionally, pitfall traps were left open between trapping events in June and July to increase sample sizes.

Twenty folding Sherman™ live-traps (7.6 X 7.6 X 25.4 cm) and five pitfall traps (clear two-liter soda bottles with tops cut off) were used to sample small mammals at each site. Pitfall traps were sunk in the ground with the lip of the trap just below the surface and covered with plywood tops supported by nails to keep out debris while allowing small mammals free access to the trap. The grid design was a five-by-five plot with an inter-trap interval of five meters. Pitfall traps were located at each corner and in the middle of the grid (Figure 2). Traps were set in the afternoon, baited with sunflower seeds, lined

Figure 2. Trapping grid design used for small mammals. Sherman™ live-traps (n = 20) are denoted by an X. Pitfall traps (n = 5) are denoted by an O. Inter-trap distance along rows or columns was 5 meters.

	1	**2**	**3**	**4**	**5**
A	O	X	X	X	O
B	X	X	X	X	X
C	X	X	O	X	X
D	X	X	X	X	X
E	O	X	X	X	O

with cotton bedding and checked the following morning. A maximum/minimum thermometer was placed in the center of the grid to record high and low temperatures throughout a trapping event.

Captured animals were transferred to a nylon mesh bag and weighed with Pesola™ spring scales. To identify recaptures, colored nail polish was applied to the animal's pinna. Traps were rebaited and fresh bedding supplied as necessary. Individuals were not sexed or aged. Each animal was released at the point of capture. Numbers of each species captured were recorded daily.

Statistical Analyses

Prey were enumerated from pellet dissections. These prey were subjected to a chi-square (χ^2) contingency analysis (species by year) to determine if prey composition changed between years (Norusis 1991).

Three methods were used to assess prey preferences. The first method, Ivlev's (1961) electivity index *E* (with Jacobs (1974) modification), compares the relative availability of food items in the environment with their relative utilizations in the diet (Refer to Appendix A for equations). The second method, Johnson's (1980) PREFER, ranks prey abundance and use by each owl. The differences in rank between usage and availability were then used to test two hypotheses: 1. Selection for all prey are equal. 2. Selection for prey *i* equals that for prey *j*.

Hypothesis one was tested with Hotelling's T^2 statistic (Johnson 1980). Hypothesis two was subjected to a Waller-Duncan K ratio t test (Johnson 1980). In this test, a K value of 100 was used, which is analogous to an alpha of 0.05 (Waller and Duncan 1969). All mammalian prey items from pellets were included in these analyses. A second PREFER run was performed without the rarest prey item (*Napaeozapus insignis*) in order to determine what effect, if any, deletion of a rare item had on observed preferences. The third method of preference assessment was the Neu et al. (1974) method. This test compared actual prey proportions with expected proportions by means of a χ^2 test and determined preference by whether observed prey usage proportions lie within confidence intervals of availability, determined from Bonferroni z statistics (Haney and Solow 1988). This method tested two null hypotheses: 1. usage occurs in proportion to availability, considering all prey simultaneously; and 2. usage occurs in proportion to availability, considering each prey individually (Alldredge and Ratti 1986).

Expected proportions (abundances) of small mammals in 1993 were calculated from summer trapping data of Jones and Wilhere (1994). Results of trapping data from the present study were used to calculate 1994 expected proportions. Live-traps are more effective at capturing rodents than are pitfalls, and pitfalls are better at capturing insectivores (Williams and Braun 1983). Because of these biases, capture rates by trap type (number captured per 100 Sherman trapnights or pitfall trapnights) were also used as a measure of prey availability. Thus, each of the three preference tests were run using both relative abundances and relative trap rates as expected proportions. Relative abundance was calculated by dividing the number of each species captured by the total of all species captured. The terms capture rates and trap rates are equivalent. Relative capture rates are calculated by dividing a species' capture rate by the total of all species' capture rates summed together.

Kendall's coefficient of concordance, *W*, measures the agreement between *k* rankings of *N* objects (Siegel 1956; Kirk 1969). Mammalian prey species in the diet were ranked for each owl. *W* was used to determine if dietary agreement existed among the owls.

The Shannon index, H', was used to determine the food niche breadth of saw-whet owl diets (Ludwig and Reynolds 1988). E5, known as the modified Hill's ratio (Alatalo

1981), was used to determine evenness of the diet. These indices were used for comparison with other saw-whet owl diet studies. BASIC programs (Ludwig and Reynolds 1988) were used to calculate these indices (Appendix A).

In addition to calculating H′ and E5 for this study, I also calculated these statistics for all 14 other studies of saw-whet owl diets (Table 18) which published actual prey numbers necessary to calculate H′ and E5. For each study, the finest level of prey resolution available was used to calculate diversity and evenness values (Greene and Jaksic 1983). To determine if the food niche breadth of the present study differed statistically from the 14 studies, H′ values were subjected to *t*-tests (Zar 1974). The sequential Bonferroni technique was used to control type I error rates among the *t*-tests (Rice 1989).

Spearman correlation coefficients, r_s, were computed to determine whether trapping rates or relative abundances were correlated with prey proportions in the diet.

SPSS for Windows (version 5.0) was used to calculate all statistics unless otherwise noted (Bryman and Cramer 1997). Statistical significance was declared when $p < 0.05$.

RESULTS

Study Area Vegetation

Red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) were the dominant tree species found on the study sites (Milling in prep.). Hemlock (*Tsuga canadensis*) was present, but occurred less frequently and usually at lower altitudes. Yellow birch (*Betula lutea*) was the most frequent deciduous tree along with northern red oak (*Quercus rubra*). Mountain maple (*Acer spicatum*) and striped maple (*Acer pennsylvanicum*) were abundant in some areas. *Rhododendron maximum* and *Rhododendron catawbiense* were common on exposed slopes and along riparian corridors.

Owl Trapping

Fifteen saw-whet owls were captured during the two year study (Table 1). Nine owls were captured in the Mt. Mitchell area. Three owls each were captured on Roan Mountain and in the Southern Great Balsam Mountains. Eight owls were captured in 1993 and seven in 1994. All owls were caught in mist nets; bal-chatri traps were ineffective. Most owls were captured singly, however, two owls were caught simultaneously during one trapping event.

Table 1. Saw-whet owl capture dates and locations.

Owl[a]	Location[b]	Date Captured	End Date[c]	Number of Pellets From
859	Roan Mt.	5/17/93	8/14/93	6
926	Roan Mt.	5/23/93	6/12/93	2
101	Roan Mt.	5/27/93		0
114	MMA	5/30/93	8/19/93	9
132	MMA	6/02/93		0
067	MMA	6/03/93	7/22/93	9
176	MMA	6/03/93	6/19/93	5
278	MMA	8/20/93	9/18/93	3
200	MMA	9/05/93		0[d]
260	MMA	3/11/94	4/04/94	2
185	MMA	3/12/94	5/18/94	14
856	Balsams	4/23/94		0
725	Balsams	5/22/94		0
767	Balsams	5/28/94	7/02/94	3
747	MMA	6/03/94		0
223	MMA	6/04/94	7/10/94	4

[a] Corresponds to transmitter frequencies.
[b] MMA refers to Mt. Mitchell and nearby areas such as Mt. Gibbes, and Bald Knob Ridge.
[c] Last date a pellet was found for the owl.
[d] Recapture of owl 067.

Small Mammal Trapping

Site 1, the high elevation site, was a mixture of woods and open fields. Approximately 50% of this site was wooded and the rest was mostly herbaceous. In the wooded section, dominant tree species were *Abies fraseri* and *Picea rubens*. *Acer spicatum* were also present. Under the spruce-fir canopy, open areas were often covered with moss, (*Polytrichum* sp.). The field was primarily vegetated by the fern, *Dryopteris campyloptera*. Other common field species included *Dryopteris intermedia, Polygonum cilinode, Carex tolliculata,* and *Hypericum mitchellianum.*

Site 2 was wooded with no field elements. *Picea rubens* was the dominant conifer present. *Betula lutea* was the most common hardwood present. *Rhododendron catawbiense* was present in small numbers. *Acer spicatum* was also found at this site.

Small mammals were trapped from April through July, 1994. A total of 115 animals of six species were captured during 985 trapnights (435 pitfall/540 Sherman™). Twenty-seven recaptures are included in this total (Table 2). The high elevation site (1847 m) yielded four less original captures than the low elevation site (1675 m). *Peromyscus maniculatus* was the most commonly trapped species with 35 animals marked and 11 recaptures. Among shrews, *S. cinereus* was trapped most often (n = 11). *Blarina brevicauda* was captured less than any other animal trapped (n = 4). *Napaeozapus insignis* was only captured at the high elevation site. Sherman™ traps captured more animals than pitfalls, 65 vs. 23 (Table 2). However, pitfalls captured 22 of 23 shrews (96%). Pitfall traps captured a single *N. insignis*, and Sherman™ traps caught but a single shrew, a *B. brevicauda*. First captures increased each month from four in April to 51 in July (Table 3).

Table 2. Summary of small mammals trapped on Mt. Mitchell in 1994. Table includes numbers of new animals captured. Numbers of recaptures are included in parentheses.

	Site		Trap Type	
SPECIES	High	Low	Sherman™	Pitfall
Clethrionomys gapperi (Red-backed vole)	10 (3)	13 (13)	23 (16)	0
Peromyscus maniculatus (Deer mouse)	14 (4)	21 (7)	35 (11)	0
Napaeozapus insignis (Woodland jumping mouse)	7	0	6	1
Sorex cinereus (Masked shrew)	5	6	0	11
Sorex fumeus (Smoky shrew)	4	4	0	8
Blarina brevicauda (Short-tailed shrew)	2	2	1	3
Totals	42	46	65	23

Table 3. Monthly mammal captures on Mt. Mitchell, 1994.

	Month				
Species	April	May	June	July	Totals[a]
C. gapperi	1	7	6	9	23
P. maniculatus	3	5	10	17	35
N. insignis	0	0	0	7	7
S. cinereus	0	0	2	9	11
S. fumeus	0	1	1	6	8
B. brevicauda	0	0	1	3	4
Totals	4	13	20	51	88

[a] Does not include recaptures.

Pellet Analysis

A total of 143 pellets was collected from a minimum of ten owls. Fifty-seven pellets were collected from beneath roosting owls and 82 were found at two habitual roost sites. Although the owl(s) were not seen at habitual roosts (except on one occasion), pellet measurements indicated that they were of the same size as known saw-whet owl pellets. While eastern screech-owls have similar size pellets, it is doubtful habitual roosts were those of screech-owls, which were neither seen nor heard during the two year study. Habitual roosts were at an elevation of 1585 m (5,200 ft); screech-owls are usually found below 1219 m (4,000 ft) in the southern Appalachian Mountains (Stupka 1963; Alsop 1991; Simpson 1992). Four pellets that were not associated with a specific owl or roost site were also collected. Fifty-three pellets were found from May to October 1993, and 90 from March to August 1994 (Table 4). The Mt. Mitchell area was responsible for 132 of the 143 pellets collected (92%). Of these 132, 82 (62%) pellets were from the two habitual roosts.

Identifiable mammalian remains were found in 59% of 1993 pellets and 67% of 1994 pellets (Table 4). Forty-four prey were identified in 1993 ($\overline{x}$ = 0.83 mammalian prey per pellet). In 1994, 76 prey were identified ($\overline{x}$ = 0.84 mammalian prey per pellet).

The number of identifiable prey per pellet ranged from zero to three (Table 5). Prey species in 39% of pellets could not be identified as the pellets contained only mammalian hair and/or unidentifiable bone fragments. Pellets containing one prey item comprised 43% of the sample, 14% held two prey and 4% contained three prey. The 99 intact pellets averaged 25.6 by 14.7 mm, respectively.

Table 4. Pellet summary statistics from 1993 and 1994.

Site[a]	Pellets Found 1993	Pellets Found 1994	Number of Prey[b] 1993	Number of Prey[b] 1994
Roan Mountain	8	0	8	0
Mt. Mitchell Area				
Habitual Roost 1	11	37	14	31
Habitual Roost 2	8	26	7	21
Other Sites	26	24	15	22
Balsam Mts.	0	3	0	2
Totals	53	90	44	76

[a] Habitual roosts 1 and 2 are part of Mt. Mitchell Area totals.

[b] Vertebrate prey only.

Description of Diet

Seven mammalian species were found in the pellets (Table 6). Two bird species were identified from pellets, caches, or prey remains. Mammals and birds comprised 93% and 7%, respectively, of vertebrate prey found in pellets.

Table 5. Mean pellet measurements (mm) and number of mammalian prey per pellet for all sites and years.

n Prey[a]	n Pellets	Pellet Length[b]	Pellet width[b]
0	55	25.2	14.1
1	62	26.1	14.8
2	20	24.5	15.4
3	6	28.9	18.0

[a] Identified prey only.

[b] Length and width are from 99 intact pellets.

Sorex cinereus, S. fumeus, B. brevicauda and unknown shrews (*Sorex* spp.) made up 60% of all mammalian prey. *Clethrionomys gapperi, P. maniculatus* and *N. insignis* (hereinafter, collectively called mice) comprised 39% of mammals taken, while *Parascalops breweri* (hairy-tailed mole) made up the remaining one percent. Dark-eyed juncos (*Junco hyemalis*) were the only birds found in pellets. The other bird species identified as a saw-whet owl food item was a decapitated veery (*Catharus fuscescens*) found at a roost site. Three pellets contained fragments of insects (beetle elytra).

Common prey items comprising more than 10% each of the owls' diet by biomass (red-backed voles, deer mice, smoky shrews, and dark-eyed juncos) represented 77% of total biomass (Table 6). Masked shrews, smoky shrews, deer mice, and red-backed voles comprised 82% of prey, and each

Table 6. Frequencies, biomass (g), and biomass percentages of saw-whet owl vertebrate prey found in pellets from all study sites for both years.

Species	n	Freq %	Mass Prey[a]	Biomass Total[b]	Biomass %
Mammals					
Red-backed vole (*Clethrionomys gapperi*)	15	12	29	435	27
Deer mouse (*Peromyscus maniculatus*)	30	23	14	420	26
Woodland jumping mouse (*Napaeozapus insignis*)	2	2	19	38	2
Masked shrew (*Sorex cinereus*)	36	28	3.8	137	9
Smoky shrew (*Sorex fumeus*)	25	19	8.5	213	13
Short-tailed shrew (*Blarina brevicauda*)	7	5	16	112	7
Hairy-tailed mole (*Parascalops breweri*)	1	1	52	52	3
Unidentified shrews[c] (*Sorex* spp.)	4	3	5.7	26	2
Birds					
Dark-eyed junco (*Junco hyemalis*)	9	7	19	171	11
Totals[d]					
Mice	47	36		893	55
Shrews	72	56		488	31
Mammals	120	93		1433	89
Birds	9	7		171	11
All	129	100		1604	100

[a] Prey masses (g) used are means from animals trapped in this study, except for the hairy-tailed mole (Whitaker 1980), and dark-eyed junco (Dunning 1993).

[b] Biomass totals are rounded to integers.

[c] Weighted mean of *Sorex* species.

[d] Totals may not equal sums from table due to rounding.

accounted for greater than 10% of the diet. Shrews comprised 56% and 31% of the diet by frequency and biomass respectively. Mice were less frequent in the diet (37%) but comprised more total biomass (55%). Prey use varied between years. Frequencies of mice and shrews in pellets differed between years ($\chi^2 = 6.14$, df = 1, p = 0.01; Table 7). This difference was most evident for the MMA where frequencies of shrews and mice differed greatly between years ($\chi^2 = 13.86$, df = 1, p = 0.0002; Table 8). For all sites combined, shrews contributed 22% more of the total biomass in 1993 than in 1994, while mice comprised 18% more of the biomass in 1994 than in 1993. For all sites combined, red-backed voles were the most important single source of biomass in 1993 (23%), but deer mice were more important in 1994 (30%; Table 7). In the MMA only, smoky shrews contributed the most biomass in 1993 (24%), but most of the biomass in 1994 was from deer mice and red-backed voles (31% each; Table 8).

On Roan Mountain, 94% of dietary biomass in 1993 was mice (of 8 prey items, four were deer mice, three were red-backed voles, and one was a smoky shrew). For all sites, mice contributed 43% of biomass in 1993 compared to 46% for shrews. In 1994, however, the relative importance of these

Table 7. Annual comparison of vertebrate prey found in saw-whet owl pellets.

	1993			1994		
Species[a]	n	% Freq	% Biomass	n	% Freq	% Biomass
C. gapperi	4	9	23	11	13	29
P. maniculatus	6	13	16	24	29	30
N. insignis	1	2	4	1	1	2
S. cinereus	15	32	11	21	26	7
S. fumeus	11	23	18	14	17	11
B. brevicauda	4	9	13	3	4	4
P. breweri	0	0	0	1	1	5
Sorex spp.	3	6	4	6	1	2
Birds						
J. hyemalis	3	6	11	6	7	10
Totals[b]						
Mice	11	24	43	36	43	61
Shrews	33	70	46	44	48	24
Mammals	43	94	89	81	92	90
Birds	3	6	11	6	7	10

[a] Refer to table 6 for complete scientific names.

[b] May not equal 100% due to rounding.

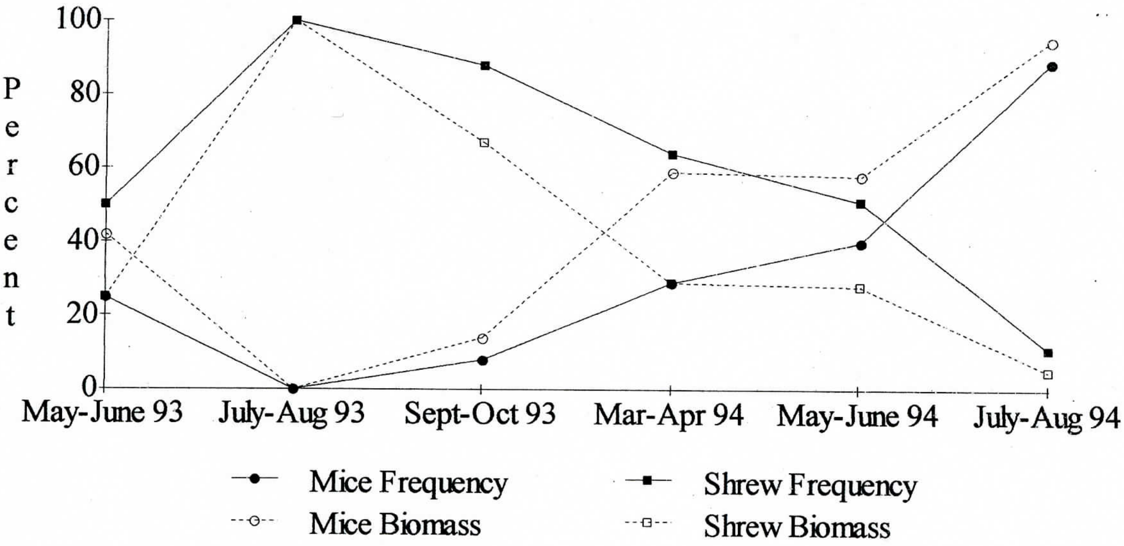
Table 8. Annual variation in counts and biomass percentages (in parentheses) of vertebrate prey in pellets from the MMA.

	1993		1994	
Mammals	n	(%)	n	(%)
Clethrionomys gapperi	1	(8)	11	(31)
Peromyscus maniculatus	2	(8)	23	(31)
Napaeozapus insignis	1	(5)	1	(2)
Sorex cinereus	15	(16)	21	(8)
Sorex fumeus	10	(24)	14	(12)
Blarina brevicauda	4	(18)	3	(5)
Sorex ssp.	3	(5)	1	(<1)
Birds				
Junco hyemalis	3	(16)	6	(10)
Mice Totals	4	(21)	35	(64)
Shrew Totals	32	(63)	39	(26)
Grand Totals	39	(100)	80	(100)

two prey types had switched, with mice comprising 61% of the biomass and shrews only 24% (Table 7).

To see whether prey choices varied temporally, mice and shrew frequencies in pellets were examined bimonthly. Mice declined in the diet from May to October, 1993 while shrews increased during the same period (Figure 3). In 1994, mice occurrence in the diet rose from March to August as shrews declined.

Figure 3. Temporal variation in frequencies and biomass of mice and shrews in the diet for the MMA.



Prey caches and/or partial remains of 19 prey were found at 17 sites (Table 9). Cached prey were usually on a branch at approximately the same height as the roosting owl, but prey remains were also found under roost sites. Six cached items lacked the anterior portion of the body; e.g., the head and front legs or wings. Prey entrails, usually intestines and/or stomachs, were found hanging on a branch next to the owl at several roosts. Entrails could not be identified to species and thus do not contribute to species counts in Table 9.

Table 9. Caches and prey remains found at saw-whet owl roost sites.

Date	Species	Site	Owl[a]	Type
6/11/93	*B. brevicauda*	Roan	101	Remains
10/14/93	*B. brevicauda*	MMA	HS2	Remains
6/06/93	*C. fuscescens*	MMA	132	Remains
6/30/93	*C. gapperi*	MMA	176	Cache
4/04/94	*C. gapperi*	MMA	260	Cache
5/18/94	*C. gapperi*	MMA	185	Remains
5/24/94	*C. gapperi*	Bals.	856	Cache
5/24/94	*C. gapperi*	Bals.	856	Cache
7/01/94	*C. gapperi*	Bals.	725	Cache
6/18/93	*J. hyemalis*	MMA	067	Remains
6/19/93	*J. hyemalis*	MMA	176	Cache
7/22/93	*J. hyemalis*	MMA	114	Cache
4/03/94	*J. hyemalis*	MMA	260	Remains
5/28/94	*S. cinereus*	Bals.	725	Cache
8/03/93	*S. fumeus*	MMA	278	Cache
8/14/93	*S. fumeus*	Roan	859	Cache
3/26/94	*S. fumeus*	MMA	185	Cache
5/24/94	*P. maniculatus*	Bals.	856	Cache
6/20/94	*P. maniculatus*	Bals.	725	Cache

[a] Refers to transmitter frequencies; HS2 refers to habitual roost site number two.

Prey Preference Analysis

Ivlev's electivity indexes (with Jacob's 1974 modification) for 1993 data showed preferential predation on *S. cinereus, S. fumeus,* and *B. brevicauda*. *Sorex cinereus* and *S. fumeus* were the only preferred prey in 1994 (Table 10). For 1993, *P. maniculatus* was the least preferred prey, while *N. insignis* was least preferred in 1994. Using relative trap rates as availability measures, *S. cinereus* was no longer preferred in 1993 (Table 11).

Table 10. Ivlev's electivity indices of prey species for the MMA in 1993 and 1994. Abundance data are from relative abundances.

	1993[a]			1994[b]		
Species	Use	Abundance	D[c]	Use	Abundance	D[c]
S. fumeus	.30	.02	.93	.19	.09	.41
B. brevicauda	.12	.01	.84	.04	.05	-.12
S. cinereus	.45	.17	.65	.29	.12	.46
N. insignis	.03	.07	-.52	.01	.08	-.79
C. gapperi	.03	.25	-.83	.15	.26	-.33
P. maniculatus	.06	.48	-.87	.32	.40	-.17

[a] Relative abundance data from Jones and Wilhere (1994).
[b] Relative abundance data from this study.
[c] Positive values indicate preference, while negative values indicate non-preference.

Table 11. Ivlev's electivity indices of prey species for the MMA in 1993 and 1994. Abundance data are from relative trap rates.

	1993[a]			1994[b]		
Species	Use	Abundance	D[c]	Use	Abundance	D
S. fumeus	.30	.05	.80	.19	.11	.31
B. brevicauda	.12	.02	.80	.04	.05	-.17
S. cinereus	.45	.48	-.06	.29	.15	.40
N. insignis	.03	.05	-.26	.01	.08	-.79
C. gapperi	.03	.14	-.68	.15	.25	-.31
P. maniculatus	.06	.27	-.71	.32	.37	-.11

[a] Abundance data from Jones and Wilhere (1994).
[b] Abundance data from this study.
[c] Positive values indicate preference, while negative values indicate non-preference.

Program PREFER (Johnson 1980) found no overall significant differences in prey use in either 1993 ($F_{(5,1)} = 20.7$, $p > 0.10$) or 1994 ($F_{(5,1)} = 2.8$, $p > 0.25$). However, if *N. insignis* is omitted from the analyses, significant differences were found for 1993 ($F_{(4,2)} = 130.3$, $p < 0.01$), but not for 1994 ($F_{(4,2)} = 3.7$, $p > 0.10$). Although main effects were nonsignificant (except for 1993 with *N. insignis* omitted), planned comparisons did show significant differences among specific prey (Tables 12, 13). All three species of shrews were shown to be preferred in both years whether *N. insignis* was included or not (Tables 12, 13).

As with the Ivlev index, PREFER found neither *P. maniculatus* nor *C. gapperi* to be preferred in either year. When relative trap rates were used to generate expected values (Table 14), prey preferences changed slightly. Overall significant differences were not found for either year (1993, $F_{(5,1)} = 8.00$, $p > 0.25$; 1994, $F_{(5,1)} = 2.67$, $p > 0.25$). Planned comparisons, however, still showed significant differences among specific prey, although the rankings changed to a small degree. Indeed, *S. cinereus* is no longer preferred in 1993. *Blarina brevicauda* and *S. fumeus* are the most preferred both years (Table 14).

Table 12. PREFER ranking and preferences[a] of mammalian prey in 1993 and 1994 for the MMA using relative abundance data.

Species	1993 Rank	1993 Preferences[b]	1994 Rank	1994 Preferences[b]
S. fumeus	1	-3.42 A,B	2	-1.00 A
S. cinereus	2	-1.58 C,D,E	3	-0.75
B. brevicauda	3	-1.25 F	1	-1.25 B,C
N. insignis	4	0.58 E	4	0.08 B
C. gapperi	5	2.08 A,C	5	0.83
P. maniculatus	6	3.58 B,D,F	6	2.08 A,C

[a] Negative values connote preference, positive values non-preference.

[b] Preferences designated by like letters are significantly different from each other at $p < 0.05$.

Table 13. PREFER ranking and preferences[a] of mammalian prey (excluding *N. insignis*) in 1993 and 1994 for the MMA using relative abundance data.

Species	1993 Rank	1993 Preferences[b]	1994 Rank	1994 Preferences[b]
S. fumeus	1	-2.08 A	1	-1.08 A
B. brevicauda	2	-1.58 B	3	-0.67 B
S. cinereus	3	-1.08 C	2	-0.75
C. gapperi	4	1.67 A	4	0.75
P. maniculatus	5	3.08 A,B,C	5	1.83 A,B

[a] Negative values connote preference, positive values non-preference.

[b] Preferences designated by like letters are significantly different from each other at $p < 0.05$.

Table 14. PREFER ranking and preferences[a] of mammalian prey in 1993 and 1994 for the MMA using relative trap rates.

Species	1993 Rank	1993 Preferences[b]	1994 Rank	1994 Preferences[b]
S. fumeus	1	-2.42 A	2	-1.08 A
B. brevicauda	2	-2.25 B	1	-1.25 B,C
S. cinereus	3	0.42 A	3	-0.58
N. insignis	4	0.58	4	0.08 B
C. gapperi	5	1.08	5	0.75
P. maniculatus	6	2.58 A,B	6	2.08 A,C

[a] Negative values connote preference, positive values non-preference.

[b] Preferences designated by like letters are significantly different from each other at $p < 0.05$.

The chi-squared technique identified slightly different preferences. Overall prey use was significantly different from availability for 1993 ($\chi^2 = 663.23$, df = 4, $p < 0.0001$) and 1994 ($\chi^2 = 31.05$, df = 5, $p < 0.0001$). This method found *S. cinereus* to be preferred both years (Table 15). Although *S. fumeus* was also preferred in 1993, it was used in proportion to availability in 1994. *Clethrionomys gapperi and P. maniculatus* were found to be avoided in 1993 and used in proportion to availability in 1994 (Table 15).

Table 15. Summary of prey species on the MMA that were preferred (+), used in proportion to availability (=), or avoided (-), based on relative abundance data. Preference was determined by the χ^2 technique of Neu et al. (1974).

Prey Species	1993[a]	1994[b]
Clethrionomys gapperi	-	=
Peromyscus maniculatus	-	=
Napaeozapus insignis	=	-
Sorex cinereus	+	+
Sorex fumeus	+	=
Blarina brevicauda	=	=

[a] $\chi^2 = 663.23$, Df = 4, $P < 0.0001$.

[b] $\chi^2 = 31.05$, Df = 5, $P < 0.0001$. Note that the degrees of freedom are less in 1993 due to the collapsing of *S. cinereus* and *B. brevicauda* into one category because of low expected frequencies.

When prey availability was determined from trap rates instead of relative abundances, only a single difference was evident. In 1993, *S. fumeus* was no longer preferred, but was used in proportion to availability. Neither method of assessing small mammal abundance changed observed preferences in 1994.

There were slight differences in results of the three preference measures (Tables 16, 17). When relative trap rates were used as measures of prey availability instead of relative abundances, at least one shrew species changed from preferred to nonpreferred prey for each of the three preference methods (Tables 16, 17). Mice were not shown to be preferred by any method.

Table 16. Comparison of methods used to determine saw-whet owl prey preferences in the MMA, using relative abundance data. A yes indicates preference and no implies nonpreference for both years. A yes* denotes preference in 1993, but not in 1994.

Prey Species	Ivlev's Method	PREFER Method	Neu Method
Clethrionomys gapperi	No	No	No
Peromyscus maniculatus	No	No	No
Napaeozapus insignis	No	No	No
Sorex cinereus	Yes	Yes	Yes
Sorex fumeus	Yes	Yes	Yes*
Blarina brevicauda	Yes*	Yes	No

Table 17. Comparison of methods used to determine saw-whet owl prey preferences in the MMA, using relative trap rate data. A yes indicates preference and no implies nonpreference for both years. A yes* or no* denotes preference or nonpreference in 1993 when the opposite was found in 1994.

Prey Species	Ivlev's Method	PREFER Method	Neu Method
Clethrionomys gapperi	No	No	No
Peromyscus maniculatus	No	No	No
Napaeozapus insignis	No	No	No
Sorex cinereus	No*	No*	Yes
Sorex fumeus	Yes	Yes	No*
Blarina brevicauda	Yes*	Yes	No

To assess possible prey choice differences among owls, Kendall's W, the coefficient of concordance, was calculated (Siegel 1956). Rankings of eight prey species were similar among four radio-tagged owls and the owl(s) using the two habitual roosts in 1993 ($W = 0.48$, $df = 7$; $p = 0.005$) and in 1994 ($W = 0.43$, $df = 7$; $p = 0.011$). Thus, owls appeared to choose the same prey species and in the same rank order within each year.

Prey Abundance and Use

Both relative abundance and relative trap rates were used as measures of prey availability. Only trap rates were highly correlated with prey use in 1993 (trap rate, $r_s = 0.81$, n = 33 prey, $p < .001$; relative abundance, $r_s = 0.30$, n = 33 prey, p = .086). In 1994, both trap rates and relative abundances were equally correlated with prey use (both measures, $r_s = 0.71$, n = 73 prey, $p < .001$). Relative abundances of mice and shrews changed little from 1993 to 1994 (Figure 4). Trap rates for mice increased dramatically but shrew capture rates were similar in both

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Figure 4. Relative abundance of mice and shrews in the MMA for 1993 and 1994.

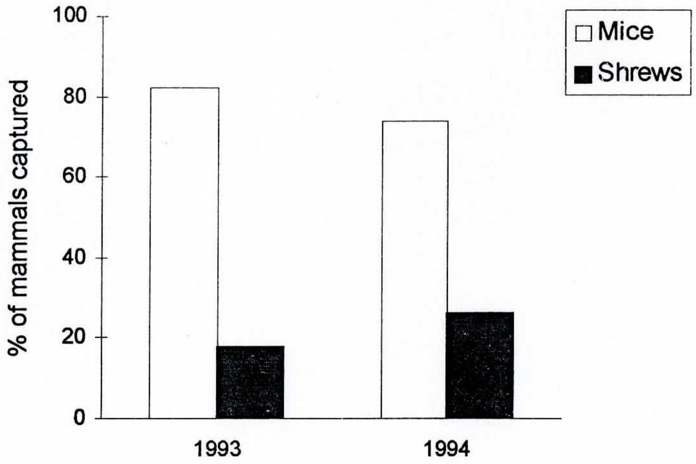


Figure 5. Trap rates of mice and shrews in the MMA for 1993 and 1994.

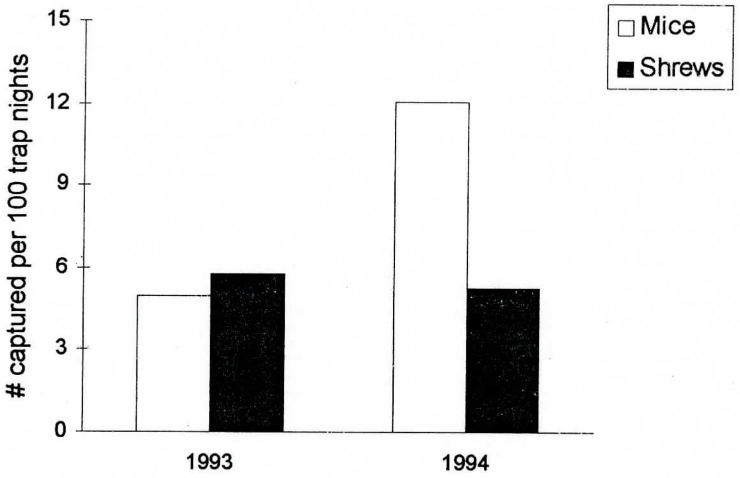
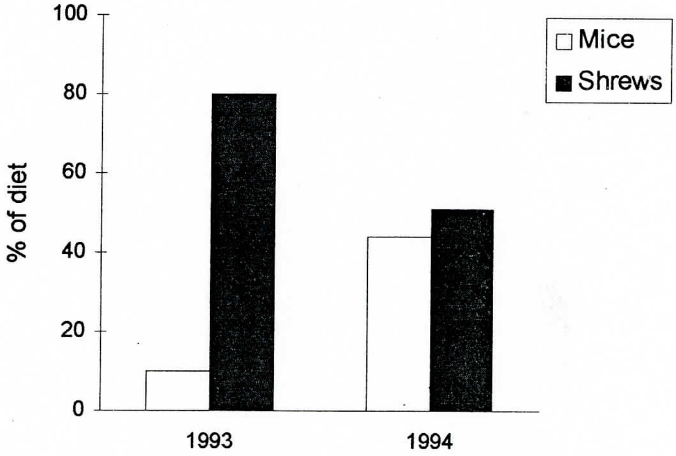


Figure 6. Percentages of mice and shrews in the diet for the MMA in 1993 and 1994.



years (Figure 5). The increase in mice capture rates parallel the increase of mice in the diet (Figure 6). Thus, small mammal trap rates were more predictive of owl diet than were relative abundances.

Food Niche Metrics

Food niche breadth (FNB) and dietary evenness of southern Appalachian owls were compared with other published dietary studies of saw-whet owls (Table 18). FNB of owls in the present study was significantly higher than that of any other study (1.73 vs. 1.56 for next highest). Student *t*-tests (Zar 1974) showed southern Appalachian saw-whet owls had a significantly larger FNB than all 14 other studies (Table 19). Dietary evenness was the third highest found (0.87 vs. 0.95 for the highest E5), but statistical comparisons were not performed on these values.

Table 18. Prey and taxon counts, food niche breadth and evenness of saw-whet owl diets from 15 studies.

Location	N[a]	T[b]	FNB[c]	Even-ness[d]	Source
North Carolina	124	8	1.73	0.87	This Study
Ohio	113	9	1.56	0.66	Randle and Austing 1952
Idaho	714	5	1.37	0.95	Marks and Doremus 1988
Washington	767	10	1.27	0.66	Grove 1985
Connecticut	240	8	1.25	0.73	Smith and Devine 1982
Montana	366	7	1.21	0.91	Holt and Leroux 1996
British Columbia	576	8	1.18	0.66	Cannings 1987
Wisconsin	533	10	1.12	0.50	Swengel and Swengel 1992
Oregon	77	9	1.01	0.40	Boula 1982
Wisconsin	162	8	0.97	0.46	Swengel and Swengel 1987
Missouri	136	3	0.86	0.87	Toland 1984
Massachussetts	225	5	0.78	0.70	Holt et al. 1991
Ontario	173	4	0.75	0.72	Catling 1972
Indiana	56	5	0.69	0.48	Dancey 1992
Tennessee	47	4	0.31	0.40	Parmalee and Klippel 1987

[a] Number of prey used in calculations.
[b] Denotes number of taxa used, insects were not included.
[c] Calculated with the the Shannon-Weiner Index.
[d] Calculated with the modified Hill's ratio.

Table 19. FNB comparisons between the present study and 14 other diet studies. All studies were compared to the overall FNB from the present study using individual *t*-tests (Zar 1974).

Location[a]	FNB[b]	*t*	df	n	P-value[c]
This study	1.73	--	--	125	--
Ohio	1.56	2.38	233	113	<.020
Idaho	1.37	6.87	162	714	<.001
Washington	1.27	8.70	168	735	<.001
Connecticut	1.25	6.92	328	239	<.001
Montana	1.21	8.66	259	366	<.001
British Columbia	1.18	9.99	196	569	<.001
Wisconsin	1.12	11.59	165	689	<.001
Oregon	1.01	2.06	76	74	<.050
Wisconsin	0.97	10.43	330	216	<.001
Missouri	0.86	11.62	258	136	<.001
Massachusetts	0.78	12.69	342	225	<.001
Ontario	0.75	11.97	293	173	<.001
Indiana	0.69	3.86	59	56	<.001
Tennessee	0.31	3.41	48	47	<.005

[a] For sources, see table 18.

[b] FNB computed using Shannon's H'; see methods.

[c] Sequential Bonferroni analysis (Rice 1989) found table-wide significance for all P values at $P \leq 0.05$.

DISCUSSION

Overall (pooling across 1993 and 1994), small mammals dominated the diet of saw-whet owls in this study. Birds were secondary prey items, and very few insect parts were found in pellets. This result agreed well with other research on saw-whet owls. However, shrews comprised more than half of the diet by frequency, in marked contrast with all other studies of saw-whet owl diets (Table 20). Although less numerous than shrews in the diet, mice represented most of the biomass in my study (Table 6).

Shrews dominated the diet in 1993 in both frequency and biomass. Numerically, shrews were still more common than mice in the diet in 1994, but proportionally contributed only half as much biomass as they did in 1993. Mice increased in both frequency and biomass in the diet from 1993 to 1994. Thus, pronounced differences were found in mice and shrew proportions (and biomass percentages) within and between each year.

The shift in the diet from shrews in 1993 to mice in 1994 was surprising. Relative abundances of mice and shrews trapped on Mt. Mitchell in both years were very

Table 20. Percentages of birds, mammals, *Peromyscus* and shrews in 15 saw-whet owl diet studies.

% Birds	% Mammals	% *Peromyscus*	% Shrews	n Prey	Source[a]
7	93	23	56	125	This study
1	99	48	0	113	Randle and Austing 1952
0	100	26	4	173	Catling 1972
4	96	77	3	77	Boula 1982
< 1	> 99	45	5	276	Smith and Devine 1982
0	100	38	0	136	Toland 1984
10	90	24	< 1	770	Grove 1985
2	98	58	2	584	Cannings 1987
0	100	94	4	47	Parmalee and Klippel 1987
4	96	81	5	243	Swengel and Swengel 1987
0	100	15	< 1	714	Marks and Doremus 1988
0	100	69	4	225	Holt et al. 1991
0	100	83	6	56	Dancey 1992
5	95	69	9	740	Swengel and Swengel 1992
< 1	> 99	35	4	388	Holt and Leroux 1996

[a] See table 18 for study locations.

similar. Mice comprised 81% of the total catch in 1993 (Jones and Wilhere 1994), and 74% in 1994 (Figure 4). However, when relative proportions were calculated based on shrews per 100 pitfall nights (PN) and mice per 100 trapnights (TN), a different picture emerged (Figure 5). Shrew capture rates were 5.7 in 1993 and 5.3 in 1994. However, in the same time period, mice capture rates increased from 4.9 to 12 per 100 TN. Mice were apparently more available relative to shrews in 1994 than in 1993, which may explain why saw-whet owls ate more mice in 1994 (Figure 6). Differences in numbers of traps, trap types (Shermans™ vs. pitfalls), and trappability of mice and shrews precluded direct comparison of shrew trap rates with mice trap rates (Pucek 1969; Andrzejewski and Rajska 1972). Observed predation proportions for these taxa covaried with capture rates, so capture rates had some utility as measures of prey availability.

The percentage of shrews in the diet declined gradually from 100% in July, August and September, 1993 to 0% in July 1994 for the MMA (Figure 3). The percentage of mice in the diet varied inversely with shrews. This dietary shift may have been due to annual or multiannual cycles of prey availability.

While the time frame of the present study did not allow examination of population cycles, results of earlier studies provide some relevant insights. Populations of some small mammal species experience cycles of abundance, but there is little data for any of the small mammal species in the present study. Over a 14-year period in Illinois, Getz (1989) showed that *B. brevicauda* displayed annual cycles but not multiannual cycles. DeGraaf et al. (1991) found that numbers of four shrew species increased in New Hampshire from one year to the next, while three species of mice decreased in abundance over the same period. This study was only two years long but the authors suggested that this pattern represented normal population fluctuations. Peak numbers of *Clethrionomys* and *Peromyscus* in Quebec did not coincide or show regular patterns over 11 years of study by Grant (1976). *Clethrionomys gapperi* has not been found to be cyclic (Bondrup-Nielsen 1987; Bondrup-Nielsen and Ims 1988). Miller and Getz (1977) suggested that *P. maniculatus* and *C. gapperi* in Vermont displayed random peaks of abundance but without annual cycles. However, a four year cycle was found in a population of *P. maniculatus* from a mixed deciduous forest in Virginia (Wolff 1985). Ylönen (1994) asserted that non-cyclic populations of microtines experience regular declines during winter and increases during the breeding season (regardless of initial spring densities), with small inter-year fluctuations. Korpimäki (1986) found that mammalian and raptor predation caused synchronous declines in mice and shrews in Finland. However, Buckner (1966) argued that shrew dynamics in Manitoba were not affected by predation. Thus, populations of mice and shrews seemed to exhibit annual or multiannual cycles of abundance in some places but not others, and the influence of predation in driving these cycles has not been resolved.

The increase of mice in the diet from 1993 to 1994 tentatively suggested that mice may have been in an upswing phase of a local population cycle. Clearly, the two years of data in the present study are insufficient to identify patterns of cyclicity for small mammals in the southern Appalachian Mountains. More research on small mammal population dynamics in the southern Appalachians is needed to determine whether these mammals exhibit cycles. Northern saw-whet owl pellet analyses may be a good way to assess these cycles. Wendland (1981), for example, used pellet analyses of tawny owls (*Strix aluco*) and long-eared owls (*Asio otus*) to demonstrate that short-tailed voles

(*Microtus agrestris*), common voles (*M. arvalis*), and yellow-necked field mice (*Apodemus flavicollis*) exhibited cycles at 5, 4, and 3 year intervals, respectively, over a 28 year period in Berlin, Germany.

Prey Preferences

There were subtle differences between results of the three different preference tests: Ivlev's (1961) electivity index (EI) (with Jacob's 1974 modification), PREFER (PR) (Johnson 1980), and Neu et al.'s (NE) (1974) method. When availability of prey is estimated by relative abundances, *S. cinereus* was shown to be preferred in both years by all three methods (Table 16). *Sorex fumeus* was preferred in 1993 (EI, PR, NE) and 1994 (EI, PR). *Blarina brevicauda* was preferred two (PR), one (EI) or no years (NE), depending on which test was used. No mouse species were found preferred by any method.

PREFER was rerun without *N. insignis* to evaluate the effect of deletion of a rare prey item on the analysis. The main difference between the two analyses was the statistically significant effects on *C. gapperi* and *S. cinereus* in 1993. With *N. insignis* included, preference for *C. gapperi* was less than that of *S. fumeus* and *S. cinereus*, while preference for *S. cinereus* was greater than that for *C. gapperi*, *P. maniculatus*, and *N. insignis* (Table 12). When *N. insignis* was omitted from the analyses, *C. gapperi* was only preferred less than *S. fumeus*, and *S. cinereus* was preferred only to *P. maniculatus* (Table 13). However, overall prey preferences did not differ between the two analyses; i.e., all three shrew species were preferred both years. For these data, PREFER seemed more robust to inclusion/exclusion of rare prey items, as has been reported (Johnson 1980).

When relative trap rates are used as estimates of prey availability, results of the preference tests changed slightly (Table 17). *Sorex cinereus* was preferred by saw-whet owls in 1993 by only the NE method. The most striking difference was found in the PREFER analyses. In 1993, *S. cinereus* was preferred significantly more than only *P. maniculatus*. But in 1994, *S. cinereus* was not preferred significantly to any other prey species (Table 14).

The two different availability measures had little effect on preferences generated by the Neu method. Only *S. fumeus* was affected, changing from preferred (using relative abundances) to use equaling availability in 1993 (using relative trap rates).

So which preference test, if any, was best? Ivlev's index (as modified by Jacobs 1974) employed ratios of prey eaten to prey available. It was sensitive to sampling errors related to rare items and was inappropriate for comparison between different samples unless only two food types are under consideration (Lechowicz 1982). The PREFER method was based on species ranks and was better when use and availability data were approximate (Alldredge and Ratti 1992). However, if proportions of prey use and abundance differed greatly, yet still had the same rank, the chance of accepting a false null hypothesis increased (type II error; Alldredge and Ratti 1992). The Neu et al. method (1974) had one troubling assumption. Availabilities had to be known without error; i.e., they could not be estimates (Thomas and Taylor 1990). Violation of this assumption resulted in a greater chance of rejecting a true null hypothesis (type I error; Thomas and Taylor 1990).

For the present study, species availabilities were estimated from trapping, so the Neu method was suspect. Also, rare items were included in the diet, and Ivlev's index was of low utility. PREFER was probably the most appropriate preference method for studies like this one.

Prey use was highly correlated with trap rates. Changes in trap rates between years and taxa were mirrored in the saw-whet owl diets. Owls seemed to include prey in the diet based in part on availability, as suggested by Griffiths (1975) that sit-and-wait predators take prey as they are encountered. Abundant prey would have been encountered more often than less abundant prey, and the diet should reflect this difference. Saw-whet owls (in this study) seem to fit this model. Shrews were more abundant in the environment relative to mice in 1993 and the reverse was true in 1994. Owl diets reflected these changes in prey abundances.

Food Niche

The FNB (H′ = 1.73) of southern Appalachian saw-whet owls was higher than that reported in any other study (Table 18). Dietary evenness was equally high (Table 18). Saw-whet owls were not relying on one or a few prey species, but consumed many prey species. Four (of eight total) prey species comprised 82% of all prey consumed. Most earlier studies reported only one or two species as major dietary components.

Why do southern Appalachian saw-whet owls take more shrews and have a broader food niche breadth than owls from other parts of their range? Three possible explanations for these differences are: (1) shrew populations are larger in the southern Appalachians; (2) mice populations are smaller in the southern Appalachians; or (3) overall, small mammal density is low in the southern Appalachians, forcing owls to take prey according to availability. In the main areas of the owls' range, high small mammal densities may allow owls to be more selective, ignoring tiny prey items like shrews to prey only on larger, more profitable mice. Tentative evidence in support of hypothesis 3 is provided by considering the results from two small mammal trapping studies in light of Cannings (1993) review of saw-whet owl diets. Lee (1995) found relative abundances of 58% mice and 42% shrews in Washington. DeGraaf et al. (1991) noted relative abundances of 55% mice and 45% shrews in New Hampshire. Cannings (1993) summary of 11 dietary studies of saw-whet owls identified 6,507 prey items from western and northeastern portions of the owls' range. Of these, only 4.2% were shrews. If shrews were as abundant (or nearly so) as mice, based on the two small mammal trapping studies, why did shrews typically comprise such a small part of the saw-whet owl diet? Perhaps mice were abundant enough that, over most of the owls' range, saw-whet owls can afford to be selective.

However, a fourth explanation for the high shrew predation rates in the southern Appalachian Mountains deserves discussion - the 'differential consumption' hypothesis. Great gray owls have been shown to eat smaller prey at the point of capture and take larger prey back to the nest (Bull et al. 1989). If saw-whet owls behaved similarly, the high shrew proportions in the diet in 1993 might have been because male owls were taking larger prey (i.e., mice and birds) back to their nests. In 1994, more mice were eaten by male owls, perhaps because less nesting occurred. Evidence in support of the proposed differences between breeding and nonbreeding male diets was provided by Barb (1995). On Roan Mountain in 1994, three nest boxes used by saw-whet owls had caches of 43 mice, 7 birds, and only one shrew (Barb 1995). Unfortunately, there were no pellet data (from male owls) on Roan Mountain in 1994 to compare with the nest box data. Still, less than 2% of prey found in these nests were shrews, which is much less than the 48% found in pellets from the MMA in 1994 in my study. The 'differential consumption' hypothesis will remain untested until pellets are found from breeding male owls and compared with cached prey from their nests.

Optimal foraging theory predicts that a predator should take scarce items relative to their abundance in the environment when overall prey are scarce; i.e., feed as number maximizers (Schoener 1971). Higher prey densities favor an energy maximizer feeding strategy (Griffiths 1975). This theory includes two primary ideas: (1) If prey are abundant, predators should take the preferred prey species exclusively, this strategy returns the most calories per time unit; (2) When prey are rarer, less profitable prey should contribute more to the diet.

Hughes (1979) suggested that inclusion of a particular food type depended on its abundance and on the abundances of more preferred food types. Changes in prey relative abundances resulted in a switch from one food type to another (e.g., shrews to mice). Dietary preferences may change gradually from preferences for shrews (when mice are uncommon) to no preferences (when mice are moderately common) to preference for mice (when mice are common). Under this hypothesis, shrews and mice both should be included in the diet if equally rare. However, if all prey are abundant, preferences for the 'optimal' prey should develop regardless of relative abundances.

Saw-whet owl diets in this study probably reflected the sit-and-wait strategy, although the data also agree with optimal foraging predictions. More mice were available in 1994 than 1993 (from trap rates), and this difference showed up in the diet. I would predict that if mice increased even more they would dominate the diet; and shrews would be taken only secondarily.

Trap rate data show that mice numbers increased from 1993 to 1994, while shrew numbers stayed about the same. This increase in mice availability is shown in the diet, with a corresponding decrease in shrew predation. Perhaps shrews are the primary alternate prey. Mice may actually be preferred but due to reduced numbers of these in 1993, shrews were taken most often. The only obvious difference in prey availability between the two years was the increase in mice. If the owls really preferred shrews, shrews should have continued to dominate the diet in 1994. By frequency, shrews did outnumber mice in the 1994 diet on the MMA (49% to 44%). But the 1993 diet on the MMA was 82% shrews and only 10% mice! A switch was also noted in terms of biomass, from 63% shrew biomass in 1993, to 64% mice biomass in 1994 (Table 8). Summing up, shrew availability remained stable from year to year, while mice populations increased and were likely responsible for the observed differences in diet between the years. Thus, both mice and shrews are important components of saw-whet owl diets in the southern Appalachian Mountains though preference tests indicate shrews are preferred.

Research and Management Implications

Fir Die-off and Small Mammal Abundance

What effect has fir decline in the southern Appalachian Mountains had on both prey and saw-whet owl populations? Only one study, conducted on Mt. Mitchell, has compared small mammal populations before and after the fir decline. According to Adams and Hammond (1991), fall numbers of deer mice and red-backed vole populations doubled from 17.88 per 100 TN in 1959 (pre-decline) to 39.27 per 100 TN in 1985. This was very different from what Jones and Wilhere (1994) and the present study found during the summers of 1993 and 1994, respectively. The combined trap rates of red-backed voles and deer mice in 1993 and 1994 were only 4.41 and 10.74 per 100 TN, dramatically lower than the values reported by Adams and Hammond (1991). Why the large discrepancies between

1959/85 and 1993/94? Time of year has a large effect on capture rates and species composition. In addition to trapping in the spring and summer, Jones and Wilhere (1994) also trapped small mammals in the fall of 1993. In October 1993, capture rates of red-backed voles and deer mice were 41.81 per 100 TN, which compares favorably with Adams and Hammond (1991) data from August, 1985. Unfortunately, neither study used pitfalls to capture shrews, so discussion is limited to mice only. Autumn numbers of red-backed voles and deer mice in 1985 (39.27 per 100 TN) and 1993 (41.81 per 100 TN), were much higher than autumn numbers in 1959 (17.88 per 100 TN). This suggests that small mammal populations are higher now than before fir decline.

If one can assume from the previous data that small mammal numbers may have increased as a result of fir decline, have the numbers of saw-whet owls increased as well? Simpson (1972) censused portions of the southern Great Balsam Mountains in North Carolina before the fir die-off began in the late 1970's (Dull et al. 1988). More recently, Milling et al. (in press) performed a similar study in the same area, after most of the fir had died. Simpson (1972) reported that nine territories were found during both of his study years of 1968 and 1969. Milling et al. (in press) found ten and eight territories in 1993 and 1994, respectively. Based on these data, it appears that the fir die-off has had minimal effects on numbers of saw-whet owl territories in the Balsam Mountains. However, it is not known whether the fir decline has affected the saw-whet owls survivability, recruitment, or reproduction.

Saw-whet Owl Breeding Densities and Small Mammal Abundance

Milling et al. (in press) also mapped territories in 1993 and 1994 for the MMA based on vocal responses of male owls. The number of territories declined slightly from seven in 1993 to five in 1994. Assuming these singing males eventually bred, it is interesting that the number of territories was higher in 1993 when summer prey populations were reduced (relative to 1994). This may reflect that 1992 was a good mouse year and the owls were responding to that; i.e., a time-lag numerical response (unfortunately, no data exist on prey or owl numbers in 1992). However, mice were not abundant in 1993 and the number of territories declined to five in 1994. Therefore, it may be the previous year's prey base that determines initial saw-whet owl abundance the following year. However, saw-whet owls (Palmer 1987; Swengel and Swengel 1995) and boreal owls (Korpimäki 1985, 1994) have been shown to rapidly track changes in prey abundance. These studies suggest that saw-whet owls and boreal owls do not exhibit time-lagged responses, perhaps because in other places they are mice and vole specialists. However, southern Appalachian saw-whet owls may have to assess the entire prey base, which would take longer than determining the abundance of only one or two species.

Alternatively, the decrease in observed territories in 1994 may have been because of the observed increase in mice. The mice increase might have allowed earlier pairing of owls. Since saw-whet owls are most vocal during courtship and in the early breeding season (Swengel and Swengel 1995) early pairing could have resulted in fewer male owls heard during 1994, hence fewer "observed" territories.

Auditory censuses may indeed be more effective at sampling bachelor male owls than paired ones. Korpimäki (1986) states that monitoring boreal owl density using singing male owls is unreliable, because most singing males are unpaired 'floaters'. Therefore, greater numbers of singing males might actually reflect fewer territories. Also, saw-whet owls are more vocal in good prey years than in poor prey years (Palmer 1987; Swengel and Swengel 1995). Due to these phenomena, it is difficult to determine the population status of saw-whet owls solely on auditory census data. Therefore, it remains unclear what effect differences in prey abundances may have on saw-whet owl breeding density across years in the southern Appalachian Mountains. More research on this topic is needed to elucidate the connections between numbers of territories and small mammal abundances.

Uniqueness of Southern Appalachian Saw-whet Owl Diets

Most studies to date have found *Peromyscus* spp. to be the most common prey of saw-whet owls (Table 20). Indeed, *Peromyscus* was the dominant prey in nine of the 14 studies listed. In contrast, the present study found a preponderance of shrews in the diet of saw-whet owls (56% by frequency). Shrews were not so important in the diet of saw-whet owls from other areas, with values ranging from 0 to only 9%.

The dietary differences of saw-whet owls from the southern Appalachian Mountains and from other areas may suggest a limited prey base in the southern Appalachian Mountains. Only 500 pair of saw-whet owls are estimated to live in the southern Appalachian Mountains (Milling et al.

in press). The fact that such a small population may be food-limited is distressing. What can be done to increase prey numbers? Milling (in prep.) found that southern Appalachian saw-whet owls avoid degraded stands of fir. Although degraded fir stands may be used extensively by small mammals (Kirkland 1977; 1990) these stands may be impenetrable to foraging owls due to the dense regrowth in these degraded stands, composed primarily of thickets of fir saplings (Witter and Ragenovich 1986). A similar scenario has been suggested for dusky-footed woodrats (*Neotoma fuscipes*) and vulnerability to predation by northern spotted owls (Sakai and Noon 1997). This study found that woodrats residing in the dense second growth were only preyed upon during movements to adjacent older growth forest. For saw-whet owls, swaths cut in the dense stands of fir saplings may allow access to the prey in these patches. One way to test the efficacy of this idea would be to cut two small (4 - 9 meters) corridors through the fir saplings at each of two sites. Radio-tagged saw-whet owls could then be monitored at both sites to determine if foraging owls use these openings. The gaps should be made fairly close to the ecotone with older growth forest because openings created in the middle of a large degraded fir stand may never be utilized by the owls.

In conclusion, the abundance and diversity of small mammals may be critical to the conservation of saw-whet owls in the southern Appalachian Mountains. Thus, land-use practices that alter the abundance, or even species composition, of these small mammals could threaten the existence of saw-whet owls in the region. Management strategies must, therefore, be carefully researched prior to implementation so that consequences of such practices do not further endanger the owl, other inhabitants of the spruce-fir forest, or the spruce-fir forest itself.

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APPENDIX A.

Equations

APPENDIX A. Equations used for prey preference analyses, calculations of food niche breadth, and evenness indices. Descriptions are adapted from original author(s).

Preference Analyses

Ivlev's (1961) Electivity Index, E

$E = (r_i - p_i) \div (r_i + p_i)$

where r_i is the percentage of a species in the diet, and p_i is the percentage of the same species found in the environment.

Jacob's (1974) Modification of Ivlev's Electivity Index, D

$D = (r_i - p_i) \div (r_i + p_i - 2r_ip_i)$

where r_i and p_i are the same as above, and $2r_ip_i$ is used to reflect differential mortality rates of each prey species. The value of the statistic D may range from -1 (total lack of use of a species), through 0 (indicates use proportional to availability), to 1 (maximum use of a species).

Johnson's (1980) PREFER test

X_{ij} represents usage of prey species i by individual owl j, and Y_{ij} represents availability of species i to owl j. Let r_{ij} represent the rank of X_{ij} within owl j, and s_{ij} represent the rank of Y_{ij} within j. Taking the difference between r_{ij} and s_{ij} yields t_{ij}, the preference of species i by j. Next, average the t_{ij} across all owls. A ranking of these averages will indicate relative preference among prey species by the entire sample of owls.

The statistics are computed by means of a F test (see Johnson 1980 for specifics). F is distributed with I - 1 and J - I + 1 degrees of freedom. To determine if statistical differences exist among usage of individual prey species, the Bayesian decision procedure of Waller and Duncan (1969) is used. This method calls two means significantly different if the difference exceeds Ws_d, where S_d is the standard error of the difference and W is a function of the number of means, the degrees of freedom, and the F statistic. Chances of type I and II errors are reduced due to the dependence of W on F. When F is small, W must be large to be significant, and if F is large, W will be significant at much smaller values.

Neu et al.(1974) Method

To detect overall differences in prey usage, the χ^2 test of independence is used: $\chi^2 = \Sigma \underline{(o - e)^2}$

e

where o is the observed frequency and e is the expected frequency. To calculate Bonferroni statistics the following formula is used: $z_{(1-\alpha/2k)}$, where α is the level of significance, (0.05 was used in this study), k is the number of simultaneous estimates being made (6 for this study). The resulting confidence intervals are constructed:

$$p_i - z_{(1-\alpha/2k)}\sqrt{p_i(1-p_i)/n} \le p_i \le p_i + z_{(1-\alpha/2k)}\sqrt{p_i(1-p_i)/n}$$

where p_i is the proportion of species i in the sample, and n is the total of all prey species observed in the sample. These intervals are then compared with expected proportions (i.e. availability) from small mammal trapping. If the expected proportion lies within the confidence interval, usage is said to be equivalent to availability. If the expected value is greater than the interval, then usage is less than availability (i.e. avoided), and vice versa for expected values below the confidence interval, which represent preference.

Kendall's Coefficient of Concordance (Siegel 1956), W

This is computed as $W = s/_{1/12}k^{2}(N^{3} - N)$, where

$s = \Sigma(R_j - \Sigma R_j/N)$, and R_j is the sum of ranks,

k = number of sets of ranks e.g. the number of owls,

N = number of entities (prey species) ranked, and

$_{1/12}k^2(N^3 - N)$ = maximum possible sum of squared deviations. The value of W expresses the degree of agreement among the owls in their selection of prey species.

Shannon's Diversity Index, (Ludwig and Reynolds 1988) H'

$H' = \sum_{i=1}^{s} (p_i \ln p_i)$ where

s = number of taxa used,

P_i = proportion of the i^{th} taxon in the sample, and

ln = natural logarithm.

In calculating H', I used discrete taxa only, e.g. if *Peromyscus leucopus*, *P. maniculatus* and *Peromyscus* spp. were listed, I did not use *Peromyscus* spp. If however, *Peromyscus* spp. was the only category of *Peromyscus* listed, I did include it in the analysis. H' has two properties which have made it a popular diversity measure. First, H' = 0 if and only if there is but one species represented. Second, H' is maximum only if all species are equally represented (Ludwig and Reynolds 1988).

Modified Hill's Ratio (Alatalo 1981) of Evenness, E5

$E5 = \frac{N2 - 1}{N1 - 1}$ where, $N1 = e^{H'}$ and $N2 = 1/\lambda$.

E5 tends to be robust to the addition of rare species, and thus is relatively independent of sample size. E5 approaches one for even diets and zero for diets dominated by a single species (Ludwig and Reynolds 1988). Only discrete taxa were used in the calculation of E5, see above for example.

Students' *t*-tests (Zar 1974), used to compare FNB values.

$t = H'_1 - H'_2 / S_{H'_1 - H'_2}$ where,

H'_1 is the FNB of the present study (1.73).

H'_2 is the FNB of the other study compared.

$S_{H'_1}$ is the variance of the present study (0.0024).

$S_{H'_2}$ is the variance of the other study compared.

S_H is approximated as: $\dfrac{\sum f_i \log^2 f_i - (\sum f_i \log f_i)^2/n}{n^2}$

where f_i is the frequency of species i in the diet, and n is the sum total of all individual prey items. Base 10 was used for logarithms; calculations of $f_i \log^2 f_i$ and $f_i \log f_i$ were taken from tables in Lloyd et al. (1968).

Sequential Bonferroni tests (Rice 1989), to control type I error rates when comparing several statistical probabilites (used for the t-tests of FNB's).

Let α be the significance level, and *k* the number of of tests (probabilities) to be compared. P_i is the probability of a difference calculated by the individual test. Rank these probabilities from smallest (P_1) to largest, (P_k). If $P_1 \leq \alpha/k$, then P_1 is judged significant at the table-wide significance level, α. If the inequality is not met then declare all probabilities nonsignificant. If significance is achieved, determine if $P_2 \leq \alpha/(k-1)$. If so, continue on until the inequality is no longer satisfied, subtracting one more from *k* with each iteration. When significance is no longer achieved, then that P value and all larger values are declared nonsignificant.

VITA

Bennie L. Cockerel, Jr. was born in Albany, Georgia, on March 14, 1965. As part of a military family, he moved several times, including stays in Guam, Michigan, and Arkansas. Prior to the fifth grade, the family moved to Batesburg, South Carolina. He graduated from Batesburg-Leesville High School in June, 1983. The following September he enrolled in Newberry College, S.C. After one year at Newberry, he enlisted in the U.S. Air Force. After the military, he entered the University of South Carolina at Aiken, S.C. He graduated with a Bachelor of Science degree in Biology in 1991.

In 1992, he accepted a teaching assistantship at Appalachian State University and began graduate work. A Master of Science degree in Biology with a concentration in ecology was awarded in August, 1997. Mr. Cockerel's address is 408 Atomic Road, Jackson, S.C., 29831.