INFLUENCE OF HABITAT STRUCTURE AND PREY ABUNDANCE ON WEASELS IN A FORESTED LANDSCAPE

by

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ABSTRACT

Most studies of weasel habitat selection have been conducted in agricultural regions: therefore, knowledge of weasel habitat requirements in forested landscapes is limited. Weasels are considered specialist predators of small mammals, and it is believed that habitat selection and quality for weasels can be defined by the abundance and distribution of prey. In the Appalachian Highlands of northwestern New Brunswick, a systematic grid was superimposed on two 50 km^2 landscapes, a mixed-forest landscape that had not been disturbed by forest cutting for approximately 40 years (Landscape A), and a landscape which had been disturbed by recent harvesting practices (Landscape B).

In the current literature, few studies have indicated that habitat structure influences weasel distribution. I hypothesized that prey abundance and distribution would be the primary factors affecting weasel distribution with habitat structure as a secondary influence. In winter 1997-1998 on both Landscapes A and B, weasel tracks were recorded on the systematic grids at stations one km apart. Models produced by logistic regression analysis for Landscapes A and B together ($p=0.004$) and Landscapes A ($p=0.013$) and B ($p=0.04$) separately, significantly distinguished between presence or absence of a weasel at a station. Weasel abundance and distribution were influenced by understory stems of sugar maple (*Acer saccharum*) 2-4 m in height ($p=0.08$, $p=0.14$), American beech (*Fagus grandifolia*) 0.5-1 m in height ($p=0.09$), total hardwood understory stems 2-4 m in height ($p=0.07$) and total basal area of all live standing trees ($p=0.03$).

Measurement of habitat use with snow track information is difficult to interpret because different behaviours cannot be readily separated. The track pattern tortuosity can be used to quantify foraging effort of weasels. Tortuosity of weasel track patterns was quantified by calculating the fractal dimension. Multiple regression analysis identified extremely decayed coarse woody debris ($p=0.01$), total hardwood understory stems 1-2 m in height ($p=0.01$), and total white birch (*Betula papyrifera*) basal area ($p=0.08$) as variables influencing weasel movement patterns.

Since no prey abundance variables were selected by either analysis, it is inferred that habitat structure influenced both weasel distribution and the tortuosity of weasel movement patterns. Logistic and multiple regression analyses identified increased weasel activity with sites having high amounts of hardwood understory. Disturbed areas, which are often associated with gaps in the canopy, appear to be important habitat components for weasels in forest-dominated landscapes. These areas are often associated with a regeneration of hardwood understory stems due to selective cutting operations, roads, and windthrow.

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CHAPTER 1

GENERAL INTRODUCTION

Concerns have been raised as to the ecological sustainability of the boreal forest. In answer to these concerns, forestry companies have been changing from traditional forestry operations to a form of ecosystem management (Hannon et al. 1996). The changing perspective of forest management has been to view the forest more holistically with a mandate to maintain biodiversity and ecological processes along with the sustainability of Canada's forest-based economy (Hannon et al. 1996).

To assist in this development, a network of research in sustainable forest management (*Sustainable Forest Management-Network of Centres of Excellence*) (SFM-NCE), comprising various research themes, was established. One, the Landscape and Biodiversity theme, aimed at aiding forestry in determining the range of natural variability which is important in maintaining biodiversity and ecological processes (Hannon et al. 1996). The hope was to study the role of landscape structure, both natural and anthropogenic, on selected ecological processes, and to identify the effects of habitat variables on the distribution and abundance of a select group of animals of varying body sizes. Preliminary work would quantify abundance, distribution, movements, productivity and habitat use of these animals in landscapes of varying structure within a range of previous natural and anthropogenic disturbances. The work was to be conducted in cooperation with the forestry company, Fraser Paper Inc., and the provincial government in the forests of northwestern New Brunswick. Among that select group of animals to be studied were weasels (*Mustela* spp.)

The main objective of this study was to investigate the influence of prey abundance and habitat structure on weasel abundance and distribution. This thesis is presented in journal format with the main objective divided into two sub-objectives corresponding to Chapters 2 and 3. Appendix II presents an analysis of the food habits of weasels from a carcass collection by trappers in the autumn of 1996 in the forested regions of New Brunswick.

Two species of weasels are found in New Brunswick: the short-tailed weasel (*Mustela erminea*), and the long-tailed weasel (*M. frenata*) (Dilworth and Gorham 1984). Short-tailed weasels are more abundant with a distribution across the entire province, while long-tailed weasels occur in lower numbers along New Brunswick's western border with Quebec and Maine (USA) (Banfield 1974, Dilworth and Gorham 1984). The analysis of the carcasses collected from trappers in the autumn of 1996 resulted in a higher number of short-tailed weasels over long-tailed weasels (Appendix II). For the remainder of this thesis, the term "weasels" will relate to short-tailed weasels only.

Although weasels are important economically as a furbearer and are common predators of small mammals and birds, little is known about their ecological role in forested landscapes (Wilson and Carey 1996). Most research on weasels has been conducted in grass-dominated agricultural regions (Erlinge 1974, Simms 1979, King 1990). To maintain biodiversity and ecological processes while continuing to practice sustainable forest management, it is prudent that we learn more about this small predator. Small predators are common in boreal systems and likely consume large numbers of seedeating rodents.

The use of a particular area by an animal is the result of its responses to one or more specific habitat components. In Chapter 2, winter habitat use of weasels is examined to determine what components of a forested landscape are influencing weasel abundance and distribution. Presence or absence of a weasel in a particular area was determined through snow tracking. It is believed that food availability dictates weasel distribution, with very little influence occurring from habitat structure (Simms 1979).

Chapter 3 reports on the potential use of fractal analysis to further define habitat use of weasels by quantifying weasel movement patterns. Measuring habitat use is difficult to interpret because different behaviours are hard to separate. Fractal analysis can be used to calibrate potential relationships between the tortuosity of movement patterns and habitat quality.

Major conclusions and their implications to Forest Management are discussed in Chapter 4, and suggested areas for future research are proposed. Although this work stands alone, the results will be used in the context of other projects within the SFM-NCE to provide a better understanding of ecosystem processes and better maintenance of ecological variability in Canada's forest.

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CHAPTER 2

WINTER HABITAT USE OF SHORT-TAILED WEASELS, *Mustela erminea*, IN A FORESTED LANDSCAPE

ABSTRACT

Weasels (*Mustela* spp.) are resource-limited, r-selected specialist-predators that feed primarily on small rodents and birds. It is believed that food availability dictates weasel distribution. Little evidence exists in current literature to indicate that their distribution is affected by habitat structure. However, most studies have been conducted in highly-disturbed agricultural environments where structure may differ from natural environments. Knowledge of weasel abundance, distribution, and habitat use in forested landscapes is limited. I hypothesized that prey abundance and prey distribution would be the primary factors affecting the distribution of weasels in these landscapes, with habitat structure as a secondary influence as it is in agrosystems.

In the Appalachian Highlands of northwestern New Brunswick, a systematic grid was superimposed on two 50 km^2 landscapes, with one representing a relatively undisturbed forest (Landscape A), and the other, an intensively managed forest (Landscape B). In winter 1997-1998, a snow tracking study was conducted at selected points on both grids to identify short-tailed weasel habitat use. Small mammal information, collected in autumn 1997, identified prey abundances and distributions for the area. However, results indicated that structural habitat components and not relative prey abundance were influencing weasel distribution. Models produced by logistic regression analysis of both Landscapes A and B together (p=0.004) and Landscapes A (p=0.013) and B (p=0.04) separately, significantly differentiated between the presence or absence of a weasel at a station. When Landscapes A and B were analysed together, weasel presence was correlated with sugar maple (*Acer saccharum*) understory stems 2-4 m in height(p=0.08) and total hardwood understory stems 1-2 m in height (p=0.07). When analysed separately weasel activity on Landscape A was correlated with total basal area of all live standing trees (p=0.03), and American beech (*Fagus grandifolia*) understory stems 0.5-1 m in height (p=0.09) and with sugar maple understory stems 2-4 m in height (p=0.14) on Landscape B. Sites with the above characteristics were often associated with gaps in the canopy which can be the result of selective cutting operations, roads, and windthrow.

Key words: weasel, *Mustela* spp., predator-prey dynamics, habitat use, forested landscape

INTRODUCTION

Weasels (*Mustela* spp.) evolved on the alpine grassland of the Pleistocene glacial tundra, an environment where a predator of small mammals would need to be able to forage along runways and tunnels in search of prey (King 1990). Since that time, they have adapted to a wide diversity of habitat types, and their geographical range has increased, with short-tailed weasels (*Mustela erminea*) occupying much of the northern hemisphere including all parts of mainland Canada. In New Brunswick, short-tailed weasels are distributed throughout the province (Banfield 1974, Dilworth and Gorham 1984).

Weasels occupy a variety of habitats from open country tundra and grasslands to wooded environments (Banfield 1974, Dilworth and Gorham 1984). This wide variety in habitat types has resulted in a mosaic of habitat structures, climates, and prey distributions among the many areas where weasels are found and has resulted in the weasel being classified as a habitat generalist (Adler and Wilson 1987). Habitat generalists have the ability to exploit a diverse range of resources and to respond readily to changes in their environment. A wide niche breadth and the capability of attaining high rates of increase with the potential for reaching high densities characterize these organisms as good colonists (Van Horne 1983, Adler and Wilson 1987), and likely explains, in part, the wide geographical distribution of these animals.

Though weasels are known to inhabit a range of habitat types, little is known about weasel population dynamics and habitat use in Nearctic boreal forests. What constitutes habitat requirements for weasels is unclear; and this lack of knowledge is even more pronounced for weasels inhabiting forested landscapes (Simms 1979, Thompson 1988, Thompson et al. 1989). Squires (1968) reported that short-tailed weasels are primarily found in wooded areas characterized as coniferous or mixed forests, but have also been observed in pastures and fence-rows near cultivated fields. Simms (1979) stated that short-tailed weasels chose early successional over late successional areas since these areas had the highest occurrence of voles, the weasel's principal prey. In one of the few forest-habitat selection studies, Thompson et al. (1989) observed no preferences by weasels for different stand age classes in Ontario boreal forest. These studies demonstrate that weasels occupy a variety of different habitats and that habitat structure, when compared to prey abundance, has had a secondary effect on habitat selection (King 1989, Oksanen and Schneider 1995).

Weasel distribution within a forest, or across a landscape, likely is a function of several influences; most notably, the distribution of prey and the ease of accessing prey during periods of snow cover. The effect of snow cover on distribution relates to foraging efficiency in subnivean environments and to size limitations of northern weasel species (Simms 1979, King 1989). Weasels have shorter fur and a greater body surface to volume ratio than other animals similar in size (Brown and Lasiewski 1972). In northern climates, where environmental conditions above the snow are severe, weasels need to minimize exposure to ambient temperatures and their daily energy expenditure. This is accomplished by increasing foraging efficiency and reducing time above the snow (Simms 1979, King 1990). The weasel's slender serpentine body suggests a specialization for feeding on small mammals, and a specialization for predation on voles

(Simms 1979, Hanski and Korpimaki 1995). Although weasels are small enough to access subnivean and subterranean environments, they must also be large enough to overcome prey. The weasel's small body size allows it to exploit these spaces where voles spend most of the winter months (Simms 1979, King 1989).

The physical structure of a forest stand has been shown to influence marten (*Martes americana*), a larger but related mustelid species. Quality marten habitat is associated with mature coniferous forest and/or areas high in coarse woody debris (Koehler and Hornocker 1977, Soutiere 1979, Hargis and McCullough 1984). The amount of coarse woody debris has been related to the potential access to prey living below the snow. Sherburne and Bissonette (1994) suggested that homeothermy, escape from predators, and increased prey availability were reasons for use of subnivean space by marten in Yellowstone National Park, Wyoming. They determined that the use of subnivean access holes was mainly associated with high prey biomass. Since weasels depend on voles as prey, which are active in winter below snow, weasels may also be associated with areas with high abundance of coarse woody debris.

Simms (1979) demonstrated that prey availability was not the only determining factor because in some areas where deer mice (*Peromyscus maniculatus*) were in high concentrations, weasels preyed mainly on voles (*Microtus pennsylvanicus* and *Clethrionomys gapperi*). Weasels will concentrate their activities in areas where these preferred prey species are at highest densities (Erlinge 1974, 1975, Henttonen 1987, Hanski and Henttonen 1996). It is believed that specialist predators should evolve to hunt in the optimal habitat of their selected prey and, as a result, distribution should correlate with such areas (Hansson 1989). Erlinge (1974) found that for weasels in grass-dominated habitats, food was the main determinant of habitat selection. Abundance and density of prey were related to distribution and territorial boundaries of weasels.

OBJECTIVES, HYPOTHESES AND PREDICTIONS

The objective of this research was to determine what components of a forest-dominated landscape influence weasel abundance and distribution. If weasels in a forest habitat are resource-limited and prey determines habitat use, (as demonstrated in agricultural areas) then weasel distribution should correlate with prey abundance. I propose the following hypothesis:

H Weasel abundance and distribution in forest-dominated landscapes are determined primarily by prey abundance and secondarily by habitat structure.

P_1 Weasel abundance will be related to prey abundance and habitat structure.

P_2 Prey abundance will explain more variance in weasel abundance than does habitat structure.

METHODS

Study Area

The study was conducted in the Appalachian Highlands of northwestern New Brunswick (47°22'N, 67°25'W), on private land owned by Fraser Papers Inc.. The region is characterized by mixed hardwood highlands and mixed softwood lowlands and categorized as Acadian forest (Rowe 1972), and more recently, Laurentian mixed forest (Bailey 1995). Two 50-km^2 systematic grid systems were superimposed on areas representative of the greater landscape, which allowed for a species-defined approach to studying habitat use. Track and trap stations were located one km apart. Home ranges of weasels typically are within a one km^2 area (King 1990), and I am confident that stations generally were occupied by different individual weasels. The grid design follows a parallel study in Alberta for the Landscape and Biodiversity Project of the Sustainable Forest Management- Network of Centres of Excellence (SFM-NCE) (Hannon et al. 1996). Within the two 50-km^2 grids, 65 out of 128 stations were surveyed. Stations were selected using a systematic-cluster design suggested by Fortin et al. (1989). This subsampling design is useful for studying biological populations within a large area because more stations may be sampled numerous times while still sampling a large area. The cluster pattern of this design also allows for the detection of ecological processes at varying scales (Fortin et al. 1989). Of the 65 stations sampled, 32 were on a relatively unmanaged landscape (Landscape A), and 33 were on a heavily-managed landscape with continued harvesting practices (Landscape B).

Snow tracking

Snow tracking has been used widely to determine relative distributions of weasels, generally because habitat-limiting factors are best expressed in winter (Erlinge 1977, Bull et al. 1992, King 1990, Raphael 1994, Zielinski and Kucera 1995), and (1) there is no bias associated with bait attraction; (2) replication is possible for estimating variance; (3) it provides both scale and scale-free measures of habitat use; and (4) it is cost-effective. A potential drawback of snow tracking is that unsuitable snow conditions may limit replication of the surveys. Analysis is based on presence or absence because individuals cannot be identified using snowtracks.

Weasel presence was recorded during the snow cover months of December 1997 to the end of February 1998. Following this date, snow conditions were not suitable for identifying weasel tracks as the snow crusted over at night. Each station was surveyed for weasel activity along four 100-m transects originating at a center point, forming a cross, and corresponding to the four cardinal directions. Stations were surveyed twice during the snow-tracking season to increase the probability of detecting a weasel in the local area and to account for some temporal changes (Zielinski and Kucera 1995). Environmental measurements such as temperature and snow conditions (snow depth, distance to crust, and crust thickness) were recorded for each station by averaging three measurements taken randomly within a 5-m radius of each station.

Prey sampling

Small mammals were trapped during the snow-free months of early fall 1997 using Victor multiple-capture live traps (*Woodstream*, Lititz, PA, 17543 U.S.A.). Five traps were placed at each station with one trap at the origin and the remaining four traps, at 35 meters in the four cardinal directions similar to the snow-tracking design. Relative abundance of different species were estimated through a mark-recapture session (Lancia et al. 1994) of three pre-bait 24-hour periods followed by four 24-hour rounds of trapping using picric acid as the marking agent. The marking procedure was in accordance with the technique described in Nietfeld et al. (1994).

Habitat Sampling

During June-August, vegetation was sampled within a 100-m radius of each station. A plot, measuring 10 by 20 m, was positioned within 50 m of the station, and two plots of the same size were positioned between 50 and 100 m. If the plot position was unsatisfactory because of a topological feature (i.e., road or body of water), then the plot was moved to avoid the feature while maintaining the integrity of the design. Aspect and slope as well as the overall community composition were recorded for each plot.

Canopy cover was recorded using an ocular tube. The relative occurrence of each species of tree, shrub, dead hardwood and dead softwood or snag within the designated strata was recorded. A shrub was defined as any woody species, including tree species, less than 2 m in height. Stratum designations were as follows: (1) 0.5 to 1 m; (2) 1 to 2 m; (3) 2 to 4 m; (4) 4 to 6 m (5); and trees > 6 m (Hagan et al. 1996). The Relevé technique was used to classify and categorize by abundance and percentage cover, each shrub and type of ground cover including: lichens, herbs, graminoid, bryophytes, leaf litter, bare ground, and standing water for each plot (Appendix I). This technique involves classifying each shrub species and type of ground cover within each plot according to the following scheme: 1 = rare in plot; < 1% cover, 2 = few occurrences in plot; 1-10% cover, 3 = several occurrences; 10-20% cover, 4 = frequent throughout plot; 20-50% cover, and 5 = very common throughout plot; > 50% cover (Mueller-Dombois and Ellenburg 1974). The mean height and percent cover for ground cover, shrubs, subcanopy and canopy were measured. Measurements of coarse woody debris included species type, maximum diameter and decay class (Maser et al. 1979). Coarse woody debris was defined as dead downed material > 8 cm in diameter at the widest point and ≥ 50 cm in length. The number of recent and old stumps was also recorded.

Statistical Analysis

A two-sample t-test was used to determine if environmental conditions were significantly different between the first and second surveys on both Landscape A and Landscape B. The relationship of structural habitat and prey abundance variables and weasel presence or absence was assessed using stepwise logistic regression analysis ($\alpha = 0.05$) (Wright 1994). Independent variables were tested against the dependent variable, which was the presence or absence of a weasel at a sampling station. Analysis was performed using SYSTAT LOGIT. Variance was expressed as McFadden's rho, where the smaller values between 0.2 and 0.4 are considered satisfactory, which is a measure of strength of association and corresponds to r^2 for multiple regression (Tabachnick and Fidell 1996). Preliminary analysis included both Landscapes A and B combined, which were later separated to determine if the predictors of weasel presence or absence would differ depending on whether the forest was managed or unmanaged.

A Pearson correlation matrix was used to identify and eliminate correlated variables ($r \geq 0.6$). Logistic regression analysis of paired variables and weasel presence or absence was used to identify which of the correlated paired variables were significant. Eighteen independent variables (Table 2.1) out of 110 structural habitat variables (Appendix I) and six relative prey abundance variables (Table 2.2) were identified for inclusion in the analysis.

RESULTS

The first round of tracking was conducted between 10 December 1997 and 29 January 1998; environmental measurements were as follows: temperature (-12.7 °C), mean snow depth (70.9 cm), mean distance to snow crust (9.1 cm) and mean snow crust thickness (0.63 cm). The second round of tracking was conducted between 2 February and 24 February 1998 and environmental measurements were as follows: temperature (-9.9 °C), mean snow depth (85.1 cm), mean distance to snow crust (10.1 cm) and mean snow crust thickness (1.5 cm). Results indicated that the environmental conditions for each round were significantly different with the exception of distance to snow crust ($p=0.37$).

Table 2.3 identifies relative proportions of prey species using the mark-recapture method for selected points on Landscapes A and B (1300 trap nights) together and Landscape A (640 trap nights) and Landscape B (660 trap nights) separately (Table 2.3). Trends in consumption of prey species are discussed in Appendix II and indicate mice and voles comprise a large proportion of weasels' diet.

Evidence of weasel activity was observed at 14 of 32 stations (43.8%) on landscape A and 16 of 33 stations (48.5%) on landscape B. The use of logistic regression requires a set of conditions to exist before valid conclusions can be made. An analysis of both Landscapes A and B together and separate using a significance for inclusion of $p=0.15$ and a significance for omittance of $p=0.25$, none of the prey abundance variables measured were found to significantly predict the presence of weasels. However, structural habitat variables were found to be significant.

Preliminary tests using stepwise logistic regression analysis were conducted on both landscapes as a whole and (following deletion of three cases with missing values) data from 62 stations were available for analysis. The final model included two predictors to define the influence of habitat and/or prey on the presence or absence of a weasel at a station.

The set of predictors produced by the regression were adequate to influence weasel use of each station. The regression identified sugar maple (*Acer saccharum*) with understory stems 2 to 4 m in height (ACSA24, $p=0.08$) and hardwood with understory stems 1 to 2 m in height (HW12, $p=0.07$) as predictors of weasel presence (Table 2.3). A test of the full model for both landscapes together with the remaining two predictors against the constant-only model was statistically significant ($X^2 = 11.0$, $df = 2$, $p=0.004$) indicating that the predictors, as a set, influence presence or absence of a weasel at a station. The odds ratio of 1.4 for ACSA24 and 1.0 for HW12 showed the likelihood of a weasel being present on the basis of one unit change of the predictor variables. The variance in weasel presence or absence provided a McFadden's rho = 0.13. The prediction success of the model resulted in 54% of weasel presence and 62% of the weasel absence being correctly predicted, with an overall prediction success rate of 58%.

Following analysis of presence of weasels on both landscapes as a whole, a stepwise logistic regression was further performed on each landscape separately. On Landscape A, after deletion of one case with missing values, data from 31 stations were available for analysis. The final model included two predictors to define the influence of habitat and/or prey on the presence of a weasel at a station in the relatively unmanaged landscape.

The two predictors defined by the regression, total basal area of all live standing trees (TOTLIVEBA, p=0.03) and American beech (*Fagus grandifolia*) with understory stems 0.5 to 1 m in height (FAGR51, p=0.09), influenced weasel use at each station (Table 2.4). A test of the full model for Landscape A together with the remaining two predictors against the constant-only model was statistically significant ($X^2 = 8.7$, df = 2, p=0.013), indicating that the predictors, as a set, influenced presence or absence of a weasel at a station. The odds ratio of 1.0 for TOTLIVEBA and 1.3 for FAGR51 shows the likelihood of a weasel being present on the basis of one unit change of the predictor variables. The variance in weasel presence or absence provided a Mcfadden's rho = 0.21. Prediction success resulted in 56% of weasel presence and 68% of the weasel absence being correctly predicted, for an overall success rate of 63%.

When Landscape B, the intensively managed forest, was tested, two cases with missing values were deleted and data from 31 cases was available for analysis of weasel presence or absence. The final model included one predictor; sugar maple with understory stems 2 to 4 m in height (p=0.14), to define the influence of habitat on the presence of a weasel (Table 2.6). A test of the full model for Landscape B together with the predictor (ACSA24) against the constant-only model was statistically significant ($X^2 = 4.1$, df = 1, p=0.04), indicating that the predictor influenced presence or absence of a weasel at a station. The odds ratio of 1.9 indicated the likelihood of a weasel being at a station on the basis of one unit change of the predictor. The variance in weasel presence or absence provided a McFadden's rho = 0.10. The prediction success of the model resulted in 54% of weasel presence and 57% of the weasel absence being correctly predicted, for an overall prediction success rate of 56%.

DISCUSSION

Contrary to predictions, the results indicated that structural habitat components and not prey abundance significantly influenced weasel abundance and distribution. No relationship was observed between weasel presence or absence and relative prey abundance variables, grouped or separate. Weasel activity was predominantly identified with sites having a high abundance of hardwood understory. These results agree with Wilson and Carey (1996) whose capture rates were higher in thinned forests and suggested that in forests managed for wood products, management history may be more important than seral stages in determining weasel abundance. They attributed this to increased understory development as a result of artificial disturbance. These conditions are similar to industrial forestry practices within our intensively managed landscape where selective cutting is the standard harvesting practice for hardwood-dominated stands. However, natural disturbance such as windthrow and the creation of gaps in the canopy can produce similar results (Gray and Spies 1996). The process of creating gaps in the canopy and reducing overstory allows for high regeneration of hardwood and the maturation of seedlings (Runkle and Yetter 1987, Gray and Spies 1996).

Gaps are created by the death of one or more trees or by the breaking of overstory branches and are critical in the community dynamics of various forest types (Runkle 1990, Gray and Spies 1996). Similar to this study, Grey and Spies (1996) observed increasing amounts of shade-tolerant species like sugar maple in young or single-layer forests as compared to old-growth or multi-layer forests. A comparison between the gap and the surrounding forest community has shown that the patches differ in small mammal and bird diversity (Forman 1995).

Inherent in the creation of a gap in a contiguous forest landscape by an anthropogenic or natural disturbance is the creation of edges. Weasels approaching an edge from the forest interior will concentrate activity within the created ecotone (Bider 1968, Marini et al. 1995). In one small mammal-edge study, Sekgororoane and Dilworth (1995) found that the relative abundance of small mammals was greater in recent rather than older harvest cuts. In this study, no direct relation to edge was observed for deer mice and red-backed voles, but relative abundance was higher within the ecotone created by the harvest cut, particularly on the forest side. Within the context of my study, weasel distribution was correlated to sites classified as tolerant hardwood which had been selectively harvested. Wilson and Carrey (1996) reported that prey abundance and increased understory development in thinned forests were the main components of habitat use by short-tailed weasels in an intensively managed forest. Although the design of this study did not account for edge-related prey abundance, none of the prey abundance variables included in our analysis were selected as predictors of weasel presence. This suggests that some variable other than foraging efficiency was influencing habitat selection.

Interference interactions with marten, a larger mustelid that preys on small- and medium-sized mammals and birds, may be causing weasels to use sub-optimal habitat. Interference interactions between sympatric mustelid species have not been thoroughly investigated (Simms 1979). Polderboer et al. (1941) and Rosenweig (1966) suggested that predation or competitive exclusion through interference by larger weasels on smaller weasels resulted in the absence of smaller weasels from an area. Simms (1979) reported that two resident female short-tailed weasels disappeared when a female long-tailed weasel (*M. frenata*) arrived in the area. Oksanen and Schnieder (1995) stated that least weasels (*M. nivalis*) were forced to forage in less productive habitats by the socially dominant short-tailed weasel. Marten use of the forest interior may have resulted in weasels moving to sites of recently disturbed forests with increased amounts of edge and increasing amounts of hardwood understory. This type of structural habitat component present within the forest ecotone may provide increased cover from avian predators while foraging (Chasko and Gates 1982, Fenske-Crawford and Nieni 1997). However, only 13% of the variance was explained by the model for both the relatively unmanaged and managed landscapes together. The inability of the model to fully explain weasel distribution based on the available information further demonstrates the classification of the weasel as a habitat generalist. The importance of habitat structure compared to prey however, suggest also that some specific components of habitat influence weasel distribution.

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Table 2.1. List of structural habitat variables used in the analysis of predictors of presence of weasels in forests of northwestern New Brunswick, 1996-1997.

Variable
Tree and shrub species abundance (no. of stems for 3 plots/ point)
Sugar maple (*Acer saccharum*) understory stems 2-4 m
American beech (*Fagus grandifolia*) understory stems .5-1 m
Hobblebush (*Viburnum alnifolium*) understory stems 1-2 m
Raspberry (*Rubus* sp.) understory stems 2-4 m
Softwood understory stems 1-2 m
Hardwood understory stem 1-2 m
Hardwood understory stem 4-6 m
Relevé: classification of abundance for shrubs (< 2 m in height) and ground cover by % occurrence for 3 plots/ point.
American beech (*Fagus grandifolia*) relevé
Yellow birch (*Betula alleghaniensis*) relevé
Herbaceous relevé
Lichen relevé
Leaf litter relevé
Total basal area of all live standing trees
Total trembling aspen (*Populus tremuloides*) basal area
Total white birch (*Betula papyrifera*) basal area
Total number of live balsam fir (*Abies balsamia*) stems for 3 plots/ point
Total number of spruce sp. (*Picea* sp.), *P. glauca*, *P. mariana* stems for 3 plots/ point
Total coarse woody debris (logs and tree tops) for 3 plots/ point

Table 2.2. List of prey abundance variables used in the analysis of predictors of presence of weasels in forests of northwestern New Brunswick, autumn 1997.

Variable
Total number of deer mice (*Peromyscus maniculatus*)
Total number of red-backed voles (*Clethrionomys gapperi*)
Total number of woodland jumping mice (*Napaeozapus insignis*)
Total number of short-tailed shrews (*Blarina brevicauda*)
Total number of all species at a sampling point
Total prey biomass

Table 2.3 **Relative prey proportions from mark-recapture sampling for both relatively unmanaged (Landscape A) and intensively managed (Landscape B) combined and separate in northwestern New Brunswick, autumn 1997.**

Prey Species	Landscape A and B (%)	Landscape A (%)	Landscape B (%)
Deer mouse (*Peromyscus maniculatus*)	44.5	47.9	40.3
Red-backed vole (*Clethrionomys gapperi*)	25.9	22.3	30.3
Woodland jumping-mouse (*Napaeozapus insignis*)	28.8	28.7	29.0
Short-tailed shrew (*Blarina brevicauda*)	0.8	1.1	0.4

Table 2.4. Results of logistic regression analysis for presence or absence of weasels as a function of structural habitat and prey abundance variables for both relatively unmanaged and intensively managed landscapes combined.

Variables	b	S.E.	Wald test (z-test)	p	Odds Ratio	95% Confidence Interval for Odds Ratio	
						Upper	Lower
Sugar maple understory stems 2-4 m	0.31	0.18	1.73	0.084	1.36	1.93	0.96
Hardwood understory stems 1-2 m	0.01	0.01	1.85	0.065	1.01	1.03	1.00
(Constant)	-1.04	0.41	-2.57	0.01			

Table 2.5. Results of logistic regression analysis for presence or absence of weasels as a function of structural habitat and prey abundance variables for the relatively unmanaged landscape.

Variables	b	S.E.	Wald test (z-test)	p	Odds Ratio	95% Confidence Interval for Odds Ratio	
						Upper	Lower
Total basal area of all live standing trees	-0.02^{-2}	0.01^{-2}	-2.22	0.03	1.00	1.00	1.00
American beech understory stems 0.5-1 m	0.25	0.15	1.68	0.09	1.28	1.71	0.96
(Constant)	0.85	0.75	1.13	0.26			

Table 2.6. Results of logistic regression analysis for presence or absence of weasels as a function of structural habitat and prey abundance variables for the intensively managed landscape.

Variables	b	S.E.	Wald test (z-test)	p	Odds Ratio	95% Confidence Interval for Odds Ratio	
						Upper	Lower
Sugar maple understory stems 2-4 m	0.61	0.42	1.48	0.14	1.85	4.18	0.82
(Constant)	-0.44	0.42	-1.05	0.30			

CHAPTER 3

TRAIL TORTUOSITY AS AN INDICATOR OF RESOURCE USE BY SHORT-TAILED WEASELS, *Mustela erminea*

ABSTRACT

Measurement of habitat use by animal movement patterns is difficult to interpret because different behaviours cannot be readily separated. The track pattern (tortuosity) can be used to quantify habitat use; however, high tortuosity could be the result of either high or low habitat quality. An independent measure of habitat quality can calibrate potential relationships between tortuosity and habitat quality. A snow tracking study was conducted to investigate short-tailed weasel behaviour and habitat use in the Appalachian Highlands of northwestern New Brunswick. In winter of 1997-1998, 73 separate weasel tracks were followed for a minimum distance of 30 m each. Tortuosity of the track patterns was quantified by calculating the fractal dimension. Results indicated that structural habitat components, and not relative prey abundance was influencing weasel track tortuosity. A multiple regression model (r^2=0.56) identified coarse woody debris with a decay class of five (p=0.01) and 1 to 2 m high hobblebush understory stems (p=0.01) as variables which influenced movement patterns. Since no prey abundance variables were selected by the analysis, it is inferred that the complexity of the habitat and not food availability affected the tortuosity of weasel movement patterns.

Key words: short-tailed weasel, *Mustela erminea*, tortuosity, fractals, habitat quality, New Brunswick, habitat use

INTRODUCTION

Animal movement patterns have the potential to provide a means of better understanding the mechanistic link between the ecological process being investigated and the structure of the environment (Kareiva and Shigesada 1983, Johnson et al. 1992, Lorimer et al. 1994, With 1994 a, b; Bascompte and Vila 1997). Because animal movement patterns are indicative of interactions between habitat structure and food, security, and resources (e.g. nest sites), all of which occur at different spatial scales, analysis of these patterns require a scale-independent measure (Dicke and Burrough 1988, Loehle 1990, With 1994 a, b; Milne 1997). Animal distribution is dependent on the size of the animal and on the texture of the substrate suggesting that animal home ranges have fractal dimensions (Loehle 1990). At smaller scales, complex and hierarchical predator behaviour also may have characteristics that could be defined with fractal dimensions (With 1994 a).

The use of fractals in ecological research is being investigated in a variety of areas (Sugihara and May 1990, Lorimer et al. 1994), including: 1) measuring habitat space in relation to leaf shape, tree branching, and crown closure (Vlcek and Cheung 1986, Crawford and Young 1990, Zeide 1990); 2) allometry of organisms related to their habitat (Wiens and Milne 1989); 3) species diversity in relation to community ecology, geographical distribution and resource partitioning (Williamson and Lawton 1991); and 4) animal movement patterns and habitat use (Loehle 1990). The fractal dimension (fractal D) of an animal's movement path may vary at different scales and, through the recognition of changes in the pattern's level of complexity, structural hierarchies may be detected (Sugihara and May 1990). These variations in the fractal D are believed to provide evidence of distinct scale-dependent processes and a comparison of an animal's path tortuosities in different habitats with varying characteristics may serve as a predictor of habitat use (Bascompte and Vila 1997, Sugihara and May 1990, With 1994 a, b).

The short-tailed weasel (*Mustela erminea*) is a specialist predator that inhabits a wide variety of habitat types (Simms 1979, Erlinge 1983, Erlinge et al. 1984, King 1990, Hanski et al 1991). Erlinge (1974) reported that the abundance of small rodents was the most important quality in the selection of habitats. Within the weasel's home range, there will exist a certain area which is used more than the rest (Erlinge 1974, Loehle 1990, King 1990). Although weasel home range size may vary among populations, this specialist predator concentrates its foraging to these areas with high prey abundance (Norrdahl and Korpimaki 1995, Erlinge 1974). Prey abundance and high energy expenditure limits the weasel's foraging range. Therefore, weasel home range size is believed to be related to the abundance of small rodents, and foraging will be limited to areas with the highest prey availability (Erlinge 1974, Simms 1979, King 1975, King 1990). Prey availability is a crucial component of quality habitat for weasels and is a function of both prey abundance and the predator's ability to capture prey. In colder winter months, this strategy is even more crucial because of the weasel's high metabolic rate (Brown and Lasiewski 1972, Erlinge 1974). Energy conservation and efficient foraging means less time exposed to harsh inclement weather and more time spent in the den which in turn increases the weasel's chances of survival (King 1990). It is for these reasons that the weasel's foraging behavior should be more complex in areas of high prey availability and movement between these patches will be less complex and more linear.

When a predator encounters prey, broad searching behaviour is replaced by localized hunting behaviour and straight linear movement is replaced by stochastic tortuous movement. These variations in movement patterns reflect encounters with structural components of habitat or, are in response to correlates of patch structure, such as habitat quality (Kareiva and Shigesada 1983, With 1994 a, b). A straight path suggests that the animal is crossing an area, but not choosing it for purposes other than traveling; however, a tortuous path indicates an area of increased use (With 1994 a, b; Bascompte and Vila 1997). The degree of tortuosity could be a good measure of the quality of a habitat in relation to weasel foraging behaviour. Therefore, a higher tortuosity of weasel movement patterns should reflect higher habitat quality.

OBJECTIVE AND HYPOTHESIS

The objective of this research was to investigate whether the variability of weasel movement patterns was the result of encounters with habitat structure and/or with areas of high prey abundance, and whether fractal analysis of the tortuosity of animal movement patterns is a reliable technique in defining habitat quality. I propose the following hypothesis:

H Weasel trail complexity is determined more by prey abundance than habitat structure.

P_1 Prey abundance will explain more variance in weasel trail complexity than does habitat structure.

METHODS

Study Area

The study was conducted in the Appalachian Highlands of northwestern New Brunswick (47°22'N, 67°25'W), on private land owned by Fraser Papers Inc.. The region is characterized by mixed hardwood highlands and mixed softwood lowlands and categorized as Acadian forest (Rowe 1972), and more recently, Laurentian mixed forest (Bailey 1995). Two 50-km^2 systematic grid systems were superimposed on areas representative of the greater landscape, which allowed for a species-defined approach to studying habitat use. Track and trap stations were located one km apart. Home ranges of weasels typically are within a one km^2 area (King 1990), and I am confident that stations generally were occupied by different individual weasels. The grid design follows a parallel study in Alberta for the Landscape and Biodiversity Project of the Sustainable Forest Management- Network of Centres of Excellence (SFM-NCE) (Hannon et al. 1996). Within the two 50-km^2 grids, 65 out of 128 stations were surveyed. Stations were selected using a systematic-cluster design suggested by Fortin et al. (1989). This subsampling design is useful for studying biological populations within a large area because more stations may be sampled numerous times while still sampling a large area. The cluster pattern of this design also allows for the detection of ecological processes at varying scales (Fortin et al. 1989). Of the 65 stations sampled, 32 were on a relatively unmanaged landscape (Landscape A), and 33 were on a heavily-managed landscape with continued harvesting practices (Landscape B).

Snow tracking

Characteristics of weasel movement patterns were recorded during the snow-cover months beginning in December 1997 to the end of February 1998. Snow conditions in March were not suitable for identifying weasel tracks as the snow typically crusted over at night. Evidence of weasel activity was surveyed at each station along four, 100-m transects originating at a center point, forming a cross, corresponding to the four cardinal directions. When weasel tracks intercepted the transect line, the trail was followed in the direction of travel. Tracking continued until a subnivean access hole was identified, or to a distance no greater than 30 meters. Bourgeois (1997) determined that a 30-m minimum trail pattern length for marten (*Martes americana*) in New Brunswick, a slightly larger mustelid of the northern forest, was necessary to calculate fractal D for this species. To calculate fractal D, the track is measured by dividing it into segments called "dividers". A minimum of 3 dividers are necessary to obtain an estimated length and produce a fractal D. Weasels are smaller in size and have a shorter average gait than marten (Banfield 1974) and therefore, 30 m was considered long enough to get accurate measures of tortuosity. When tracks went below snow, tracking would continue where the weasel came back to the surface. The nature of the subnivean access hole was identified and recorded, and attempts were made to find the exit point, at which point tracking resumed. Changes in the weasel's direction of travel and the distance traveled were recorded for each 30-m track length. A new measurement of distance and degree bearing commenced at the first deviation of >10 degree change in direction. This 10 degree limit was determined in a previous study on tortuosity of fisher (*Martes pennanti*) trail patterns where direction changes of < 10 degrees were too subtle to affect tortuosity (O'Blenis 1997).

Fractal Analysis

Weasel track patterns were reconstructed and plotted by using the recorded travel directions and distances traveled between each change of direction. Nams' (1996 b) Fractal 3.0 program was used to calculate the fractal D using the dividers method (Mandelbrot 1967, Dicke and Burrough 1988, Milne 1991, Nams 1996 a). The range of divider sizes used to measure path lengths for the calculation of Fractal D was 0.01 m to 10.0 m. The lower limit was defined by the precision of the recorded data, and the higher limit was based on the length of the longest tracks used in the analysis.

For fractal analysis, the geometric dimension of a line is equal to 1, and that of a surface is equal to 2; the fractal D for a path lies somewhere between 1 and 2. A '1' indicates that the landscape offers relatively little resistance to the animal's travel path and a '2' suggests that movement is so tortuous that it completely covers a plane. Therefore, as the tortuosity of an animal's trail increases, the fractal dimension approaches 2 (Mandelbrot 1983, Crist et al. 1992, With 1994 a, b; Nams 1996 a, b).

Variations in the overall length of a path will occur with changes in the divider length. When a large divider size is used, smaller scale details in the track may be omitted. With a decrease in divider size, more details are recognized in the track, and the measured path length increases. Estimates of path length may vary with different starting positions along the path (Nams 1996 a, b). This variation was reduced by moving the dividers over the paths multiple times, starting at different points each time and calculating the fractal mean. Where more than one weasel path was recorded at each point, the individually calculated fractal mean was then averaged to produce only one fractal value for weasel movement at each point.

Prey sampling

Small mammals were sampled during the snow-free months of early fall 1997 using Victor multiple-capture live traps (*Woodstream*, Lititz, PA, 17543 U.S.A.). Five traps were placed at each station with one trap at the origin and the remaining four traps, at 35 m in the four cardinal directions similar to the snow tracking design. Relative abundance of different species were estimated through a mark-recapture session (Lancia et al. 1994) of three pre-bait, 24-hour periods followed by four 24-hour rounds of trapping, using picric acid as the marking agent. The marking procedure was in accordance with the technique described in Nietfeld et al. (1994).

Habitat Sampling

During June-August, vegetation was sampled within a 100 m radius of each station. A plot measuring 10 by 20 m in size, was positioned within 50 m of the station, and two plots of the same size were positioned between 50 and 100 m. If the plot position was unsatisfactory because of a topological feature (i.e., road or body of water), then the plot was moved to avoid the feature while maintaining the integrity of the design. Aspect and slope as well as the overall community composition were described for each plot.

Canopy cover was recorded using an ocular tube. The relative occurrence of each species of tree, shrub, dead hardwood and dead softwood or snag within the designated strata was recorded. A shrub was defined as any woody species, including tree species, less than 2-m in height. Stratum designations were as follows: (1) 0.5 to 1 m; (2) 1 to 2 m; (3) 2 to 4 m; (4) 4 to 6 m (5); and trees > 6 m (Hagan et al. 1996). The Relevé technique was used to classify and categorize by abundance and percentage cover, each shrub and type of ground cover including: lichens, herbs, graminoid, bryophytes, leaf litter, bare ground, and standing water for each plot (Appendix I). This technique involves classifying each shrub species and type of ground cover within each plot according to the following scheme: 1 = rare in plot; < 1% cover, 2 = few occurrences in plot; 1-10% cover, 3 = several occurrences; 10-20% cover, 4 = frequent throughout plot; 20-50% cover, and 5 = very common throughout plot; > 50% cover (Mueller-Dombois and Ellenburg 1974). The mean height and percent cover for ground cover, shrubs, subcanopy and canopy were measured. Measurements of coarse woody debris included species type, maximum diameter and decay class (Maser et al. 1979). Coarse woody debris was defined as dead downed material > 8 cm in diameter at the widest point and ≥ 50 cm in length. The number of recent and old stumps was also recorded.

Statistical Analysis

The influence of structural habitat and prey abundance variables on the tortuosity of the weasel's movement pattern was assessed using stepwise multiple regression analysis (α=0.05) (Wright 1997). These independent variables were tested against the dependent variable, which was the calculated fractal mean for weasel movement patterns at a sampling station. Mean fractal dimensions from weasel movement patterns on both the relatively unmanaged and the intensively managed forests were combined because of the small sample size.

A Pearson correlation matrix was used to identify which variables were correlated with each other ($r \geq 0.6$), and eliminated variables that were not correlated. A linear regression analysis of paired variables and the fractal mean identified which of the correlated paired variables was more significant. Thirty-four (Table 3.1) out of 110 structural habitat variables (Appendix I) and six relative prey abundance variables (Table 3.2) resulted from the linear regression analysis.

RESULTS

Sixty-two weasel movement patterns from 27 sampling stations were used in fractal analysis. Fractal scores from each point were averaged to comply with structural and prey sampling protocols resulting in 27 separate fractal mean scores. The total length of these movement paths was 1,920 m.

Prey sampling for over 540 trap nights at selected points identified the following prey species and their relative proportions present among the selected sampling stations: 48.1% deer mouse (*Peromyscus maniculatus*); 20.3% red-backed vole (*Clethrionomys gapperi*); and 37.6% short-tailed shrew (*Blarina brevicauda*). It should be noted that one prey species, woodland jumping-mouse (*Napaeozapus insignis*), hibernates in the winter, and therefore, was not used in the regression analysis. Trends in consumption of prey species are discussed in Appendix II and indicate mice and voles comprise a large proportion of weasel diet.

None of the prey abundance variables measured were found to significantly influence track tortuosity. This was contrary to the hypothesis that weasel trail complexity would be positively related to prey abundance and not other habitat variables. The multiple regression model ($r^2=0.56$) identified the abundance of coarse woody debris with a decay class of five ($p=0.01$), 1 to 2 m high hobblebush (*Viburnum alnifolium*) understory stems ($p=0.01$), and to a lesser degree total basal area of white birch (*Betula papyrifera*) ($p=0.08$) as structural habitat factors that significantly influenced track tortuosity (Table 3.3). Track tortuosity decreased with the amount of coarse woody debris with a decay class of five (Fig. 3.1) and increased with the amount of hobblebush stems between 1 and 2 m in height (Fig. 3.2). Coarse woody debris with a decay class of five referred to the most advanced stage of decay (Maser et al. 1979).

Weasel tracks encountered obstacles in 37% of track patterns. These obstacles included: tree bases (N = 10; 6 of which were coniferous); coarse woody debris (N = 11); and a snag (N = 1) (Table 3.4). In one instance, the weasel's track went through the snow surface with no apparent associated structural component.

DISCUSSION

Contrary to predictions, the results indicated that the structural components of habitat and not relative prey abundance significantly influenced the tortuosity of weasel movement patterns. No relationship was observed between the tortuosity of weasel movement patterns and the six prey abundance variables measured, grouped or separate. The small sample size of weasel track patterns precluded any analysis of responses to components of the intensively-managed and the unmanaged forests separately.

Weasel track tortuosity was significantly influenced by sites with a low abundance of extremely decayed coarse woody debris and high regeneration of hardwood. The results did not indicate that relative prey abundance influenced the tortuosity of weasel trails suggesting that variations in movement patterns do not reflect habitat quality based on food quantity. Maser et al. (1979) suggested that coarse woody debris of increasing decay class should support a higher abundance of small mammals. The soft decayed wood provides a medium for the growth of hypogeous fungi, a food and water source for red-backed voles as well as good substrate for rodent burrowing (Maser et al. 1979, Nordyke and Buskirk 1991). My results indicated reduced tortuosity of weasel movement patterns with increasing abundance of coarse woody debris of decay class five-extremely decayed wood. Nordyke and Buskirk (1991) reported a positive correlation between red-backed voles and increasing decay class of coarse woody debris. However, their study only included coarse woody debris, up to and including, decay class 3.5.

Observations in the field identified weasel tracks encountering obstacles in a third of the tracks. When weasel trails went below the snow, they were predominantly in association with some structural component of the habitat. Of these structural habitat components, 48% were coarse woody debris and 43% were living tree stems which broke through the surface of the snow. During the snow cover months of winter, coarse woody debris of decay, class one to three, provides breaks in the snow for weasels to gain access to subnivean habitat (Powell 1978, Sherburne and Bissonette 1994).

Weasel movement pattern tortuosity was also correlated with an increase in the amount of hobblebush understory stems, 1 to 2 m in height. Physical structures of the vegetation can have the potential to modify the motivation of an animal and change its response to landscape structure by presenting physical barriers that increase patch viscosity and result in increased complexity of movement patterns (With 1994a, b). Within these areas, the tortuosity of movement patterns will increase (Wiens and Milne 1989, Crist et al. 1992, With 1994b). With (1994a) suggested that if a patch provided refuge from predators then movement within the patch would increase. Although assigning causation is difficult, my results suggest that an increasing abundance of hobblebush understory stems obstructed the weasel's movement and increased tortuosity. Though predator avoidance may be a factor, these deciduous shrubs would provide limited cover in winter to aerial predators. There was no evidence of higher food abundance in these habitats.

The focus of this study was on the relationship between weasel behaviour and the structure and productivity of a habitat. It was hypothesized that prey abundance would influence the tortuosity of weasel movement patterns by showing an increase in tortuosity in areas with higher productivity (provided that small mammal numbers are similar in winter to those in autumn). However, the results did not support this hypothesis. The fractal approach provides a scale-independent means of quantifying movement patterns at a level that is meaningful to the animal under investigation. The results from this study indicate that the use of fractal analysis to define the tortuosity of an animal's movement pattern can be a reflection of the resistance offered by the structural components of a landscape rather than an abundance of prey or the quality of the habitat.

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Table 3.1. List of structural habitat variables used in the analysis of predictors for increased weasel track tortuosity in forests of northwestern New Brunswick, 1996-1997.

Variable
Tree and shrub species abundance (no. of stems for 3 plots/ point in a given height class)
All understory stems (4-6 m)
All understory stems (> 6 m)
Hobblebush (*Viburnum alnifolium*) understory stems (1-2 m)
Hobblebush understory stems (2-4 m)
Hobblebush understory stems (4-6 m)
Hobblebush understory stems (> 6 m)
Sugar maple (*Acer saccharum*) understory stems (4-6 m)
American beech (*Fagus grandifolia*) understory stems (> 6 m)
Beaked hazel (*Corylus cornuta*) understory stems (4-6 m)
Beaked hazel understory stems (> 6 m)
Beaked hazel total understory stems
Rasberry (*Rubus* sp.) understory stems (2-4 m)
Rasberry (*Rubus* sp.) understory stems (4-6 m)
Rasberry (*Rubus* sp.) understory stems (> 6 m)
Softwood understory stems (0.5-1 m)
Softwood understory stems (1-2 m)
Softwood understory stems (4-6 m)
Softwood understory stems (> 6 m)
Hardwood understory stem (2-4 m)

Coarse Woody Debris: abundance of coarse woody debris (> 8 cm in diameter at widest point and ≥ 50 cm long for 3 plots/point.   Coarse woody debris (decay class: 5)   Diameter of coarse woody debris   Mean decay class of coarse woody debris   Total number of downed tree tops
Relevé: classification of abundance of each shrub species (< 2 m in height) and ground cover by % occurrence for 3 plots/point.   Rasberry relevé   Bare ground relevé   Bryophyte relevé   Leaf liter relevé
Total red maple (*A. rubrum*) basal area
Total yellow birch (*Betula alleghaniensis*) basal area
Total white birch (*B. papyrifera*) basal area
Total number of live balsam fir (*Abies balsamea*)
Total number of sugar maple stems
Total number of eastern white cedar (*Thuja occidentalis*) stems
Total number of spruce sp. (*Picea* sp.), stems
Snow depth: mean value of 3 measurements recorded at each sampling station for each round of tracking

Table 3.2. List of prey abundance variables used in the analysis of predictors for increased weasel track tortuosity in forests of northwestern New Brunswick, autumn 1997.

Variable
Total number of deer mice (*Peromyscus maniculatus*)
Total number of red-backed voles (*Clethrionomys gapperi*)
Total number of woodland jumping mice (*Napaeozapus insignis*)
Total number of short-tailed shrews (*Blarina brevicauda*)
Total number of all species at a sampling point
Total prey biomass

Table 3.3: Results of multiple regression analysis for tortuosity of weasel movement patterns as a function of structural habitat and prey abundance variables in forests of northwestern New Brunswick, December 1997 - February 1998.

Variable	**df**	**F**	**p**
Coarse woody debris: decay class of 5	1	7.51	0.01
Hobblebush (*Viburnum alnifolium*) understory stems (1-2 m)	1	9.47	0.01
Total white birch (*B. papyrifera*) basal area	1	3.38	0.08

Table 3.4: Types of subnivean access structures used by weasels in forests of northwestern New Brunswick, December 1997 - February 1998.

Access structures	n
Tree bases	
Coniferous	6
Deciduous	4
Coarse woody debris	11
Snag	1
Hole in snow	1
Total	23

Figure 3.1: Frequency of coarse woody debris with a decay class of five and fractal mean D of weasel movement patterns in forests of northwestern New Brunswick, December 1997 - February 1998.

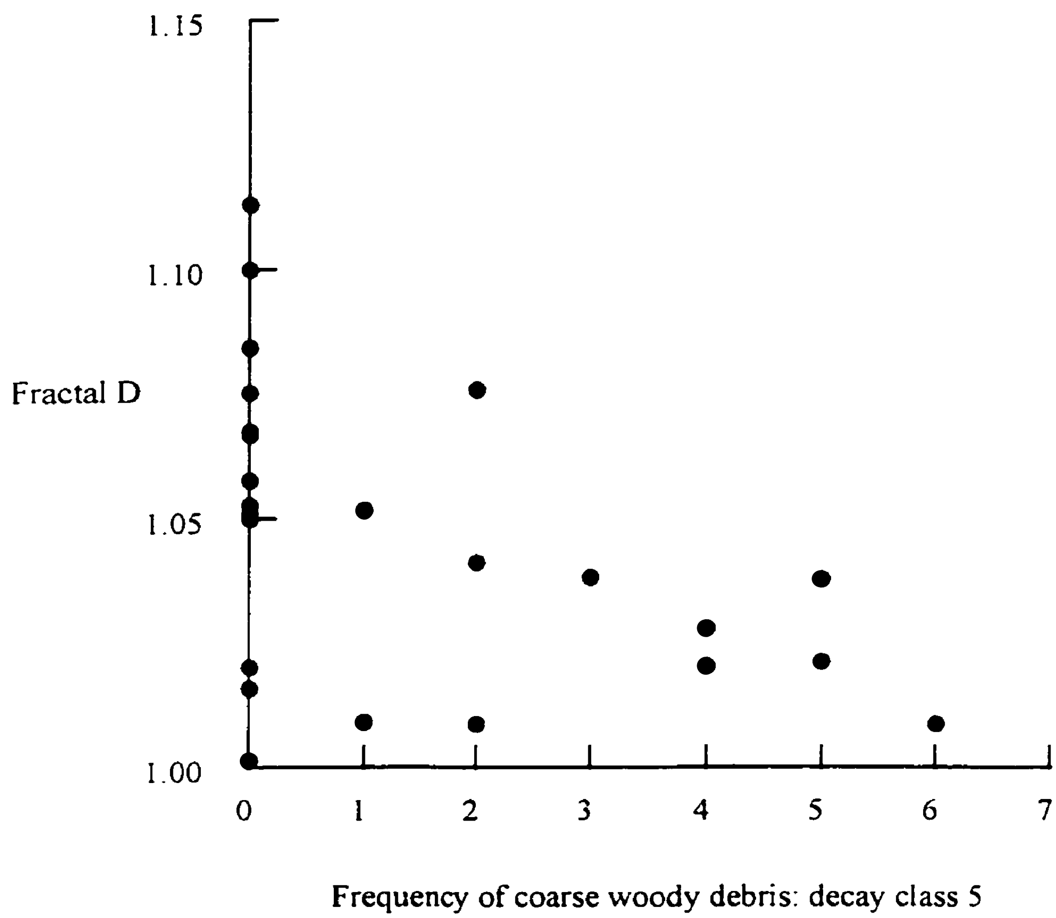
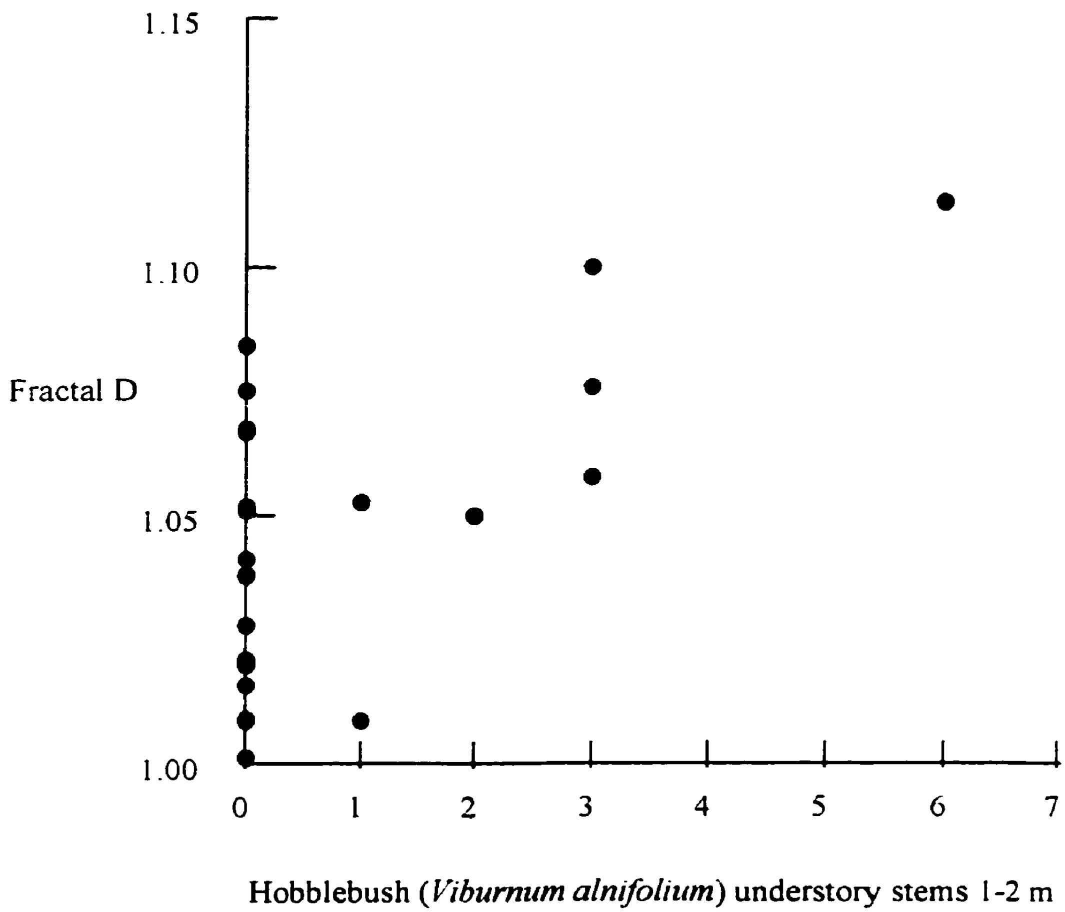


Figure 3.2: Frequency of hobblebush (*Viburnum alnifolium*), 1 to 2 m in height and fractal D of weasel movement patterns in forests of northwestern New Brunswick, December 1997 to February 1998.



CHAPTER 4

GENERAL DISCUSSION AND FOREST MANAGEMENT IMPLICATIONS

Previous studies conducted in primarily agricultural areas have indicated that relative prey abundance and availability are the most important factors influencing weasel abundance and distribution (Erlinge 1974, Simms 1979). The results of the present study indicate that weasels in a forested landscape were influenced by structural habitat components and not relative prey abundance. Weasel activity was identified with sites with a high abundance of hardwood understory. These sites were characterized by the occurrence of a disturbance, whether anthropogenic or natural. Within the forests of northwestern New Brunswick, disturbed sites are often the result of selective-cutting operations, road creation or windthrow. These areas might have provided protective cover from aerial predators and/ or refuge from interference competition from larger predators, even though food was not the main attractant.

Fractal geometry was used to identify habitat quality as a factor of resource use by weasels. The high metabolic rate of weasels would suggest that food abundance and availability is the resource defining habitat quality for weasels (Brown and Lasiewski 1972, King 1989). However, weasel track pattern tortuosity was not influenced by prey abundance, and therefore, did not reflect areas of higher use and/ or higher quality. Weasel track tortuosity was significantly influenced by sites with a low abundance of extremely decayed coarse woody debris and a high regeneration of hardwood understory. This suggested that the complexity of the habitat was influencing weasel behaviour and increasing track complexity and time spent in an area. Avoidance from predators may have been a factor and could have resulted in increased movement within these areas. However, these deciduous shrubs would provide little escape cover in winter from aerial predators. Increased track tortuosity may simply be a function of the physical complexity of the habitat.

Although the results present different predictors for weasel presence and track pattern complexity, they are not contradictory. Predictors of track tortuosity were only included from sites where weasels were present. However, predictors influencing weasel presence were sampled from all stations whether a weasel was present or not. The responses for each model were different and should not be viewed otherwise. Finally, the low amount of variability taken into account by the models suggests that other factors are influencing weasel presence and track tortuosity.

The forestry industry is concerned with the sustainability of Canada's forests and is changing to a form of ecosystem management. This changing philosophy is aimed at maintaining biodiversity and ecological processes to ensure ecosystem health (Hannon et al. 1996). This study describes the responses of weasels to habitat structure and prey abundance in forested landscapes. Weasels are major consumers of small mammals and birds (Erlinge 1974, Hanski et al. 1991), are prey to larger carnivores (Simms 1979), and are therefore key elements in the trophic dynamics of a forest ecosystem. Maintaining ecological variability within Canada's managed forests requires a better understanding of processes and trophic dynamics. Predator-prey interactions are one process which affect these trophic dynamics (Hannan et al. 1996). The interaction of weasels and the various components that make up their habitat, including both prey abundance and structural habitat components, provided a means of investigating this relationship.

Weasel habitat selection has been related to early successional stages where similar characteristics exist within the gaps and edges formed by selective-cutting operations, road creation, and windthrow (Simms 1979). Results of this study indicated that within an industrial forest, weasel habitat selection may be better defined by describing an area in terms of management history. Harvest operations that increase habitat diversity and edge may be beneficial to weasels. Small mammal abundance was shown to be greater in recent rather than older harvest cuts and within the created ecotone (Sekgororoane and Dilworth 1995). These habitats may be providing refuge for weasels from interference interactions from larger predators as well as enough prey to sustain the population. However, knowledge of intra- and interspecific interactions among sympatric *Mustelid* populations is limited (Simms1979, King 1990). It should be noted that the design of this study was not intended to account for the edge-related effects of anthropogenic and natural disturbances. The sampling grid was laid out in a systematic design, and edge was not known to be important to weasels in forested environments. There exists the potential to further define the response of weasels to habitat structure and prey abundance in forested landscapes. Future research should investigate these interactions with finer-scaled observations of movement, foraging behaviour and denning in both unmanaged and managed forests. This should help to further improve our understanding of this predator's role in the trophic dynamics of forest ecosystems.

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APPENDIX I

List of Structural Habitat Variables: Description of structural habitat variables sampled from three, 10 X 20 m quadrats at each sampling station.

Variable
Tree and shrub species abundance (no. of stems for 3 plots/ point for a given height class)
All understory stems 0.5-1 m
All understory stems 1-2 m
All understory stems 2-4 m
All understory stems 4-6 m
All understory stems >6 m
Hobblebush (*Viburnum alnifolium*) understory stems 0.5-1 m
Hobblebush understory stems 1-2 m
Hobblebush understory stems 2-4 m
Hobblebush understory stems 4-6 m
Hobblebush understory stems >6 m
Hobblebush total understory stems
White birch (*Betula papyrifera*) understory stems 0.5-1 m
White birch understory stems 1-2 m
White birch understory stems 2-4 m
White birch understory stems 4-6 m
White birch understory stems >6 m
White birch total understory stems
Striped maple (*Acer pensylvanicum*) understory stems 0.5-1 m
Striped maple understory stems 1-2 m
Striped maple understory stems 2-4 m

Striped maple understory stems 4-6 m

Striped maple understory stems >6 m

Striped maple total understory stems

Sugar maple (*Acer saccharum*) understory stems 0.5-1 m

Sugar maple understory stems 1-2 m

Sugar maple understory stems 2-4 m

Sugar maple understory stems 4-6 m

Sugar maple understory stems >6 m

Sugar maple total understory stems

American beech (*Fagus grandifolia*) understory stems 0.5-1 m

American beech understory stems 1-2 m

American beech understory stems 2-4 m

American beech understory stems 4-6 m

American beech understory stems >6 m

American beech total understory stems

Beaked hazel (*Corylus cornuta*) understory stems 0.5-1 m

Beaked hazel understory stems 1-2 m

Beaked hazel understory stems 2-4 m

Beaked hazel understory stems 4-6 m

Beaked hazel understory stems >6 m

Beaked hazel total understory stems

Raspberry (*Rubus* sp.) understory stems 0.5-1 m

Raspberry understory stems 1-2 m

Raspberry understory stems 2-4 m

Raspberry understory stems 4-6 m

Raspberry understory stems >6 m

Raspberry total understory stems

Softwood understory stems 0.5-1 m

Softwood understory stems 1-2 m

Softwood understory stems 2-4 m

Softwood understory stems 4-6 m

Softwood understory stems >6m

Softwood total understory stems

Hardwood understory stem 0.5-1 m

Hardwood understory stem 1-2 m

Hardwood understory stem 2-4 m

Hardwood understory stem 4-6 m

Hardwood understory stem >6 m

Hardwood total understory stems

Relevé: classification of abundance of each shrub species (< 2 m in height) and ground cover by % occurrence for 3 plots/point, according to the following scheme.

1 = rare in plot; <1% cover

2 = few occurrences in plot; 1-10% cover

3 = several occurrences; 10-20% cover

4 = frequent throughout the plot; 20-50 % cover

5 = very common throughout plot; >50% cover

Hobblebush relevé

Yellow birch relevé

Striped maple relevé

Sugar maple relevé

American beech relevé

Beaked hazel relevé

Raspberry relevé

All Softwood species understory relevé

All Hardwood species understory relevé

Herbaceous relevé

Bare ground relevé

Bryophyte relevé

Lichen relevé

Leaf litter relevé

Standing water relevé

Total basal area of all live standing trees
Total basal area of dead standing trees
Total number of live stems (>8 cm dbh)
Total number of dead stems (>8 cm dbh)
Total number of live balsam fir stems
Total live balsam fir basal area
Total number of dead balsam fir stems
Total dead balsam fir basal area
Total number of sugar maple stems
Total sugar maple basal area
Total number of American beech stems
Total American beech basal area
Total number of yellow birch stems
Total yellow birch basal area

Total number of trembling aspen (*Populus tremuloides*) stems
Total trembling aspen basal area
Total number of white birch stems
Total white birch basal area
Total number of white spruce (*Picea glauca*) stems
Total white spruce basal area
Total number of eastern white cedar (*Thuja occidentalis*) stems
Total eastern white cedar basal area
Total number of red maple (*Acer rubrum*) stems
Total red maple basal area
Total number of pine sp. (*Pinus* sp.), white spruce, black spruce (*Picea mariana*) stems
Total basal area of pine sp., white spruce, black spruce
Coarse Woody Debris: abundance of coarse woody debris (> 8 cm in diameter at widest point and ≥ 50 cm long for 3 plots/point.
Coarse woody debris (decay class 1)
Coarse woody debris (decay class 2)
Coarse woody debris (decay class 3)
Coarse woody debris (decay class 4)
Coarse woody debris (decay class 5)
Mean decay class
Diameter of coarse woody debris
Total number of downed tree tops
Total number of logs
Total coarse woody debris
Total number of softwood coarse woody debris

List of Relative Prey Abundance Variables: Abundance of different prey species estimated through a mark-recapture program during early autumn 1997 at each sampling station.

Variable
Total number of deer mice (*Peromyscus maniculatus*)
Total number of red-backed voles (*Clethrionomys gapperi*)
Total number of woodland jumping mice (*Napaeozapus insignis*)
Total number of short-tailed shrews (*Blarina brevicauda*)
Total number of all species
Total prey biomass

APPENDIX II

FOOD HABITS OF SHORT-TAILED WEASELS (*Mustela erminea*) IN A FORESTED LANDSCAPE

ABSTRACT

Most research pertaining to the diet of North American weasels has been conducted in agricultural regions and is not representative of diets in forested regions. Weasel carcasses (N = 165) collected by trappers during a two-week harvest (16-30 November, 1996) in forested New Brunswick, were analyzed for food habits. Hair and bones were found in 134 weasels (81.2%). Stomachs (N = 83) and gastro-intestinal tracts (N = 109) were used in the calculation of the percent frequency of occurrence. Results suggest that soricid (27.1%), arvicolines (23.4%), and cricetines (16.7%) comprised 2/3's of their autumn diet. At a species or genus level, the deer mouse (*Peromyscus maniculatus*) (16.7%) and the *Sorex* spp. (22.9%) were shown to have the highest percent occurrence. Squirrels, including the red squirrel (*Tamiasciurus hudsonicus*) and the chipmunk (*Tamius striatus*), comprised 12.5% of the weasel's diet; a value higher than has previously been reported.

Key words: short-tailed weasels, *Mustela erminea*, food habits, diet analysis

INTRODUCTION

The majority of the literature pertaining to weasels indicates that small mammals, in particular rodents, are the weasel's principal prey (Erlinge 1983, King 1990, Hanski et al. 1991). However, this is based on studies which have been conducted in primarily agricultural regions and not in forested landscapes. The majority of weasel research has been conducted in the grass and farmland regions of Europe, southern Ontario and Quebec (Erlinge 1975, 1981, 1983, Raymond et al. 1984, King 1990, Oksanen and Schneider 1995) or in sub-Arctic regions (Maher 1967, McLean et al. 1974).

There are difficulties associated with extrapolating what weasels eat from agricultural landscapes to forested landscapes. A study by Aldous and Manweiler (1942) on the diet of short-tailed weasels (*Mustela erminea)* in the coniferous forest regions of the northeastern United States and adjoining parts of Canada determined that similar to prey selection in agricultural areas, small mammals (<80 grams) were the dominant winter food choice. Thompson and Colgan (1990) suggested that smaller prey requiring minimal energy costs, may be taken incidentally by marten (*Martes americana*) while searching for larger prey items. Although larger prey items occur less frequently in the diet of small carnivores like the weasel, they might be more important in terms of caloric intake (Cumberland and Dempsey 1993).

It has been suggested that of the available rodents present in an area, arvicolines (e.g. voles) are the principal prey of these specialist predators (Aldous and Manweiler 1942, Simms 1978, Nams 1980, King 1990). Variations in the escape strategies of small mammals have resulted in the vole being the weasel's principal prey item (Simms 1978, 1979; King 1990). In the presence of a weasel, voles responded by running and were quickly dispatched, whereas white-footed mice (*Peromyscus leucopus*) evaded capture by climbing upward or freezing (Heidt 1972, King 1990). In agricultural areas, when deer mice were present, voles were still consumed in higher proportions (Derting 1989, King 1990). It would be advantageous for weasels to prey on species that are the easiest to catch because of the high energy demands associated with catching prey. This energy demand and the weasel's high metabolic rate have been correlated to hunting in areas of high prey density (Derting 1989), which has been shown to be the case in most grassland studies. In the Boreal forest and fringe habitats, short-tailed weasels are able to hunt red-backed voles and deer mice in the subnivean space created by mosses and ericaceous shrubs (Simms 1979).

The objective of this study was to provide an index of prey use by weasels in the forests of New Brunswick, Canada. This information could be used as a foundation for other projects investigating the response of weasels to various habitat components, including prey abundance. For the purpose of this thesis, it was important to identify which species are consumed by weasels. Distribution of weasels may be related to the abundance of voles versus mice.

METHODS

In 1996, 165 weasels (trapped during the New Brunswick harvest, 16-30 November) were collected from trappers for diet analysis. To determine if the species of *Mustela* sampled was short-tailed weasel (*M. erminea*) or long-tailed weasel (*M. frenata*), which occur in small numbers along the western border of the province

(Dilworth and Gorham 1984), skulls were collected and the following body measurements were recorded: (1) weight; (2) total body length; (3) tail length; and (4) hind foot length. Although results will only be indicative of late autumn food habits and not year-round diet, this method provides an index of prey items consumed by weasels in New Brunswick.

It can be assumed that a weasel cannot eat more than the equivalent of one small rodent at one time since it's stomach has a maximum capacity of 10 to 20 g. Therefore, a single stomach or intestine will generally contain only one item (Aldous and Manweiler 1942, Heidt 1972, Simms 1978, King 1990). The contents of the stomach and gastro-intestinal (GI) tract constitute one meal each, consumed at separate time intervals and were considered separate samples. This allowed for two samples to be collected from each individual.

The contents of each stomach and GI tract were removed, rinsed separately in a plastic container, and then washed through a 35 grade sieve. The remaining stomach or GI tract contents were viewed through a dissecting microscope and identifiable items removed. During the process of mastication and digestion, many of the more obvious characteristics used in species identification may be lost. Items such as tooth and bone are often absent or too fragmented to be helpful in identification, and only hair and feathers remain (Day 1966, Gamberg and Atkinson 1988). Using hair for diet analysis is common practice since the hair is species-specific and hair enables identification (Wallis 1993). Flesh was not identified. Vegetable matter was assumed to be incidental (Erlinge 1975, Simms 1978). Hairs were imprinted on a slide treated with hair spray and observed using a compound microscope. A reference collection of study skins and various keys (Day 1966, Adorjan and Kolenosky 1969, Thompson et al. 1987) facilitated identification of prey remains. All mammalian prey were identified to species, except *Microtus* sp. and *Sorex* sp. which are difficult to identify beyond the genus level (Thompson et al. 1987, Thompson and Colgan 1990, Cumberland and Dempsy 1993, Cumberland et al. 1995). Attempts were not made to identify invertebrates and woody debris since such materials were considered incidental (King 1990). The frequency of occurrence for each food item in the diet was determined by counting the number of times each item occurred in the total sample of stomachs and GI tracts. For the analysis, total sample did not include empty stomachs and GI tracts.

RESULTS

Collection of 165 weasel carcasses resulted in 155 (93.9%) short-tailed weasels and 10 (6.1%) long-tailed weasels. Only short-tailed weasels were included in the analysis. The sex ratio was 141 (91.0%) males to 14 (9.0%) females. Seventy-four stomachs (47.7%) and 57 GI tracts (36.8%) were found to be empty. Empty stomachs and GI tracts were not included in the analysis. The resulting sample included 155 weasels and a total of 81 stomachs and 98 GI tracts. Therefore, the sample size was 81 stomachs and 98 GI tracts (N= 179). Species were lumped into 8 categories based on taxonomic association: voles and lemmings (*Microtinae*), mice (*Cricetidae*), shrews (*Soricidae*), squirrels (*Scuridae*), weasels (*Mustilidae*), feathers, other fauna and unknown (Table A.1). Other fauna included prey items where the frequency of occurrence was ≤ 2.

Mice and voles, including the arvicolines and the cricetines, comprised 41.9% of the total prey items; of which deer mice (*Peromyscus maniculatus*), with 17.3%, were the single most abundant mouse species. The remainder were as follows: 8.4% red-backed vole (*Clethrionomys gapperi*), 9.5% other voles (*Microtus* spp.), and 6.7% southern bog lemming (*Synaptomys cooperi*). *Sorex* spp. also comprised a large proportion (23.5%) of the samples. The other shrew genus in the region, the short-tailed shrew (*Blarina brevicauda*), accounted for 4.5%. Smaller amounts from a range of species accounted for the remainder of the food items collected. Members of the *Sciuridae* made up 11.2% of the total prey recovered. This included two species, eastern red squirrel (*Tamiasciurus hudsonicus*) at 8.4% and eastern chipmunk (*Tamia striatus*) at 2.8%. Feathers were recovered as well and constituted 5.0% of the total prey items. The remaining items including weasel hair (*Mustela* spp.) at 6.1%, other fauna at 2.8% and 5.0% unknown.

DISCUSSION

Numerous studies have shown that small mammals and birds make up the greater proportion of the weasel's diet (Aldous and Manweiler 1942, Erlinge 1974, King 1990). However, resulting prey proportions depend on the gender of the weasel, regional characteristics and prey availability (Aldous and Manweiler 1942, Simms 1978, Whitaker and French 1984). Many studies have indicated that voles are the principal prey of the weasel (Erlinge 1975, Simms 1979, Raymond et al. 1984). However, these studies were primarily conducted within agricultural regions. Studies within forested areas have shown that mice and shrews occur more frequently as components of weasel diet (Aldous and Manweiller 1942, Raymond et al. 1984).

A higher ratio of male to female weasels was observed from weasel carcasses obtained from trappers. This type of collection often results in gender biases toward male weasels because of spatio-temporal effects of body size, trap geometry and sex dependent behaviour (Buskirk and Lindstedt 1989). Seasonal effects resulted in a decreased representation of avian food items, and no jumping mice remains being collected. During the late autumn season, bird abundances are low as migrants have left, and woodland jumping mice (*Napaeozapus insignis*) are inactive due to hibernation. However, Northcott (1971) reported that short-tailed weasels will exhume jumping mice from their winter hibernation nests. Dietary analysis of weasel stomachs and GI tracts did indicate that small mammals including arvicolines, cricetines and shrews were the most dominant food item within the weasel's diet. Derting (1989) reported that weasels demonstrated opportunistic foraging behaviour and attacked all prey offered in an enclosure study. However, differences in escape tactics resulted in voles (*Micotus* spp.) being captured more frequently. An opportunistic foraging strategy suggests that prey will be taken in direct proportion to availability (Aldous and Manweiler 1942, Erlinge 1975, Derting 1989). Weasel feeding habits can be defined by the relative abundance and availability of prey species (Aldous and Manweiler 1942, Erlinge 1975). Availability of prey was not known since the sample originated from throughout the province of New Brunswick. Simms (1979) suggested that deer mice might be the weasel's most frequent prey choice in forested regions because of higher availability, and habitat characterized by the presence of mosses and ericaceous shrubs carpeting the forest floor. Instead of freezing and/or climbing (Erlinge 1975, Derting 1989, King 1990), deer mice in these regions may alter escape tactics and escape into the subnivean spaces created by these mosses and shrubs (Simms 1979).

Our results were similar to Aldous and Manweiler (1942) who found that shrews followed mice in terms of dominant prey species for weasels inhabiting a forested landscape. Erlinge (1975) stated that shrews as prey items for weasels were more dominant in North American studies. In New Brunswick, the most abundant shrew species available were short-tailed (*Blarina brevicauda*); masked (*Sorex cinereus*); smokey (*S. fumeus*); 4) pigmy (*S. hoyi*); and arctic (*S. arcticus*) (Gorham and Dilworth 1984). The average biomass of a shrew is approximately 45 % of a cricetine and 28 % of an arvicoline (Dilworth and Gorham 1984). Weasels have been observed avoiding shrews even when abundance was high. This avoidance behaviour is believed to be the result of the shrews aggressive behaviour when attacked and a distasteful flavour (Erlinge 1975, Vaudry et al. 1990). In a grass-dominated study, Raymond et al. (1984) reported that shrews constituted an important dietary component of the weasel; however, the whole shrew was seldom consumed.

Squirrel remains were recorded in higher proportions than have previously been reported for weasels. The high ratio of males to females in the sample and the more opportunistic foraging behaviour of larger male weasels (Raymond et al. 1984, Derting 1989) may explain the higher abundance of squirrels. Larger male weasels would be able to exploit larger prey items that would require a higher risk of injury and higher energy expenditure. A higher female component in the sample might have resulted in a larger vole component. The average biomass of a squirrel is approximately seven times greater than a cricetine and four times greater than an arvicoline (Dilworth and Gorham 1984).

The results suggest that deer mice and shrews occurred more frequently in the diets of weasels from forested landscapes than from agricultural regions. These results provided an index of prey use, during late autumn by weasels of the forested regions of New Brunswick, that will be used for other projects investigating the response of weasels to various habitat components including prey abundance.

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Table A.1. Diet of 155 weasels, trapped during the two-week harvest (16-30 November, 1996) in New Brunswick, expressed as frequency of occurrence (N=179), and percent of occurrence.

Prey type	**Frequency of Occurrence**	**Percent of Occurrence**
Voles and Lemmings		
Clethrionomys gapperi	15	8.4
Microtus spp.	17	9.5
Synaptomys cooperi	12	6.7
Mice		
Peromyscus maniculatus	31	17.3
Shrews		
Blarina brevicauda	8	4.5
Sorex spp.	42	23.5
Squirrels		
Tamiasciurus hudsonicus	15	8.4
Tamius striatus	5	2.8
Weasels		
Mustela sp.	11	6.1
Feathers	9	5.0
Other fauna	5	2.8
Unknown	9	5.0
Total	179	100.0