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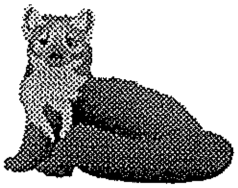
An Energetics-based Habitat Model for Marten in Western Newfoundland



Interim Progress Report
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Prepared for

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AN ENERGETICS-BASED HABITAT MODEL FOR
MARETN IN WESTERN NEWFOUNDLAND.
PROJECT#2-207-004

Introduction

The Newfoundland marten (*Martes americana atrata*) and the social and ecological values it symbolizes represent a significant challenge to integrated resource management. Conventional wisdom argues that the marten is an old-growth obligate, and as such, presents a conflict with those concerned with extracting a maximum sustainable yield of wood fiber from the landscape. Not surprisingly, the Newfoundland marten has received considerable attention during the development of the Western Newfoundland Model Forest Integrated Resource Management Plan. The recent emergence of environmental advocacy organizations such as Forest Allies ensures that the values epitomized by the Newfoundland marten will be an integral part of western Newfoundland resource management for some time to come.

Science alone does not provide answers for complex management issues. Instead, the principal role of science in ecosystem management is to provide the accurate and reliable information that is absolutely essential for sound decision making (Adair *et al.* 1995, Christensen *et al.* 1996). The most vital questions involving the Newfoundland marten (such as: How will the marten respond to experimental timber harvesting regimes? Establishing reserves? Changes in snaring techniques?) require substantial scientific insight, which itself depends on reliable information.

Modeling and Management

Adaptive management, or management through experimentation, may provide the most reliable means for answering complex and difficult questions (Walters and Holling 1990). However, from a planning perspective, adaptive management has a very significant drawback: answers are often a long time in coming. For example, an adaptive management approach to assessing the impact of experimental cutting practices on marten would require tracking several generations of marten! Clearly managers faced with a resource in crisis (such as the Newfoundland marten) must make immediate decisions. In these cases, wildlife ecologists frequently undertake short-term analyses of what are essentially long-term phenomena, assuming that the immediate responses that they observe are representative of the long-term effects. The most common example of this approach is a "space-time substitution," where a multitude of sites in various stages of development are compared. The space-time subsitution has one significant drawback, however: the method is almost impossible to "control" in an experimental sense. As a result, empirical approaches provide an insufficient means of assessing how tenuous the space-time relationship is.

Clearly managers faced with a resource in crisis cannot afford to rely on poor assumptions! As a consequence, planners have turned to predictive models as a short-term surrogate for adaptive management (Morrison *et al.* 1992). The central premise of this approach is that computer models can use existing ecological knowledge to predict future conditions. These predictions can, in fact, provide the basis for the very adaptive management programs needed to test the model.

Traditional habitat modeling approaches are descriptive rather than truly predictive. Descriptive models are truly reliable only when they are capable of addressing *all* of the possible habitat conditions that the species might face. Such a model would be essentially encyclopedic (a habitat equivalent of a "look-up table") and virtually impossible to create, simply because physical conditions, history, and management manipulation may lead to a nearly infinite array of possibilities. For this reason ecologists have turned to "mechanistic" models designed to explain the organizing principles that lead to habitat selection. Alternatively, mechanistic models describe the actual decisions made by the organism, rather than just the pattern that arises from these decisions. As a result, mechanistic models should be capable of predicting habitat selection in an infinite array of circumstances, including novel landscapes.

Most models intended to assess marten habitat suitability (*e.g.*, Allen 1982, Thompson and Harestad 1994, and many others) are descriptive. Some are pseudo-mechanistic, in that they describe the availability of key habitat features, such as resting sites and feeding areas. These models may accurately portray the habitats selected by marten in existing landscapes. However, their predictions may depend on the habitats that were available when and where the empirical study was conducted (Adair and Bissonette 1995). So long as these conditions hold, the models are accurate. Their generality (and hence utility) may suffer, however, if the test landscape conditions is significantly different from the observed landscape. In Newfoundland, this notion is especially critical: most marten habitat association studies to date have been confined to the uncut portion of the Pine Marten Study Area, which is a virgin anomaly in an otherwise intensively managed landscape.

Our mechanistic model is based on optimization, one of the most basic principles in ecology. The optimization paradigm suggests that natural selection, over evolutionary time scales, will favor those organisms and behaviors that do the best (optimal) job of obtaining resources from their environment. This does not necessarily imply that animals will behave optimally, but instead suggests that animals will make the best decisions they can given their historical constraints. Our marten model uses optimization principles to rate landscapes based on their ability to provide key features of marten habitat, such as resting sites, safe travel routes, and profitable foraging patches.

One of the most significant advantages of our optimization approach is that the model is capable of addressing habitat selection behavior at a multitude of scales. For marten, the concept of scale is essential for understanding their habitat needs. Typically, marten habitat models employ scale-independent measures (for example, percent canopy cover), and address scale only through application, where the minimum unit of resolution is the forest stand, and the extent of application is arbitrary (*e.g.*, Shulz and Joyce 1992). As a consequence these models and their predictions are strongly constrained by the database. This is logically contradictory: the database should be made capable of answering the question correctly, rather than the question constrained to meet the database.

Brief reflection will illustrate the role of spatial and temporal scales in marten habitat selection. At the smallest level of resolution (cognitive grain), foraging marten are more likely to investigate clumps of coarse woody debris than single logs. Similarly, marten use specific structures for resting sites (large diameter hollow snags and logjams). Unfortunately, this grain is clearly smaller than the smallest level of mapping resolution available for use in the model.

Our observations also suggest that marten are likely to favor some kinds of forest communities over others: Newfoundland marten rarely traverse wide open spaces (bogs, frozen lakes, and the like) and certainly do not spend much time in them, but they do spend a considerable amount of their active time foraging in defoliated blowdowns. These observations are consistent with the spatial scale mapped by most forest inventory databases. It is not surprising that this is the level of organization emphasized by most ecologists studying marten habitat selection!

However, if we expand our spatial horizons, we discover that marten show distinct habitat selection behaviors at a larger spatial scale. For example, Newfoundland marten are much more likely to forage in defoliated blowdowns surrounded by intact forest than in similar blowdowns isolated within an expansive clearcut. Similarly, these same animals may forage along the clearcut-forest interface, but generally do not venture far into clearcuts. These observations suggest that in order to represent marten habitat selection correctly, the model must be both landscape-level in scope and spatially informed. While some of these phenomena lend themselves to simple spatial rules (for example, venture into a clearcut no farther than 50m from the forest edge), some are more difficult to envision (for example, how far away from a resting site can a foraging patch be before either the foraging patch or the resting site becomes unsuitable).

Most habitat assessment models used by natural resource managers attempt to resolve the question of how individual animals interact with spatially disparate resources, and go no farther. At this point habitat assessment models implicitly assume that the species' population follows an ideal free distribution (Fretwell 1972). Under the ideal free distribution, organisms distribute themselves among habitats according to fitness, with the density of settlers proportional to the suitability of the habitat. This distribution assumes that the animals are fully capable of assessing their habitats, established residents provide no obstacle to settlement, and that movement among habitats is completely unimpeded. Newfoundland marten, as intrasexually territorial animals, clearly violate these assumptions. As a result, models that predicts fitness based on physical structure alone (as do habitat assessment models in general) will fail to predict where territorial animals like the Newfoundland marten should settle. In order to predict how Newfoundland marten will distribute themselves on the landscape, the 'habitat' model must also address population-level interactions among territory holders and dispersers. In addition, because the presence of males affects the size of the territory that females must defend (as well as who the females must defend against), a habitat model for the Newfoundland model should consider both males and females.

Newfoundland presents a markedly heterogeneous environment at the regional scale: expansive barrens, cliffs, and lakes present substantial, and essentially permanent, barriers. As a consequence, the Newfoundland marten population is likely to be spatially structured even at this scale. While dispersal may resemble a diffusion process at this scale (the marten is unlikely to know what lies 50 km ahead), even this 'diffusion' is likely to be channeled by movement corridors. Because the degree of connectivity provided by corridors is likely to be described by its physical structure, it could be adequately treated with a stand-level database!

Integrating all of the habitat selection phenomena exhibited by marten in a descriptive model (at the appropriate spatial scales) is intellectually and computationally exhausting. Instead, we have opted to model marten habitat selection at two fundamental levels of organization: within an individual's home range, and among territorial members of a population patch. The model that assesses home-range quality is the focus of our work for the Western Newfoundland Model Forest. Rick Schneider's population viability model (Schneider and Yodzis 1994) addresses distribution at the population level, although the role of intrasexual territoriality is not treated.

The 'home-range' model focuses on the habitat needs of female marten raising kits for two reasons: 1) habitat conditions for these animals during this period of their life cycle are the basic determinant of individual, and consequently population, fitness, and 2) conventional wisdom suggests that female marten should choose habitats that provide the most resources for raising kits and that male marten are likely to settle wherever the females are. The model uses a dynamic combinatorial optimization technique to assess the relationship between potential den sites and potential foraging sites. The model is dynamic because its assessment of habitat suitability depends on spatial location (spatially explicit), time of year (temporally informed), and the condition of the animal. The model is combinatorial because it actually maps the possible travel routes between den sites and associated feeding sites. Finally, the model is optimal ('ideal') because it distributes animals on the simulated landscape according to the maximum achievable fitness. The model assembles information garnered at a small scales (within stand averages) to provide a habitat assessment unique to the scale of the home range. This method of assembling information appears to be consistent with the Newfoundland marten's actual behavior.

While descriptive models typically employ an arbitrary scheme to assemble disparate patterns, our mechanistic model is actually a testable hypothesis of how marten assemble habitat information. As a consequence, we can quantitatively test both the individual elements and the assembly mechanism. Traditional descriptive models cannot be so tested.

Mechanistic models require qualitatively different habitat data than that needed by descriptive models. Because we examine the actual components of habitat (*e.g.*, thermal environment and food abundance), we can assess the relative importance of these components directly, rather than relying on their structural components. This advantage is especially significant for marten, because several components may correlate with the same structural variable (*e.g.*, closed canopies provide both security from predation and thermal cover).

Our habitat assessment model can be used to generate forest harvesting scenarios (management alternatives) during the initial planning process, as well as experimental harvesting protocols for adaptive management. It is unlikely that the Western Newfoundland Model Forest's Integrated Resource Management Plan will specify each and every harvest, but instead the plan will probably specify allowable harvest bounds and specific harvesting rules. As a consequence, during implementation each harvest will need to be assessed for impacts individually. Of course the cumulative impact of these individual harvests will need to be assessed as well. Our habitat suitability model should prove invaluable during each of these phases.

Management is of course a continuously evolving process. Our assessment model could be the tool used to evaluate the effectiveness of new ideas when they are suggested. We envision the habitat suitability model as being an objective means of providing the information that managers need to make informed decisions.

Accomplishments for the Report Period

This report summarizes work completed as part of our project during the period 1 April 1996 through 31 March 1997. We had five principal objectives for the project for this period:

1) Continue model formulation.
2) Commence thermal energetics measurements
3) Commence location of den and resting sites for marten in the Little Grand Lake area.
4) Continue vegetation measurements for the small mammal microhabitat study.
5) Complete small mammal live-trapping sessions for the spring, summer, and early fall.

Model Formulation

A more detailed description of our habitat assessment model is provided in Adair's dissertation proposal, previously submitted to the WNMF. During the report period we developed two primary advances in the model's construction. First, we explicitly recognized the importance of territorial interactions in the distribution of individuals across the landscape. This territory model (an improvement to Rick Schneider's model) is being developed in parallel with the within-home range model designed expressly for the Western Newfoundland Model Forest.

We also addressed a formidable technological problem associated with our modeling approach. Combinatorial optimization problems are subject to a phenomenon that mathematicians (rather cryptically) call "NP-hardness." An NP-hard problem may be easy to describe but impossible to solve analytically or computationally. Generally NP-hard problems are characterized by an enormous (possibly infinite) array of possible decisions, among which an optimal solution exists. Unfortunately in these cases, because there are so many possibilities, we have no way of finding out exactly what that optimal solution is!

To visualize the full implications of NP-hardness, consider a potential natal den surrounded by several potential foraging sites. In the simplest scenario, if there are (for example) 4 foraging sites near the natal den, then there are 4 possible alternative decisions (travel routes) that the lactating marten can consider. However, in the real world marten could explore any number of foraging sites during each foray from the den. If we consider all of the possible combinations of 4 foraging sites, there are 15 alternative decisions (because the marten must follow specific routes, the problem is combinatorial). The number of possible alternatives is a provides a crude description of the problem's mathematical complexity. Because the number of possible alternatives (complexity) increases explosively as more patches (or resting sites) are added, our marten habitat model is NP-hard.

However, our observations (and logic as well) suggest that a lactating marten with kits in the den is unwilling stray from the den for extended periods of time, either because the kits get cold or hungry, or because remaining at the den reduces the risk of predation. As a consequence, this marten has a restricted traveling time or distance (distance and time are related by traveling speed). This traveling time restriction may significantly reduce the complexity of our problem by eliminating most of the possible alternatives from consideration. Patches that are too far from the den, or multiple-patch routes that take too much time, need not be treated. Preliminary calculations suggest that the total foraging time may be sufficiently restrictive for Newfoundland landscapes (where foraging sites tend to be widely spaced) to ameliorate the NP-hardness problem.

Identifying foraging sites provides a second conceptual obstacle. Traditionally, optimization models of habitat selection address the distribution of foraging patches rather than the distribution of food items *per se*. In Newfoundland we can readily identify those forest stands that are most likely to provide food; these would be the patches in a conventional optimization model. However, in natural landscapes these structural patches can vary considerably in size and shape, so that some means of dividing these patches into tractable units becomes necessary. Unfortunately, marten behavior does not suggest a suitable method for subdividing these structural patches; a ‘hectare’ has no meaning to a marten. In addition, these structural patches are not internally homogeneous for the food items (individual small mammals) and subnivean access structures that they support. Modeling these components at the level of the stand would mean simulating distributions of accessible small mammals within each stand, which would add an untenable level of complexity to the model. Instead, we developed a simple method for distributing food populations (rather than structural patches) based on their stand-level structural correlates. The model then addresses actual patches of prey, rather than patches of potential prey habitat. The problems of patch size and shape are resolved with an approach that is ecologically meaningful to the marten.

Thermal Energetics

Thermal energetics comprise one of the primary decision criteria for our habitat suitability model. To date no one has actually attempted to measure thermal energetics for an animal like the marten under natural conditions experienced in the boreal forests. Our attempts during the 1996 season were largely successful.

Because we want to test hypotheses about the influence of thermal energetics on marten habitat selection, we need to examine thermal conditions simultaneously in a number of locations for extended periods of time. After considerable trial-and-error, we settled on marten-sized (1 L) aluminum camping fuel bottles, painted flat black and filled with a combination of propylene glycol and water mixed to simulate the specific heat typical of animal tissue. Bottles were fitted with a temperature-sensing data logger to provide a reasonable measurement of the complete thermal environment, including ambient temperature, direct solar and scattered radiation, forced convection, and evaporation. Environmental chambers have been used to calibrate the bottles, so we understand how their response to the thermal environment relates to the response of real martens under the same conditions. Twelve thermal devices were set out in 6 major habitat types (senescing balsam fir, balsam fir in the ZICM stage, black spruce, defoliated blowdown, regenerating clearcut, and bog), and monitored from early April through mid-September 1996.

Unfortunately marauding wildlife, possibly attracted to micronutrients in the propylene glycol, destroyed a several apparatus. The problems were solved by the addition of copious amounts of cayenne pepper sauce, but not until after several weeks of data in 2 sites were lost. Nevertheless, the resulting data provide some interesting patterns.

Because of the massive size of the database (over 450,000 data points), we cannot present all of the data here. Instead, we will present a subset of the data to illustrate the major points. Figure 1 illustrates the data for 6 sites (senescing fir BFOF 1-2, black spruce BS 2-1, ZICM balsam fir SG 3-2, defoliated blowdown BK 1-2, cutover COV 3-1, and bog BOG 2-1) during the period from April 24 through May 13. The most striking pattern is that all of the habitats are very similar. Figure 2 illustrates the difference between open habitats (in this case a defoliated blowdown, BK 1-2) and closed canopy forests (a senescing balsam fir forest, BFOF 1-2): open habitats experience much larger daily fluctuations than do closed habitats, suggesting that variance may be important. Interestingly, while open habitats are generally colder at night than closed-canopy sites, the difference is not significant from the perspective of the marten. Conversely, open sites are significantly warmer than closed-canopy sites during the late afternoon; some of these sites exceed the upper critical temperature for marten (about 30 °C). All sites are strikingly similar with respect to weather patterns (cloudy days and nights can be readily identified as reduced peaks and troughs, respectively).

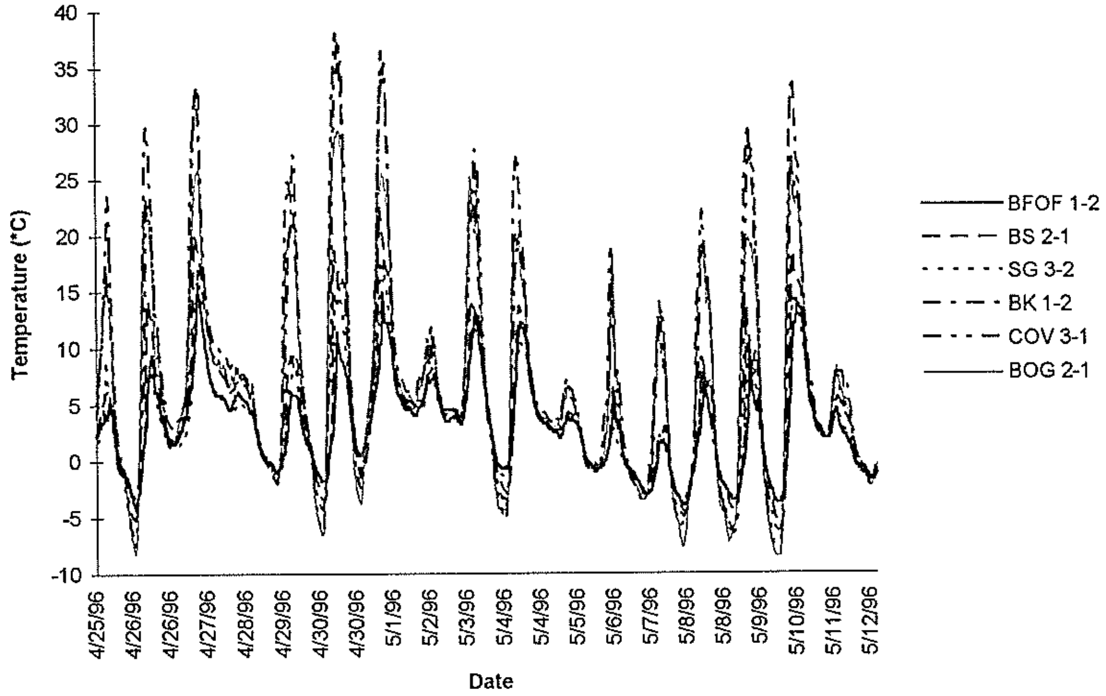

Figure 1. Thermal data for 6 representative sites (senescing fir BFOF 1-2, black spruce BS 2-1, ZICM balsam fir SG 3-2, bugkill BK 1-2, cutover COV 3-1, and bog BOG 2-1) during the period from April 24-May 13, 1996.

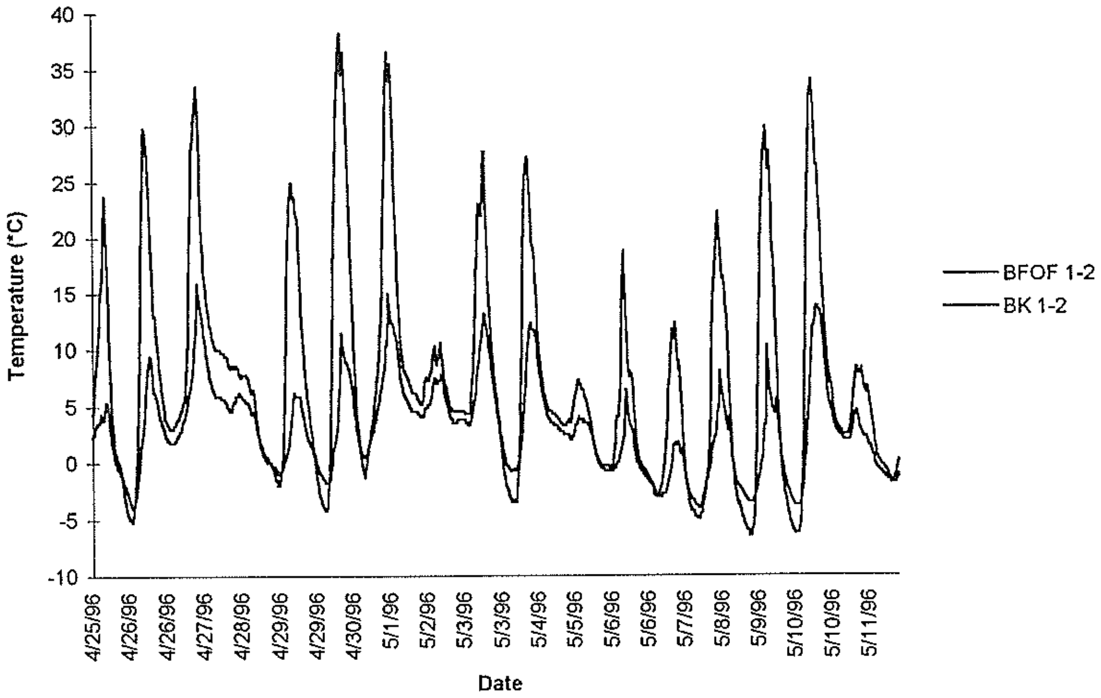

Figure 2. Thermal data for a representative open site (a defoliated blowdown, BK 1-2) and a representative closed canopy site (a senescing balsam fir forest, BFOF 1-2).

At present, the thermal data suggest that thermal energetics may not be an important component of habitat selection for marten. This conclusion, however, depends on two significant caveats: First, the spring and summer of 1996 were significantly milder than normal. Second, the period of study did not include winter conditions when thermal differences among habitats could be greatest in magnitude, and certainly most physiologically significant to marten. The period of study was largely snow-free, so ground-level vegetation may have significantly reduced forced convective losses (wind). Deep mid-winter snow conditions remove these barriers to convective loss. As a result, we cannot yet conclude that the active thermal environment is an insignificant factor in marten habitat selection. We can, however, suggest that thermal conditions are not likely to influence marten habitat selection decisions during the snow-free season.

Dens and Resting Sites

Our habitat model uses resting sites as the first determinant of habitat quality. Landscape quality is appraised by assessing the configuration of foraging sites and traveling corridors around the resting sites. As a consequence, resting site surveys not only provide us with basic information about potential resting site structures, but also provide the basis for testing the spatial relationships implied in the model. Thus, one set of data can be used for both input (specific structures) and testing (spatial relationships at the landscape scale) without risking logical circularity.

Adair employed homing telemetry to locate a natal den (kits prior to weaning) for one female marten (Kathy) and several maternal resting sites (those that sheltered weaned kits) for 2 females (Kathy and Hannah). The total effort yielded 53 resting structures used by 8 females and 6 males (Table 1). While our project contributed to the effort, almost all of the trapping and collaring required for the resting site telemetry was achieved by the Marten Demographics project. All but 2 of the resting sites listed in Table 1 were located by Adair, however this effort was greatly facilitated by the home ranges generated by the Demographics project.

Resting sites were located by using radio telemetry to home in on the animal until the animal's location was confirmed by visual observation. Only marten that had remained within one location for 1 hour or more (assumed to be resting) were investigated. Of these 165 searching efforts, 53 led to marten that were "caught napping." We assume that the remainder were either disturbed upon arrival, and consequently vacated a nearby resting site, or were simply moving slowly (possibly foraging). In the case of the two females with kits (Kathy and Hannah), the adults frequently remained active, but were typically confined to one location throughout the entire day. Resting sites were initially relatively easy to locate (April, May, and into June), as animals tended to rest for extended periods of time during these cooler periods. However, by mid-June, the marten appeared to adopt a "cat-napping" strategy, resting for only very brief periods of time. This unfortunately made detecting resting marten difficult, and consequently comparatively fewer sites were located in late June, July, August, and September. The martens with kits (Kathy and Hannah), who typically remained stationary for most of the day, provide a notable exception.

Once Adair had located a resting site, he marked a nearby structure and left immediately to minimize disturbance. All of the sites were revisited for measurement in late August. Unlike the aerial telemetry methods used by the Demographics project, our locational error is not due to uncertainty about the animal's location, but instead is due to our limited ability to map the site accurately. As a result, we estimate the the locational data for the resting sites will have an accuracy of about 100m.

At each site, the actual resting structure was described and a number of measurements of the surrounding vegetation taken. Most resting sites consisted of enlarged woodpecker or squirrel holes in hard snags or live trees, in which case the diameter at breast height (1.5m, actually Adair's neck height), species, and height of the snag or tree, as well as the height and orientation of the entrance hole, were recorded. Several marten used large witch's brooms, in which case the diameter at breast height, species, and height of the supporting tree, as well as the diameter and height of the witch's broom, were recorded. Two marten used underground cavities formed by talus, two others used squirrel middens; in these cases we were unable to obtain measurements of the actual cavity. Several marten used hollow downed logs; in these cases we recorded the diameter of the log at the cavity, the state of decay, the species, and the height off the ground.

We used several procedures to survey the forest conditions immediately surrounding the resting structure. First we recorded the species, diameter at breast height, height, vigour, and dominance/subdominance of the first 5 trees along a randomly determined 10m radius extending outward from the resting structure. We then recorded the diameter at breast height and the species or decay class for all trees and snags within 10m of the resting structure. We then estimated canopy foliar cover, midstory foliar cover, tall (>1m) shrub/forb cover, low (<1m) shrub/forb cover, ground foliar cover, grasses and sedges cover, mosses cover, bare rock/soil cover, and open water cover, using 1 of 6 ocular estimate categories (0 = 0 %, 1 = 0-5 %, 2 = 6-25 %, 3 = 26-50 %, 4 = 51-75 %, 5 = 76-95 %, 6 = > 95 %). Finally, we estimated the abundance of soft logs on the forest floor, hard, large diameter debris on the ground, hard, small diameter debris on the ground, large woody debris less than 1m high, and large woody debris greater than 1m high, using 4 ocular abundance categories (a = abundant, p = present, t = trace, and 0 = absent).

Two conclusions can be drawn from our resting site survey. First, 1996 was a dismal year for reproduction in the Little Grand Lake marten population: only 2 of 8 females monitored lactated during this year. Unfortunately, Hannah had not been collared during the natal denning period, so we were unable to locate a natal den for her. We did locate a natal den for Kathy, but were unable to ascertain how many kits were born. While Hannah was observed to have weaned two kits (which were later tagged but not collared), no more than one post-weaning kit was seen with Kathy, and this kit was neither tagged nor collared. We tentatively conclude that continued low microtine populations (especially during the previous winter) may be responsible for the dismal natality in the Little Grand Lake population. It is interesting to note that both "successful" females used cutover-forest interfaces extensively, where nesting songbirds are plentiful, but neither left the security of the forest. It is not clear whether these females used these interfaces preferentially, or simply in proportion to their abundance (both female's home ranges skirted around extensive cutovers).

Second, the Little Grand Lake marten population uses resting site structures that are extremely rare on the landscape. After a considerable effort to determine what was "available" we were unable to locate similar structures by random or systematic surveys. The only identifiable resting site structures that we were able to find were the ones that had been used by the marten. Because availability is minimal, these structures may in fact be limiting. However, if these structures were strongly limiting, we would expect to see marten repeatedly using the same structures; this was not observed. It is possible in Newfoundland the potential limitation imposed by resting sites is overshadowed by the immense territory size needed to exploit widely scattered food resources. Nevertheless, it is clear that suitable resting sites are a rare resource in western Newfoundland.

The Little Grand Lake marten population used woody structures provided by trees that are considerably larger than the average (Table 1). Some structures, such as standing hard snags and hard logs, are consistent with observations elsewhere within the marten's range. Little Grand Lake marten, however, appear to use hollow, live birch trees far more frequently than marten elsewhere. This observation may be due to the fact that in western Newfoundland, heavy balsam fir snags fall to the ground within a few years of mortality. As a consequence, even when tree mortality rates are high, the supply of suitably large, sufficiently decayed snags may be low.

Table 1. Den and resting sites located during April-September 1996.

Angela			
24 May 1100	5384150N	434350E	squirrel midden at base of white pine, 46cm DBH, 14.9m tall
2 June 0930	5385825N	431500E	hollow base of leaning paper birch, 30cm diameter at base
4 June 2000	5383162N	435775E	1.5m diameter witch's broom, 7.0m high in 52cm DBH, 17.3m tall balsam fir
20 June 1615	5384125N	437625E	live hollow paper birch, 43cm DBH, 11.1m tall
21 June 1830	5384775N	434350E	live hollow paper birch, 57cm DBH, 11.9m tall
24 July 1300	5384775N	433900E	class C larch snag, 53cm DBH, 7.0m tall
25 July 1230	5384125N	436875E	class C white spruce snag, 26cm DBH, 4.9m tall
Brutus			
9 June 1600	5384500N	429750E	hollow butt of 30cm diameter class C birch log, 1m off ground
Darren			
13 June 1030	5386700N	439600E	class C birch snag 37 cm DBH, 4.7m tall
2 August 1100	5387300N	439200E	1.5m diameter witch's broom 10.5m high in 31 cm DBH, 12.8m tall white spruce
5 September	5386700N	439600E	class C birch snag 37 cm DBH, 4.7m tall

Table 1, continued. Den and resting sites located during April-September 1996.

Ellen			
10 May	5389825N	425325E	underground chamber in overgrown talus
30 May 1530	5389500N	424450E	class D birch snag, 37cm DBH, 3.7m tall
3 June 1200	5389100N	423050E	class D fir snag, 34cm DBH, 5.8m tall
Hannah			
8 July 1100	5386725N	430150E	resting in crux of yellow birch, 70cm DBH, 27.5m tall
9 July 1000	5386925N	429950E	live hollow yellow birch, 74cm DBH, 16.6m tall
12 July 1230	5387250N	429075E	resting in branches of paper birch, 30cm DBH, 10.0m tall
13 July 1100	5385505N	427725E	resting in branches of paper birch, 40cm DBH, 16.6m tall
23 July 1350	5385505N	427725E	resting in branches of balsam fir, 31cm DBH, 13.8m tall
24 July 2000	5386150N	429100E	resting in branches of balsam fir, 35cm DBH, 14.3m tall
25 July 1630	5386225N	428400E	class C white pine snag, 58cm DBH, 7.0m tall
Hugo			
21 May	5389575N	442375E	class C fir snag, 31cm DBH, 5.5m tall
Jane			
17 May	5388850N	436010E	class C fir snag, 31cm DBH, 4.9m tall
25 June 1100	5387300N	438400E	class C fir snag, 27cm DBH, 4.7m tall
Karen			
2 June 1120	5379925N	443525E	underground chamber in talus
3 June 1120	5379600N	443700E	1.5m diameter witch's broom 10.0m high in 20cm DBH, 15m tall black spruce
Kathy			
3 May	5389100N	426825E	class D white spruce snag, 43cm DBH, 5.8m tall
10 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
14 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
17 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
18 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
19 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
20 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
21 May	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
22 May 1400	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
24 May 1800	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
28 May 1600	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
29 May 1555	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
2 June 1450	5389255N	426550E	hollow butt of live paper birch, 54cm DBH, 16.6m tall
3 June 1830	5388350N	423500E	hollow butt of 45cm diameter class C fir log, 0.5m off ground
6 June 1100	5388600N	426000E	class D fir snag, 30cm DBH, 6.2m tall
14 June 1345	5388250N	426050E	hollow butt of live paper birch, 60cm DBH, 15.2m tall
22 June 2000	5388600N	426000E	class D fir snag, 30cm DBH, 6.2m tall

Table 1, continued. Den and resting sites located during April-September 1996.

Margaret			
21 May	5385150N	429775E	class C white pine snag, 60 cm DBH, 3.5m tall
22 May 1200	5384575N	432400E	class D fir snag 27cm DBH, 6.0m tall
30 May 1000	5384600N	432675E	class D fir snag 35cm DBH, 4.2m tall
4 June 1700	5385050N	432800E	live hollow paper birch 63cm DBH, 21.4m tall
9 June 1655	5384150N	431200E	hollow butt of 40 cm diameter class D fir log, on ground
12 June 1300	5385100N	430075E	live hollow yellow birch, 52cm DBH, 11.5m tall, leaning at 49° angle
14 June 1030	5384995N	432900E	class C fir snag, 26cm DBH, 8.4m tall
15 June 1730	5385050N	432800E	live hollow paper birch 63cm DBH, 21.4m tall
Pat			
21 June 1100	5388600N	422525E	hollow butt of 45 cm diameter class D birch log, on ground
Raymond			
22 June 1000	5385025N	437075E	hollow 44cm diameter class C fir log, 0.5m off ground
26 July 0900	5383675N	435725E	squirrel midden at base of white pine, 71cm DBH, 17.3m tall
Rebeccah			
22 April	5386600N	440925E	class C larch snag, 38 cm DBH, 6.7m tall
23 April	5387725N	440900E	class C larch snag, 61 cm DBH, 7.8m tall
24 April	5385300N	440875E	hollow butt of live 26 cm DBH paper birch (nursery tree)
5 May	5386300N	442125E	hollow butt of 35cm diameter class D white spruce log, 1m off ground
16 May	5384650N	440875E	class D fir snag, 25 cm DBH, 6m tall
18 May	5387600N	440650E	class D fir snag 26 cm DBH, 3.5m tall
2 June 1130	5387450N	441300E	class C fir snag, 31 cm DBH, 6m tall
5 June 0900	5385300N	441775E	hollow butt of 35 cm diameter class D fir log, on ground
20 June 1400	5385125N	439600E	class C fir snag, 30cm DBH, 4.9m tall
Taz			
9 June 1000	5384150N	438300E	class C birch snag, 31 cm dbh, 4.7m tall
25 June 1430	5386400N	442100E	class D white spruce snag, 35cm DBH, 3.4m tall

Small Mammal Microhabitat

We developed a simple biometric approach for evaluating small mammal habitat preferences. During 1994 and 1995 we live-trapped each grid once in the early summer and then once again in the early fall. During 1996 we live-trapped these same grids, as well as 12 new grids, for one session in May, June, July, and August. Our basic approach depends on a reasonable level of trapping success: we generate our habitat relationships by correlating the microhabitat variables measured at each trap site with the number and composition of animals caught there. Landscapes (forest stands for a mouse) are then examined for their ability to provide favorable microhabitats.

We established live-trapping grids in the 6 major macrohabitat types described for the thermal environment study. For sites that we felt were unlikely to support abundant small mammal populations (senescing balsam fir, old black spruce, ZICM balsam fir, and bog sites) we located 3 stands for each type and placed 2 permanent grids within each stand. For sites that we felt were likely to support abundant small mammal populations (regenerating clearcuts and defoliated blowdowns) we located 6 stands for each type and placed 2 permanent grids within each stand. This stratified scheme results in a total of 48 grids (1200 trap sites). Trapping grids consisted of 25 trapping stations in a 5 x 5 configuration with trap sites 12.5 m apart. Two non-collapsible Sherman live traps, wrapped in a plastic bag, stuffed with polyester filling, and baited with 1 mL of peanut butter encapsulated in wax paper, were set at each station. Traps were checked twice per day and rebaited when necessary. Each grid was surveyed for one 5-night period in late-April-May, June, July, and August. The 5-night periods were timed to coincide with favorable weather events (dry, cloudy nights). The total effort amounts to 48,000 trap-nights for the 1996 season (a total of 72,000 trap nights for the project to date).

Small mammal distribution patterns were similar to those observed during the 1995 season (Table 2). Trapping success for all species was dismally low for the first two months, but rose sharply when juvenile animals entered the population in August. The August increase in masked shrews (*Sorex cinereus*) was less dramatic than in 1995, when many of the study sites were infested with hemlock loopers (*Choristoneura fumiferana fumiferana*). Similarly, while masked shrews were abundant in senescing and ZICM balsam fir forests in 1995 (during the infestation), they were largely absent from these same forests in 1996, when hemlock looper populations were comparatively low. Continued abundant populations in defoliated stands and cutovers suggests that trapping mortality may not be affecting shrew populations.

Larger prey items more consequential to the marten, including meadow voles (*Microtus pennsylvanicus terranovae*), deer mice (*Peromyscus maniculatus*), red squirrels (*Tamiasciurus hudsonicus*), and eastern chipmunks (*Tamias striatus*) are found most readily in open habitats with abundant woody debris (defoliated blowdowns and some cutovers). These prey types appear to be very patchily distributed. The continued low densities of meadow voles over the last 3 years suggest that a population irruption may be likely in 1997. The data collected to date is of insufficient quantity to make any statistically sound generalizations about habitat preferences for western Newfoundland's small mammals.

We continued collecting the vegetation structure data needed for the small-mammal microhabitat analysis during May, June, and August. We collected data on cover density, ocular coverage estimates, woody debris estimates, and flora species composition at the 300 trap sites added this year. We collected forest inventory-type data for the 650 trap sites not addressed during the 1995 season.

To measure the density of security cover, we laid 4 perpendicular 5m transects radiating outward from each trap station, with the orientation of the first radius determined randomly. A leather mouse cat toy ("Elvis the Blue Suede Mouse") was lowered to the ground at 1m, 2m, and 5m distances along each radius. The observer noted whether the mouse was visible or not.

Table 2. A simplified summary of small mammal trapping results for the 1996 season.

	April-May	June	July	August-September
Senescing balsam fir forest	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**
Masked shrews	0	0	0	5/5
Meadow voles	0	0	0	0
Deer mice	0	0	0	0
Eastern chipmunks	0	0	0	0
Red squirrels	0	0	0	0

	April-May	June	July	August
Black spruce old forest	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**
Masked shrews	0	0	0	8/8
Meadow voles	0	0	0	0
Deer mice	0	0	0	0
Eastern chipmunks	0	0	0	0
Red squirrels	0	0	0	0

	April-May	June	July	August
ZICM balsam fir forest	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**
Masked shrews	0	0	0	3/3
Meadow voles	0	0	0	0
Deer mice	0	0	0	0
Eastern chipmunks	0	0	0	0
Red squirrels	1/1	0	1/1	2/2

	April-May	June	July	August
Defoliated balsam fir	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**
Masked shrews	3/3	1/1	2/2	68/68
Meadow voles	0	0	0	6/5
Deer mice	0	3/3	2/2	14/9
Eastern chipmunks	0	1/1	0	0
Red squirrels	0	3/3	2/2	7/4

	April-May	June	July	August
Regenerating cutover	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**
Masked shrews	5/5	3/3	2/2	46/46
Meadow voles	0	3/3	0	1/1
Deer mice	0	0	0	1/1
Eastern chipmunks	0	0	0	1/1
Red squirrels	0	0	0	1/1

	April-May	June	July	August
Bogs	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**	**Capt/Ind**
Masked shrews	0	0	0	1/1
Meadow voles	0	0	0	0
Deer mice	0	0	0	0
Eastern chipmunks	0	0	0	0
Red squirrels	0	0	0	0

We used 6 percent coverage categories (0 = 0 %, 1 = 0-5 %, 2 = 6-25 %, 3 = 26-50 %, 4 = 51-75 %, 5 = 76-95 %, 6 = > 95 %) to provide visual estimate for 10 structural features within a 10m radius circle centered on trap station: canopy foliar coverage, midstory foliar coverage, tall (>1m) shrub/forb coverage, low (<1m) shrub/forb coverage, ground cover foliage, grasses and sedges, mosses, bare rock/soil, and open water.

We used 4 abundance categories (A = abundant, P = present, T = trace, and 0 = absent) to provide visual estimates for 5 structural features within a 5m radius circle centered on each trap station: soft logs on the forest floor, hard, large diameter debris on the ground, hard, small diameter debris on the ground, large woody debris less than 1m high, and large woody debris greater than 1m high.

Species composition was estimated using the 6 percent coverage categories described above. Five structural categories were used to examine species composition around the trap station:

Canopy trees (5m radius)
Midstory trees > 3m tall (5m radius)
Tall shrubs and regeneration, 1-3 m tall (5m radius)
Low shrubs, forbs, ferns, grasses, and sedges < 1m tall (2m radius)
Mosses, lycopodia, and lichens (2m radius)

Species composition data will be used to generate Damman Forest Ecosystem Classification labels for each trap site, and to develop an independent fuzzy-set Damman-based site classification system.

We collected tree species, size, health, and age information for 650 of the 900 trap stations. At each trap station, we laid one 5m transect radiating outward from the trap station in a randomly determined direction. The 2 trees (> 5 cm dbh) nearest to the radius on the counterclockwise side and within 5m of the trap station were aged with an increment borer. We determined the species, diameter at breast height (cm), height (m, measured with a clinometer), vigour, and dominance for the five trees nearest to the radius on the counterclockwise side and within 5m of the trap station (including the two trees used for aging). 'Vigour' was measured as the percent of the tree bole that supported foliage, classified according to the 6 ocular estimate categories described above. Dominance categories included "dominant" for trees that were part of the main canopy, "subdominant" for understory trees, and "super" for super-canopy trees. Finally, we counted the total number of dominant trees, subdominant trees, and snags within 5m of the trap station. Snags were further classified as recently dead (A); dead, hard, and with branches (B); dead, hard, and without branches (C); and soft (D).

The end product of our small mammal microhabitat and marten resting site surveys is a comprehensive and exacting vegetation database encompassing 1253 sites and at least 300,000 data points.

Future Directions

The 1997-98 year will be devoted to enhancing model performance. Three primary approaches will be employed: 1) assessing model performance via sensitivity analysis and application to real and simulated landscapes, 2) enhancing the accuracy of the model's input data, and 3) comparing model predictions with real marten data. All three of these approaches will be needed to create a model that accurately imitates marten habitat selection, and consequently, produces reliable information for decision-making. The first and third underscore the critical need for accurate input and testing data, which is the principal concern of our current Model Forest Proposal for the 1997-1998 fiscal year.

Sensitivity analysis, the most common approach to evaluating model performance, is accomplished by adjusting model parameters and examining the resulting output. Sensitivity analysis can be used to assess how the model processes data. For our marten habitat suitability model, we will need to examine how the model performs when we vary parameters like the availability of resting sites, access to prey, or thermal conditions in different habitat types. Finally, we will need to use sensitivity analysis to assess how the model reacts to resource fragmentation in real and simulated landscapes.

While sensitivity analysis will provide insight into how the model works, it will not tell us whether the model's predictions are correct. Making a truly predictive model absolutely depends on accurate input data. Three kinds of input data need to be improved by further field study: 1) marten resting site structures, 2) thermal energetic environment, and 3) small mammal prey distribution data.

Resting site selection

During 1996 we were able to investigate resting site selection, but because few study animals reproduced, we were unable to examine natal and maternal den site selection at the level needed by the model. Because females with kits must be able to obtain food rapidly and efficiently while confined to a single den site, we believe that these dens represent the most limiting aspect of marten habitat selection. Because den site location affects kit growth and survival directly, we suspect that this element of habitat selection contributes disproportionately to population fitness. Because the winter and spring of 1996 were mild relative to other years, we suspect that we may have seen marten use a wider range of structures than they ordinarily would during more normal years, when thermal environments are more critical. Continued study during 1997 could provide insight into whether this aspect of habitat selection is limiting during more typical weather conditions, as well as whether marten in Newfoundland select the same resting sites year after year.

At the current time, our list of resting site locations is probably suitable for creating a reasonable input database for the habitat model. However, the list in Table 1 is insufficient for an adequate test of the model.

Thermal environment

Because marten are not well insulated, we suspect that thermal environment plays an important role in habitat selection. Our operative temperature approach to thermal dynamics provided excellent data for 1996, a warmer than average year. We suspect, however, that limiting conditions will be more evident during a "normal" year, and that marten habitat selection could be more restricted. Continued study during 1997 should provide better data for assessing the relative contribution of thermodynamics to marten habitat selection.

At the current time, our thermal database is probably suitable for creating a reasonable input database for the habitat model. Our thermal database is not, however, currently sufficient for testing hypotheses about the role of the thermal environment in marten habitat selection during the reproductive season.

Small mammal prey base

Our work during the last 3 years has indicated a consistently low meadow vole populations. While marten are generalist predators capable of exploiting a wide assortment of prey, the food items generally considered to be most important have been either temporally unavailable (snowshoe hares, *Lepus americanus*, may cycle with a relatively long periodicity), abundant only seasonally (songbirds, eggs, insects and berries), or absent from the island (most notably, red-backed voles, *Clethrionomys gapperi*). Not surprisingly, data gathered by the Marten Demographics (Baseline) Project (and this project as well) suggest that Newfoundland marten are generally unable to reproduce successfully when meadow voles are rare. Consequently, meadow vole populations may be in fact be the overriding determinant of marten productivity. Meadow vole populations at this latitude generally cycle in abundance every 3-4 years (Krebs and Myers 1974), suggesting that the year 1997 should bring with it the next cycle high, and possibly the first significant reproductive effort in the marten population since 1993.

Unlike previous studies (Bissonette *et al.* 1988, Thompson and Curran 1995, Sturtevant 1996), we have been able to demonstrate that stands defoliated by insects retain meadow voles (marten prey) even during low years. However, retaining standing dead trees is not an economically optimal policy. Fortunately, our meadow vole studies have been based on microhabitat selection, providing insights into the structures that could be created (through harvest management) to attract meadow voles, and consequently enhance the martens' prey base. Because our approach focuses on microhabitat distribution, we can use our data to directly predict the implications of a red-backed vole introduction in terms of effects on existing meadow vole populations and on the marten prey base.

Unfortunately, extremely low capture rates to date hamper our ability to make broad generalizations about small mammal distribution. As a result, we have not yet been able to obtain sufficiently reliable input data for the habitat assessment model. We believe that 1997 will provide capture rates several orders of magnitude higher than in years past, resulting in a strong data set. Once we have obtained that data set, we should be able to make strong inferences about the specific structures that attract small mammal prey, and how these can be manipulated by management. Because small mammals (especially meadow voles) are the primary prey for most of Newfoundland's mammalian and avian predators, understanding their ecology has profound implications for managing biodiversity.

The success of the model depends on a strong input dataset, which in turn depends on our ability to census small mammals. Censusing small mammals is both the most time- and labor-intensive aspect of the project, and the most critical source of input data for the model. To date we have (apparently) conducted the most intensive small mammal survey, and possibly the most intensive wildlife habitat vegetation survey, yet undertaken in the Province of Newfoundland. If we are unable to survey small mammals during the 1997 season, all of this cost and effort will be for nought.

Model Testing

We intend to test the model's predictive power using home range data collected by the Demographics Project. However, testing a predictive habitat selection model with empirically created data means that we must consider territoriality, a population-level phenomena. In order to refine model output, and to facilitate testing, we will need to develop an algorithm that addresses intrasexual territoriality through a range of prey and population densities. Because no such algorithm yet exists, we expect that this development may consume several months' time.

Data Analysis

Finally, all of the field data previously collected, along with field data collected during the 1997 season, will need to be analyzed. At present this represents over 1,000,000 data points. The magnitude of the database means that processing will require a mainframe computer and a considerable amount of interpretation. The small mammal microhabitat data in particular will provide several ancillary benefits, including an independent test of the Damman Site Classification System, input data for a new classification system based on fuzzy set theory, and an independent test of the stand density management diagrams developed by Sturtevant (1996). In total, we estimate that data analysis will take approximately 1 full year.

Year 5 Project Goals

As in the past, our project has three main components, each with its own set of objectives for the year. Our ability to accomplish these goals depends on an adequate funding level for the 1997-98 fiscal year.

Winter/Spring

1) We will employ homing telemetry techniques to locate marten resting sites, natal dens, and maternal dens. We will cooperate fully with ongoing work being conducted by the Marten Demographics project conducted by the Model Forest, Natural Resources Canada, and the Wildlife Division.

Summer/Fall

1) We will continue live-trapping for small mammals on our fixed grids from mid-June through early September. This trapping will result in the most comprehensive habitat association and demographic information yet collected for Newfoundland's forest small mammals.

2) We will continue habitat structure (vegetation) measurements for resting and den sites located during the winter and spring. Maternal den sites will be continually monitored throughout the summer.

Year-round

1) Throughout the year we will continue to develop and refine the computer application of the individual-based habitat model through the testing procedures described above.
2) Throughout the field year (mid-March through early September) we will continue monitoring the thermal environment using our operative temperature apparatus.

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