Using Wildlife-Habitat Models to Estimate Hoary Marmot (*Marmota caligata*) Abundances at Regional Scales

By

William L. Harrower

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Abstract:

The Ministry of Environment initiated the Northern Wolverine Project in 1996 to document the distribution and abundance of wolverine (*Gulo gulo*) in northern British Columbia. This project identified the hoary marmot (*Marmota caligata*) as an important food source for adult female wolverine during lactation and weaning. In 1999 and 2001, I surveyed of the distribution and abundance of hoary marmots in the Northern Wolverine Project study area to develop a wildlife-habitat model that would estimate the relative abundance of marmots.

I counted marmots and marmot burrows and correlated these counts with landscape attributes. I used these correlations to develop hypotheses that describe the relationships among habitat variables and marmot density. I used univariate correlations among habitat variables and marmot density, a multivariate statistical model, and published reports on marmot ecology to develop my hypotheses. I expressed my hypotheses in the form of habitat suitability index (HSI) models that describe the relationship among habitat variables and marmot carrying capacity.

I have developed methods to describe the relationship between habitat and abundance and provide suggestions for the refinement, verification, and validation of the HSI models. Although the relationship between environmental variables and marmot density was weak, I was able to qualitatively describe a relationship between marmot densities and environmental variables to aid further model development. I suggest that a more refined identification of environmental variables at a smaller spatial scale may yield a stronger relationship between marmot density and their habitat.

TABLE OF CONTENTS:

LIST OF FIGURES:

LIST OF TABLES:

Acknowledgments:

The efforts of a number of people over the preceding years have been instrumental in the completion of this project. First and foremost, Eric Lofroth of the BC Ministry of Water, Air, and Land Protection, Wildlife Branch has provided time, money and expertise in all aspects of study design and analysis. Charlie Krebs of the University of British Columbia, Zoology Department has provided valuable input in the development of methodologies and analysis techniques and provide a number of manuscript reviews, and Dr. Don Reid of the Ministry of Environment, Lands and Parks first envisioned the sampling protocols. Dr. Scott Harrison of the University of British Columbia, Faculty of Forestry has provided many reviews of this manuscript and has provided a valuable sounding board for my ideas. Kristin Karr of the Ministry of Water, Air, and Land Protection provide her extensive GIS expertise in both mapping and data analysis. Many more people have provided support and ideas along the way. These people include: Laura Darling, Leah Ramsay, Debbie Wellwood, Christina Kereki, Tim Enis, Maria Leung, Dr. Kyle Young, Dr. Tim Karrels, and Scott McNay. Thank you all!

1.0 Introduction:

1.1 Project Background:

The British Columbia Ministry of Environment Lands and Parks initiated the Northern Wolverine Project in 1996 to document the distribution and abundance of wolverine (*Gulo gulo*) in central British Columbia. These data were sought to improve the ecological knowledge about the wolverine and assist managers in developing land-use options that conserve wolverine. The Ministry chose wolverine because it is a species that may be susceptible to changes in land-use practices (Lofroth 2001).

The wolverine is a wide-ranging, low-density species that exhibits a circumpolar distribution. In British Columbia wolverine occur at higher elevations of the boreal forest and mountain regions. Wolverine have an affinity for high elevations and a tendency for vertical seasonal migrations (Banci 1994, Lofroth 2001). Wolverine habitat is probably best defined by adequate year-round food supplies rather than by topography or plant associations. Female wolverine den at high elevation and have 1 to 5 kits (Banci 1994, Lofroth 2001). Kits are born in spring and grow to adult size by the end of summer. Natal dispersal occurs in the fall of the year of birth. The rapid growth of kits places high energetic demands on maternal females during lactation and weaning. Food habit analyses indicate that female wolverine diets during early spring and summer consist primarily of woodland caribou (*Rangifer tarandus*) and hoary marmots (*Marmota caligata*) (Lofroth 2001). Thus, the distribution and abundance of hoary marmots was identified as a key factor that might determine wolverine reproductive success.

Given the importance of hoary marmots as food for adult female wolverine, I initiated a study to estimate the distribution and abundance of hoary marmots in the alpine regions of the Northern Wolverine Project study area (Figure 1). A comparison of the regions required the development of methods to estimate the relative abundance of marmots across large areas. I accomplished the estimation of marmot densities through the development of a series of wildlife-habitat models. Habitat models will enable researchers to estimate an area's carrying capacity for hoary marmot. Since the distribution of female wolverine varies among the mountain regions in the Northern Wolverine Project study area, this prey model will provide insights into female wolverine distribution, abundance, and reproductive success.

1.2 Natural History:

Hoary marmots inhabit mountainous areas of western North America. In British Columbia, hoary marmots are active between April and September, hibernating in high elevation burrows for the rest of the year. Considerable variation exists in the dates of hibernation and emergence (Barash 1989). These dates are governed by local and annual variations that affect the emergence and cessation of food plants (Barash 1989). Marmots are social animals, and may be monogamous, or polygamous. Colonies consist of an adult male, his harem of females, young of the year, yearlings, and dispersing 2-year old animals (Barash 1989). Satellite males and transient animals may also be encountered surrounding more permanent colony towns.

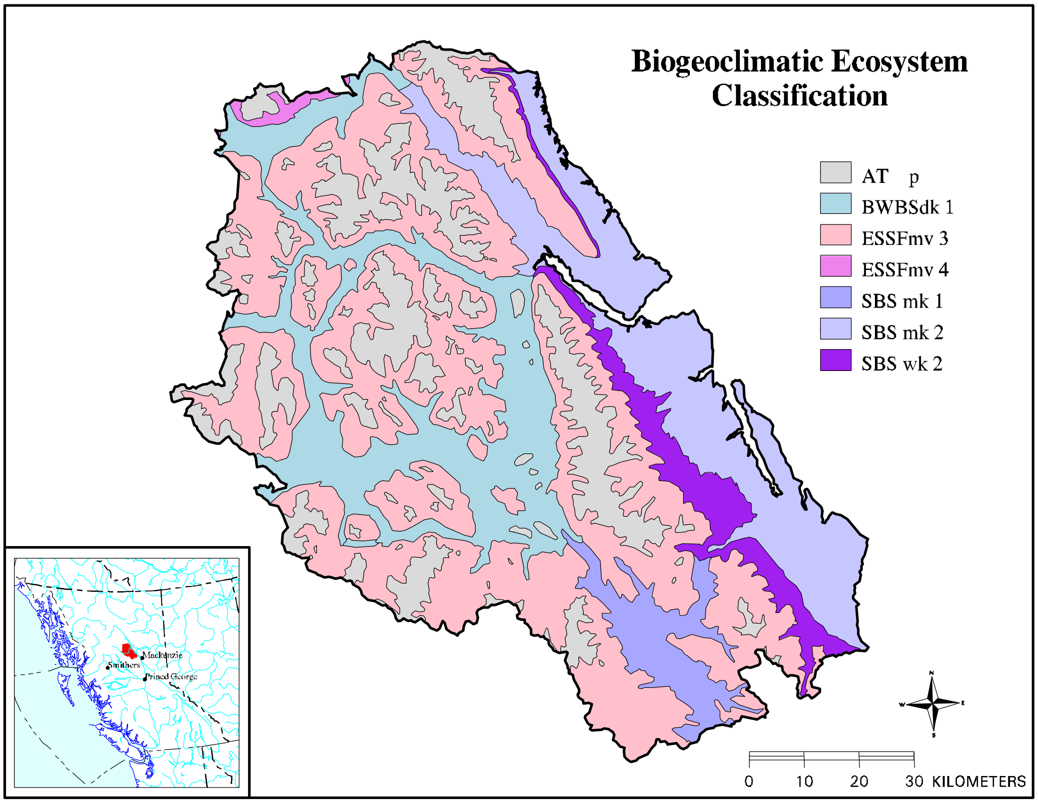

Figure 1: Biogeoclimatic subzones of the Northern Wolverine Project Area. Alpine areas are highlighted in grey. Biogeoclimatic zones occurring in the study area are: Alpine Parkland (AT p), Boreal White and Black Spruce (BWBS), Engelmann Spruce-Subalpine Fir (ESSF), and Sub boreal Spruce (SBS). Pojar (1991) provides descriptions of subzone and variant abbreviations.

The primary foods of hoary marmots are herbaceous vegetation and grasses. Feeding sign and burrows can generally be found in most high alpine bowls and meadows where these plants occur (Barash 1989). In my study area, marmots begin the season feeding in snow free patches of grass on warm, south facing slopes. As the snow continues to melt and herbaceous forbs emerge, the marmots move to lower elevations feeding in the lush alpine meadows of lower alpine bowls.

Marmots have low metabolic rates and limited thermoregulatory abilities (Barash 1989). Their daily activity patterns are governed by these temperature regulation requirements. A bimodal activity pattern has been described during mid-summer and good weather conditions (Barash 1989). This bimodal pattern consists of periods of basking and feeding activities in early morning and late afternoon. During inclement weather, early spring, and late fall, daily activity patterns switch to a unimodal pattern with the highest activities observed during mid-day (Barash 1989). In this way, marmots avoid large-scale body temperature fluctuations with limited energy expenditure.

1.3 Wildlife-habitat Models:

Morrison (1998) describes a number of habitat models and their specific application. For my study, 2 types of models were applicable: multivariate statistical models and habitat suitability index (HSI) models. Multivariate statistical models can be used to describe differences in the abundance and distribution of organisms as a function of habitat availability. Multivariate statistical techniques relate the response of a species, measured as fitness, to environmental variables. Different environmental variables meet different life history requirements. The collection of environmental variables, that meet all of the life history requirements of an organism, describe the habitat requirements of that organism. Combining variables into a single equation enables the prediction of relative abundance of an organism, or the examination of the influence of environmental variables on fitness. Multivariate statistical models are important tools in understanding the distribution of species and the relationships among species and their environment (Morrison 1998).

HSI models are a tool commonly used by wildlife managers. These models correlate an assessment of the physical and biological attributes of a landscape with the density of organisms, in an attempt to estimate the carrying capacity of a particular area. The attributes of the landscape are assumed to be proportional to the carrying capacity of an area for a particular animal (USFW 1981). Habitat, defined as the collection of environmental variables that are able to meet the life history requirements of an organism, is used to estimate the carrying capacity of an area for a particular organism. To develop an HSI model, a series of variables are identified and each is given a measure of suitability based on its influence on fitness (Van Horne 1983, Burgman 2001). The relation of each environmental variable to a measure of ecological fitness is scaled to between 0 and 1 and combined, generally through the use of their geometric mean, into an overall index of habitat suitability. In this way, the relative suitability of individual areas can be compared. A number of authors have identified concerns regarding HSI model development and assessment (Schamberger 1986, Stauffer 1986, Breininger 1995, 1998, Roloff 1999). Methods have also been developed to assess the variability in HSI models (Burgman 2001).

Measures of an organism's density or biomass have been widely used as surrogates to measurements of ecological fitness (Van Horne 1983, Burgman 2001). If density or biomass is to be used to assess the relationship between an organism and environmental variables, 2 assumptions must hold (Schamberger 1986). First, we assume that the measured density of organisms will be higher in high quality habitats. High quality habitats are areas with structural, climatic, or biological attributes that allow an organism to experience increased fitness (Van Horne 1983, Breininger 1995, 1998, Burgman 2001). However, if we define high quality habitat as those habitats with a higher density of organisms, the assumption becomes circular. Therefore, researchers must clearly identify that high quality habitats are those that increase the fitness of the organism, and that density is only used as an indicator of fitness. High density may not always correlate with increased fitness.

The second assumption is that animals are located in higher quality habitat more often. This assumption requires that density relate directly to the abundance of particular environmental variables (Van Horne 1983). It may not. Multi-annual variation in population densities, intra- and inter-specific competition, and predation pressures may result in the disproportionate use of poor habitat types. The scale, type and timing of density measurements must suit the particular ecology of the organism of interest. Therefore, density may not adequately reflect the impact each environmental variable has on fitness.

Models must also reflect the impact of each environmental variable. For example, in the absence of information on specific habitat requirements, the geometric mean is used to model the response of a species to environmental variables in HSI models. This method assumes that each variable has a similar effect on fitness and, therefore, contributes equally to the distribution of organisms. However, a single environmental variable may be limiting. The geometric mean does provide some disproportionate weighting to variables of low values. Although organisms may not be consistently located in habitats containing the limiting variable, the limiting variable may have a substantial impact on fitness (Van Horne 1983). Models must reflect the impact of each variable, and the geometric mean may be one way to do this.

All models are simplistic representations of complex systems and, as such, their predictive ability may be lost in simplification (Schamberger 1986). Wildlife-habitat models only provide estimates of the potential carrying capacity of an area and are not direct estimates of abundance. As described above, estimates of carrying capacity may be erroneous if density is not a function of habitat quality, is not measured accurately, or if the model does not take into account all limiting factors related to habitat selection (Van Horne 1983, Schamberger 1986, Bender 1996, Roloff 1999). Although many such models have been developed, few have been adequately verified or validated (Schamberger 1986, Bender 1996, Brooks 1997, Roloff 1999). Model verification requires that the relationships between fitness and environmental variables, hypothesised by the model, are correct and have been developed using quantitative descriptions. Model validation involves the application of the model to single or multiple areas and the independent verification of results. Thus, proper model development and testing are essential in determining the effectiveness of the model.

The scale at which a model is developed and applied and the particular censusing technique used will govern the effectiveness of the model (Van Horne 1983). Models are generally developed using data obtained at small spatial scales and then applied to the availability of variables across the landscape. If the influence of animal movements and home range size are not incorporated into the choice of censusing techniques, the accessibility of environmental variables may not be accounted for at larger scales (Van Horne 1983).

2.0 Objectives:

The overall objective of my study was to provide the information necessary to assess the relationship between the abundance of hoary marmots and the selection of home ranges by adult female wolverine. I developed 2 types of wildlife-habitat models that enabled the estimation of the relative abundance of hoary marmots at landscape levels. This required the development of a habitat classification system that would incorporate a series of environmental variables into predefined habitat classes. I measured the relative density of hoary marmots using 2 methods, direct counts and burrow transects, and related the relative density of marmots to the occurrence of habitat variables.

Construction of my wildlife-habitat models required 3 assumptions concerning habitat use by hoary marmot: the proportional use of each habitat reflects the ecological importance to hoary marmots of each habitat; the burrows of hoary marmots occur in habitats in proportion to the importance of that habitat in meeting marmot life history requirements, and the relative proportion of each habitat in an area represents the abundance of hoary marmots.

3.0 Methods

3.1 Study Area

The Northern Wolverine Project study area is an 8,900-km^2 area on the west side of Williston Reservoir in the Manson, Omineca, Osilinka, and Mesilinka river drainages in northern British Columbia. Four biogeoclimatic zones and 7 subzones are represented in the study area (Figure 1). The study area has considerable logging activity, a large network of logging roads, a power transmission corridor, a hydroelectric reservoir, and sixteen registered traplines. The Omineca Mountains comprise the largest extent of alpine in the area. Since marmots generally occur in alpine habitats, the Omineca Mountains are the only area that I studied. The Omineca Mountains are composed of independent mountain ranges each with unique topographical features. I examined 3 of these ranges: the northern Swannel range, southern Swannel range, and northern Wolverine range (Figure 2).

3.2 Habitat Classification:

The description of the distribution of marmots over the entire study area depends largely on a habitat classification scheme and on estimates of marmot use of each habitat type. For initial surveys, Reid (1999) developed a basic habitat classification scheme based on the

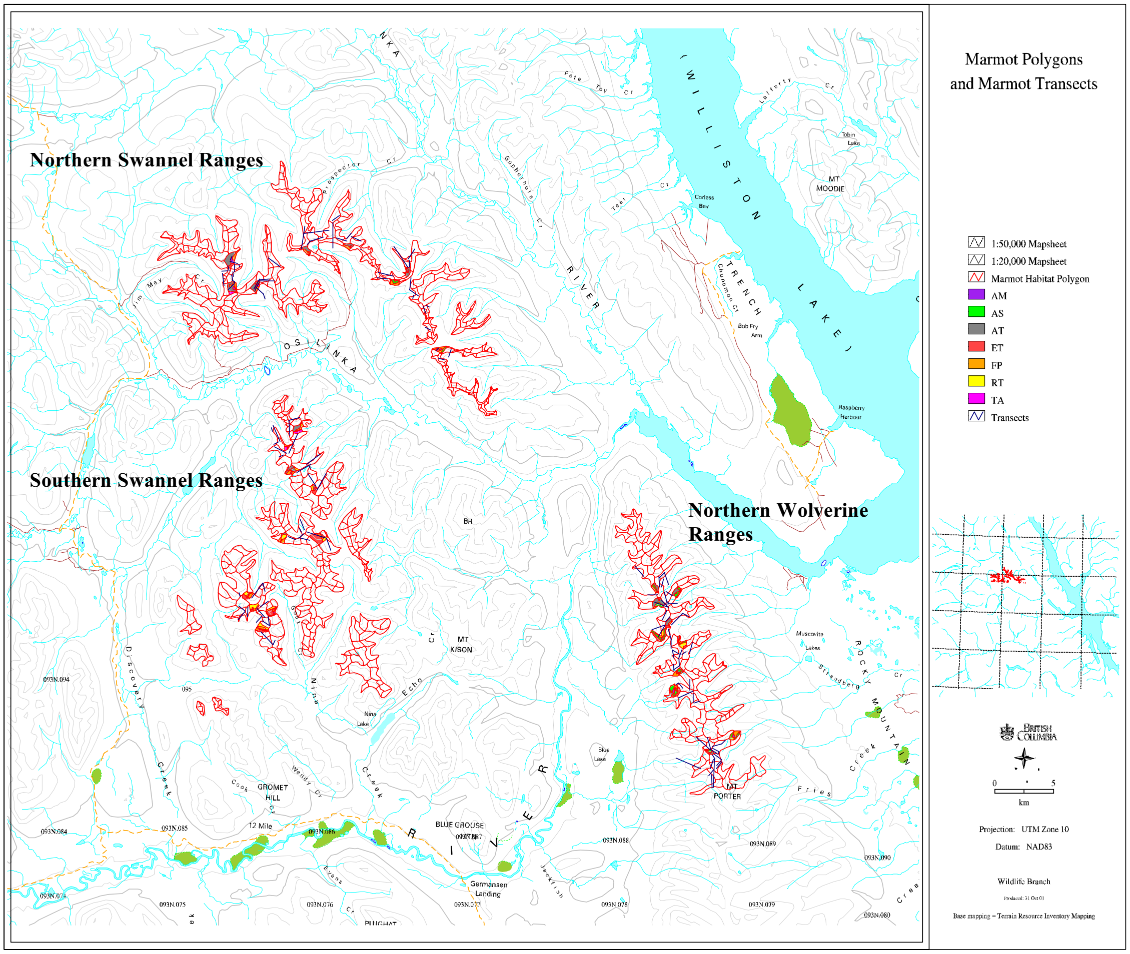

Figure 2: Northern Wolverine Project study area showing location of 3 mountain ranges sampled for hoary marmot. All polygon boundaries are outlined, sampled polygons are shaded, and transects delineated. Table 1 provides a definition of habitat unit abbreviations.

Broad Ecosystem Classification System (BEU) for British Columbia (P. o. British Columbia 1998). My modified classification scheme identifies 5 broad vegetation classes (Table 1).

Table 1: Vegetation Classification Descriptions for alpine regions of the Omineca Mountains of Northern British Columbia.

Habitat Class	**Description**	**Major Components**
Alpine Meadow (AM)	moist sites with predominately herbaceous growth	> 30% cover of *Aconitum delphinifolium, Valeriana sitchensis, Lupinus arcticus, Caltha leptosepala, Veratrum viride, Arnica cordifolia, Anemone parviflora,*and *Ranunculus eschscholtzi*
Alpine Shrub (AS)	extensive patches with greater than 50% cover of scrub birch or willow	>50% of *Betula glandulosa, Salix barrattiana* or scattered cover of *Abies lasiocarpa*
Alpine Tundra (AT)	drier sites with greater than 30% cover, of rosette or sessile forbs or sedges and grasses	> 30% cover of *Cassiope tetragonal, C. stellariana, C. mertensiana, Phyllodoce empetriformis, Empetrum nigrum* or *Poacea sp*.
Fir Parkland (FP)	areas below tree line where patches of alpine vegetation are less than 30 m in longest linear extent and are interspersed with areas with extensive tree cover	>30% cover of *Abies lasiocarpa* generally interspersed with Alpine Tundra or Talus
Talus (TA)	area where unvegetated talus extends greater than 30 m in longest linear extent	Unconsolidated rock interspersed with Alpine Tundra, Alpine Shrub or Fir Parkland where the percent cover of talus exceeds 30% of the total area

The role of aspect and slope on marmot habitat choice has been identified as important (Van Vuren 1991, Allaine 1994, Bryant 1996, Reid 1999). Therefore, I collected information on broad classes of slope and aspect. Reid (1999) identified 4 slope classes and 4 aspect classes (Tables 2 and 3). He divided the 4 aspect classes into 3 sub-classes that reflected the temperature regimes and snow melt times for each aspect.

Table 2: Slope Class Descriptions for alpine regions of the Omineca Mountains of Northern British Columbia.

Slope Class	Description
Class 1	0-20 degrees
Class 2	21-40 degrees
Class 3	41-60 degrees
Class 4	>60 degrees

Table 3: Aspect Class Descriptions for alpine regions of the Omineca Mountains of Northern British Columbia.

Aspect Class	Temperature Class	Description
North	Cool	292-67.5 degrees
South	Warm	112.5-247.5 degrees
East	Neutral	67.5-112.5 degrees
West	Neutral	247.5-292.5 degrees

Using these criteria, I defined habitat units and estimated marmot abundance in each individual unit. Undoubtedly, the occurrence of marmots in a specific habitat type is governed by many factors and marmot abundance will depend on the combination of habitat classes that occur on a site.

3.3 Direct Observations:

I observed polygons to determine the minimum number of marmots occupying these sites. I determined the proportion of slope, aspect, and vegetation classes in each polygon. I used these data to develop a series of equations that described the relation between abundance and habitat in each polygon. These equations describe how the estimate of marmot abundance is related to the habitat present in individual polygons. I used multiple regression techniques to combine the information from all polygons into a single equation representative of the entire study area. This simplified representation of how marmot abundance relates to habitat types was used to predict the estimated carrying capacity of marmots. I used the Log (y+1) transformation and Arcsin(Sqrt(x)) transformations and confirmed normality using Shapiro Wilk and D'Agostino Omnibus tests for both habitat and density data (Hintze 2001). I also checked for heteroscedasticity in the data using residual vs. predictor plots and confirmed the lack of multicollinearity using variance inflation factor, and eigenvalue correlations (Hintze 2001).

Polygons consist of contiguous alpine areas that are observable in their entirety from a single vantage point. Polygons are generally comprised of a single alpine bowl or drainage that will support 1 or 2 marmot colonies. I identified polygons prior to sampling on 1:50000 National Topographic Service (NTS) maps based on specific contour orientations and checked boundaries and defined habitats using 1:20000 orthographic photos. All polygon and vegetation class boundaries were digitised into a Geographic Information System (GIS) following delineation on 1:40000 aerial photographs. Additionally, slope and aspect data for each 25-m^2 portion of the study area were analysed using GIS, which classified data into the defined slope and aspect classes to determine the proportional representation of each type of habitat.

I observed individual polygons for 3-hour periods on relatively warm, clear days because this was the period of highest marmot activity and therefore highest sightability. Single, 3- to 4-hour observation periods were performed at mid-day on overcast and cool days.

Ideally, 3 discreet observation periods were performed at each polygon. Observations occurred over no more than 1 week with most observations occurring over a 3-day period. These methods provided approximately 9 hours of observation at each site. If inclement weather persisted through the sampling period, observations were made during mid-day to maximize the number of marmots observed. Additionally, if inclement weather negated 3 observation periods or restricted the duration of individual observations, sampling was reduced to a minimum of 2, 4-hour observation periods. Thus, I spent a minimum of 8 hours of observing each site over no less than 2 days. The number of new individuals observed, as a function of cumulative hours of observation, was recorded to determine the asymptotic number of marmots in each polygon. Individual marmots were identified by their unique pelage. This enabled me to determine the minimum number of individuals alive. Direct counts have provided a simple and relatively accurate measure of marmot abundance. (Bryant 1996) reported that 75% of Vancouver Island marmots (*Marmota vancouverensis*) in colonies are identified in 9 hours of observation; however, this number cannot be tested or adjusted without mark-recapture surveys. I examined the asymptotic increase in the cumulative number of marmots observed over time to estimate when counts had approximated the actual number of marmots occurring in a polygon (Appendix I).

I selected polygons for sampling using stratified random sampling procedures. I stratified my study area by alpine region. Polygons were also stratified by the cost of sampling and were randomly selected in each stratum. The cost of sampling was defined in terms of physical effort or man-hours required to reach a polygon from selected base camp locations. Polygon locations were selected to obtain a relatively complete coverage of the census area while maintaining independence of sampling locations (Figure 2).

3.4 Burrow Density Transects:

I measured burrow density using direct counts along variable-width line transects (Burnham 1980, Krebs 1999). The program DISTANCE (Thomas 1998) was used to develop burrow density estimates by slope, aspect, and vegetation classes. For each burrow, I recorded which side of the transect the burrow occurred and its perpendicular distance from the transect line. I assumed that all burrows along the transect line were recorded and that sightability declined with perpendicular distance from the transect line. Additionally, I recorded data on the entrance type, burrow activity, and number of entrances. I also assumed that burrow densities reflected the relative use of each habitat type by marmots. Thus, the number of burrows encountered in each area may have represented the relative abundance of marmots in that habitat type.

Transects were placed randomly across the survey area in efforts to obtain sufficient sample sizes for each habitat type. However, exact transect placement was problematic. To obtain a suitable representation of the entire study area, ensure independence of transects, and ensure randomisation, placement of transects should occur perpendicular to a single baseline traversing selected stratum in the study area. Individual transects lines should then be randomly selected for sampling. However, the nature of the topography and need to sample a larger proportion of certain habitat types precluded this type of layout. Transects were placed at oblique angles to ridge lines to ensure that transects traversed drainages and crossed as many habitats as possible. Transects were also placed at least 1 habitat unit apart to maintain sampling independence. Habitat units are defined as an area consisting of a single vegetation type as described in Table 1. Although subjective, these procedures enabled the maximization of sampling effort while maintaining some degree of randomisation (Figure 2).

3.5 Habitat Suitability Index (HSI) Models:

HSI models estimate the potential carrying capacity of an area for a species based on the structural, vegetative, and geographic characteristics of that area. HSI models assume that if organisms are occupying a particular area, these organisms are selecting that area based on the availability of the habitat types present. Thus, marmot abundance was used as an indicator of marmot habitat preference and high abundances were assumed to correlate with high marmot fitness. Likewise, if the occurrence of burrows is an indicator of marmot abundance, then the abundance of burrows in certain habitats indicates marmot habitat selection or at least the relative abundance of marmots inhabiting the area. Following this line of reasoning, one should be able to predict the relative abundance of marmots in an area based on the habitats that occur there.

I defined 3 habitat features that influence marmot abundance: slope, aspect, and vegetation (Armitage 1991, Barash 1989, Van Vuren 1991). Each of these habitat features is assumed to have some influence on the fitness of marmots. Marmots require a food source and require surficial materials that enable the marmots to dig escape and hibernation burrows. Marmots also require escape terrain such as the cracks between large boulders or talus. Suitable habitats must be free of snow for enough of the year to enable breeding, rearing, and feeding to occur prior to hibernation. Slope and aspect are assumed to have an impact the timing of snowmelt. Thus slope, aspect, and vegetation types all influence marmot abundance. However, it is unlikely that these features act as suitable indicators of marmot abundance in isolation. To meet all of their life-history requirements, marmots must use a variety of habitat types, each habitat fulfilling a specific life-history requirement.

4.0 Results:

4.1 Habitat Sampling Results:

I collected data on slope, aspect, and vegetation structure during direct observations and transect surveys. Although transect surveys cover an area larger than the polygons, I did not select transects randomly because I allocated more effort in specific habitats. I allocated more effort to specific habitats to meet the sample size requirements that yielded my desired level of error for my estimates of marmot abundance. I attempted to achieve a minimum of 25% relative error with a 90% confidence level in my estimates. For this reason, the transect data provide a better representation of sampling effort than habitat distribution. However, polygon selection was sufficiently randomised that descriptions of the habitat types comprising polygons provide an accurate representation of the availability of each habitat type in the study area.

I determined the proportion of habitat types in each polygon, stratified by region. The 3 regions identified in my study were: the northern Swannel mountains; the southern Swannel Mountains and the northern Wolverine Mountains (Figure 2). I sampled 12.4 km^2 of the entire Northern Wolverine Project study area. The percent of the total alpine area sampled in each region was 28.2%, 35.5%, and 36.3% respectively (Figure 3).

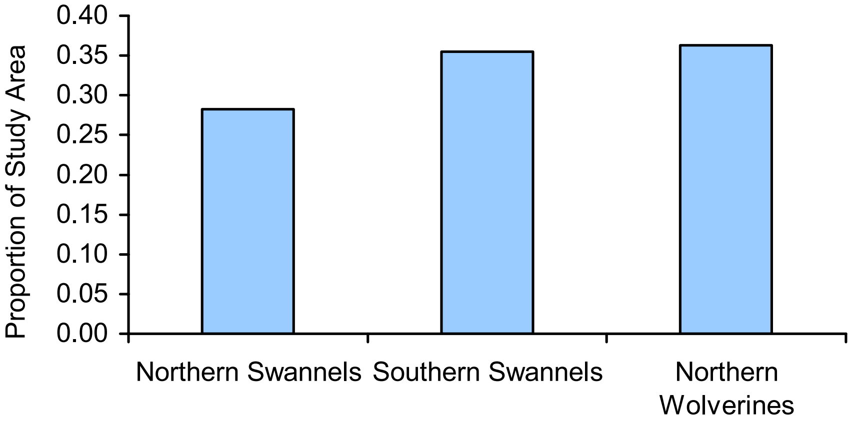

Figure 3: Proportion of total area sampled for habitat characteristics in each region of Northern Wolverine Project study area. Roughly the same area was sampled for habitat characteristics in each region of the study area.

I determined the proportions of each habitat type occurring throughout the study area and in each region. Using a GIS, I estimated that 4.7% of the total study area that I sampled was Alpine Meadow, 13.1% of the area was Alpine Shrub, 29.7% Alpine Tundra, 21.9% Fir Parkland, and 30.6% Talus.

The northern Swannels are predominated by the Alpine Tundra vegetation type with only small amounts of Talus (Figure 4). The southern Swannels have a relatively equal proportion of Alpine Tundra, Fir Parkland, and Talus with no Alpine Shrub vegetation. The northern Wolverines can be characterised by the high proportions of Talus and Alpine Shrub.

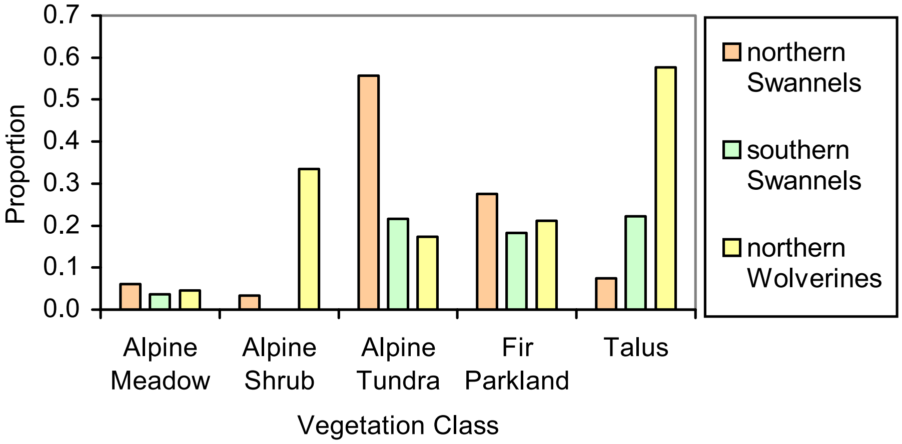

Figure 4: Proportion of each vegetation type occurring in the 3 regions of the Northern Wolverine Project study area. Alpine Meadow occurs in only small amounts in all regions. Alpine Tundra dominates the northern Swannel Ranges and the northern Wolverine Ranges are dominated by Talus, with a high amount of Alpine Shrub. Alpine Tundra, Fir Parkland and Talus dominate the southern Swannel Ranges with each of these 3 vegetation types occurring in roughly the same proportions.

Slope classes are only moderately different among the 3 mountain ranges (Figure 5). The northern Swannels is comprised primarily of 0-20 degree- and 21-40 degree-slope classes indicating moderate slopes. The southern Swannels has a high proportion of the 21-40 degree-slope class and a relatively large amount of the 41-60 degree-slope class. The northern Wolverines are intermediate between the 2 other regions with moderate amounts of the 3 slope classes that I measured.

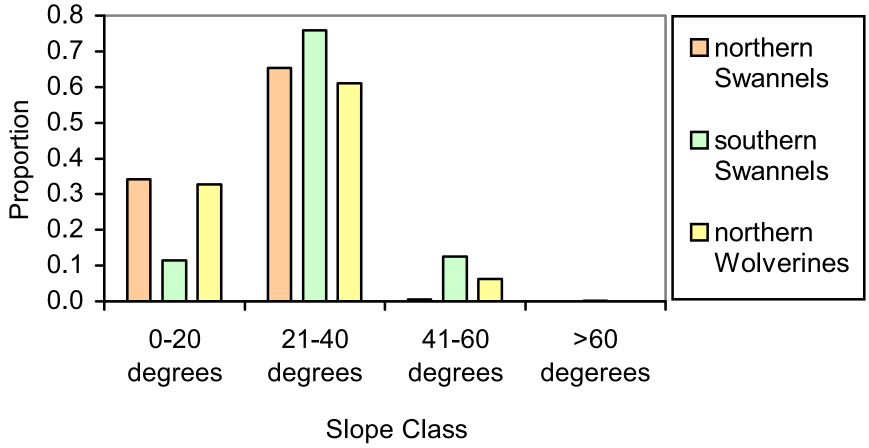

Figure 5: Proportion of slope class occurring in each region of the Northern Wolverine Project study area. A much larger proportion of slopes less than 40 degrees occur in each region. The southern Swannel Ranges contain the largest proportion of steep terrain, followed by the northern Wolverine Ranges and finally the northern Swannels. These differences are not pronounced.

Data suggesting that an area has a high proportion of north-south slopes or a high proportion of east-west slopes may indicate that the general aspect of the range or these data may only indicate a sampling bias induced by polygon selection criteria. Randomisation procedures were intended to overcome these biases, but the small sample sizes may have led to skewed results in habitat data.

The main aspects of each range are different (Figure 6). The northern Swannels have primarily south and eastern aspects while the southern Swannels have primarily northern and southern aspects. Likewise, the northern Wolverines have primarily northern and southern aspects; however, the proportion of each area is reversed from that of the southern Swannels.

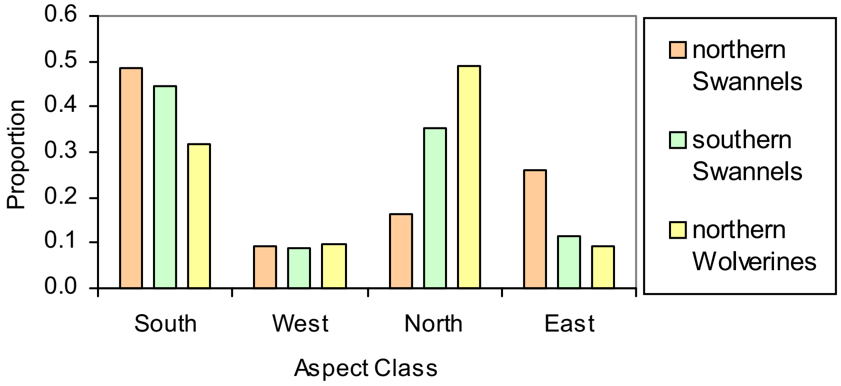

Figure 6: Proportion of aspect class occurring in each region of the Northern Wolverine Project study area. All regions contain approximately the same proportion of each aspect class.

4.2 Marmot Density Estimated by Direct Observation

I observed 25 polygons in 1999 and 2001. A total of 232 hours were spent observing polygons with a mean observation time of 9.3 hours/polygon (S.D.=1.0). Of the 25 polygons, I observed marmots in 16 polygons. There was an average of 1.6 marmots per polygon (S.D.=1.8) across all polygons and an average of 2.8 marmots per polygon (S.D.=1.5) for those polygons that had marmots. I assume that this latter average, 2.8 marmots per polygon (S.D.=1.5), as the average marmot colony size.

I used a multiple regression analysis to determine an equation that predicted the abundance of marmots by habitat type (Table 4). A forward stepwise regression was performed to determine the optimum predictors of marmot abundance (Hintze 2001). The R^2 values ranged from 0.17 to 0.71 with diminishing returns in the increase in R^2 values near 9 variables (Figure 7). Root mean square error values (MSE) were also examined (Figure 8). These MSE values suggest that the appropriate model had 6 to 7 variables. I also examined Mallow's Cp statistic. This statistic suggests that the models that I examined are consistently under parameterised, but that models with 5 variables are appropriate.

Nearly all models include the majority of vegetation classes. Western aspects (67.5-112.5 degrees) and northern (292-67.5 degree) aspects are also included in some models. Slope classes 3 (41-60 degrees) and 4 (>60 degrees) are also common. However, the determination of vegetation types present in an area is dependent upon the slope and aspect of that site (Pojar 1991). I examined a correlation matrix of these values and observed a relatively high degree of correlation among slope and aspect variables and vegetation variables (Appendix II). Therefore, only vegetation variables were included in the model. This allowed me to identify the most parsimonious model with the most predictive value and widest applicability.

I also performed a forward stepwise regression of vegetation variables (Table 5). This procedure suggested that the best model would include all vegetation types in the following order: Alpine Meadow, Alpine Shrub, Alpine Tundra, Fir Parkland, and Talus. Results suggest that models with 4 or 5 of the vegetation types are the best predictors of marmot density. The R-squared values are highest and root mean square error values are lowest for these models. Models that do include Alpine Meadow and models that exclude Alpine meadow perform similarly. Since Alpine meadow was seen as the most important single indicator of density, it was included in the final model (Appendix II).

Table 4: Top 2 best fit multiple regression models for models with 5 to 10 variables from stepwise regression performed on polygon observation data. Although root mean square error falls with a larger number of variables Mallow's Cp statistic suggests appropriate parameterisation in models containing approximately 5 variables.

Model variables in order of importance	Number of Model Variables	R-squared	Root mean square error	Mallow's Cp statistic (p+1)
AS, AT, FP, TA, >60 degrees	5	0.52	0.001893	5.73 (6)
AM, AS, AT, East, > 60 degrees	5	0.45	0.002026	8.46 (6)
AS, AT, FP, TA, West, > 60 degrees	6	0.58	0.001812	5.27 (7)
AS, AT, FP, TA, East, >60 degrees	6	0.57	0.001844	5.84 (7)
AS, AT, FP, TA, West, 41-60 degrees, >60 degrees	7	0.63	0.001754	5.39 (8)
AS, AT, FP, TA, West, East, >60 degrees	7	0.60	0.001837	6.79 (8)
AM, AS, AT, FP, TA, West, 41-60 degrees, > 60 degrees	8	0.66	0.001741	6.35 (9)
AS, AT, FP, TA West, North, 41-60 degrees, > 60 degrees	8	0.65	0.001765	6.73 (9)
AM, AS, AT, FP, TA West, North, 41-60 degrees, > 60 degrees	9	0.69	0.001717	7.18 (10)
AM, AS, AT, FP, TA, South, West, 41-60 degrees, > 60 degrees	9	0.67	0.001762	7.82 (10)
AM, AS, AT, FP, TA, West, North, 21-40 degrees 41-60 degrees, > 60 degrees	10	0.70	0.001753	8.85 (11)
AM, AS, AT, FP, TA, West, North, 0-20 degrees, 41-60 degrees, > 60 degrees	10	0.70	0.001756	8.88 (11)

*Note: Mallow's Cp statistic should equal the number of variables (p) plus 1. It is an indicator of whether the appropriate number of variables has been used in model development.

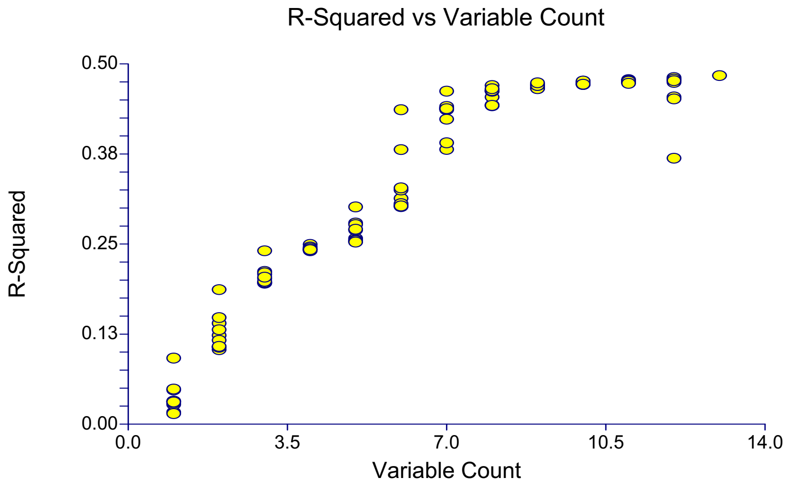

Figure 7: The R^2 values for 5 best fit multiple regressions models developed with stepwise regression with increasing number of variables for polygon observation data. Diminishing returns are seen in models containing more than 6 variables.

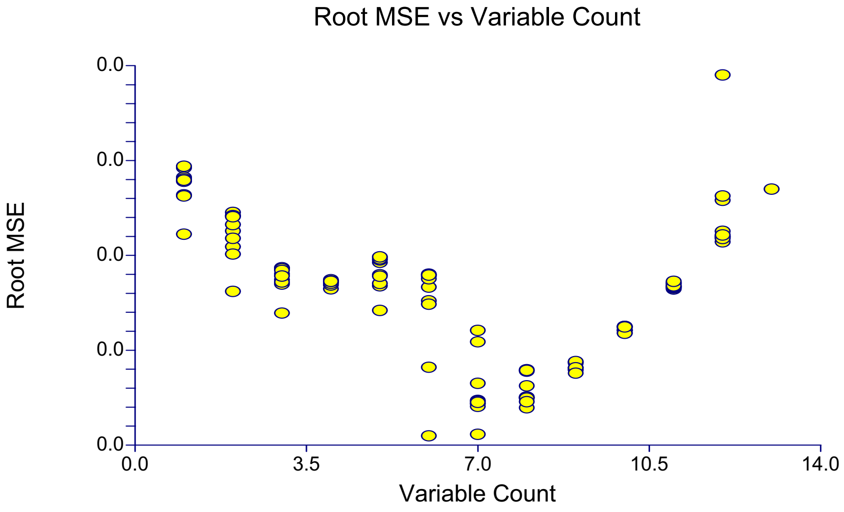

Figure 8: The root mean square error (MSE) values for 5 best fit models developed with stepwise regression with increasing number of variables for polygon observation data. Note that the root mean square error falls to its lowest values in models containing 6-7 variables.

Table 5: Best fit multiple regression models from stepwise regression of vegetation variables for polygon observation data. Note that the root mean square error falls with an increased number of terms and that Mallow's statistic suggests appropriate parameterisation with approximately 5 variables.

Model variables	Number of Model Variables	R-squared	Root mean square error	Mallow's Cp statistic (p+1)
AM	1	0.17	0.002263	5.25 (2)
AM, TA	2	0.23	0.002240	5.60 (3)
AM, AT, FP	3	0.25	0.002256	6.82 (4)
AS, AT, FP, TA	4	0.37	0.002120	5.02 (5)
AM, AS, AT, FP, TA	5	0.40	0.002119	N/A

*Note: Mallow's Cp statistic should equal the number of variables (p) plus 1. It is an indicator of whether the appropriate number of variables has been used in model development.

Alpine Meadow (AM), Alpine Shrub (AS), Alpine Tundra (AT), Fir Parkland (FP), and Talus (TA) were included as variables in the suitability model ($R^2 = 0.40$, $F_{5,24} = 2.5$, $p = 0.06$). The following equation relates marmot density (individuals/km^2) to the proportion of habitats in an area.

$$\text{Density}=2.52\text{x}10^{-4}+3.06\text{x}10^{-9}(\text{AM})-1.35\text{x}10^{-8}(\text{AS})-2.07\text{x}10^{-8}(\text{AT})-3.35\text{x}10^{-8}(\text{FP})-1.62\text{x}10^{-8}(\text{TA})$$

From the multivariate equation HSI scores can be developed using the equation:

$$\text{HSI}_1 = \text{Predicted Density/Maximum Observed Density}$$

Since the multivariate equation was developed using standardised beta coefficients, these coefficients provide a description of the relative importance of each variable in estimating marmot abundance (Figure 9). All variables have a negative influence on marmot abundance except Alpine Meadow. Alpine Meadow provides the majority of food for marmots and occurs at the lowest frequency in the study area. Additionally, variables with vegetation structure that impedes the ability of a marmot to identify predators from a distance, such as Fir Parkland, have the greatest negative influence on density.

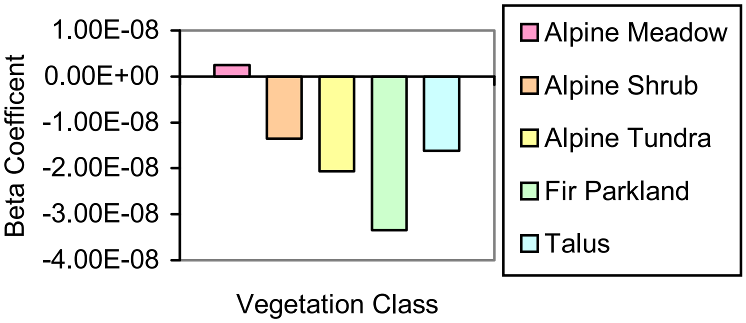

Figure 9: Relative influence of standardised beta coefficients on marmot density for a multiple regression model using 5 vegetation types as variables. The Alpine Meadow is the only variable with a positive influence on density. All other vegetation types have a negative influence with Fir Parkland having the greatest negative influence.

I derived density estimates for each region in the study area using actual counts of marmots. There were no statistical differences observed among the various regions (Figure 10).

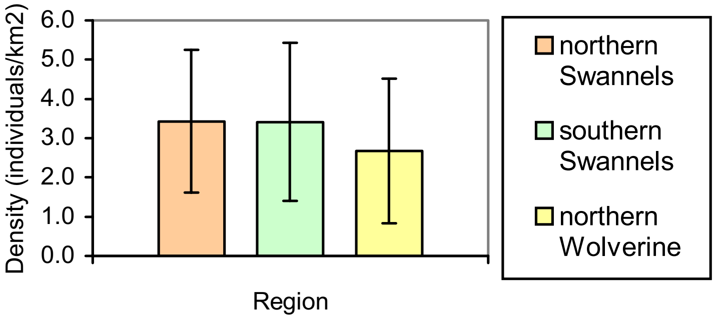

Figure 10: Density of marmots in various regions of the Northern Wolverine Project study area with 95% confidence intervals. All regions have similar estimated densities of hoary marmots.

4.3 Burrow Transect Results:

I performed variable width transects throughout the Northern Wolverine Project study area. I surveyed 102 km of transect (Figure 11).

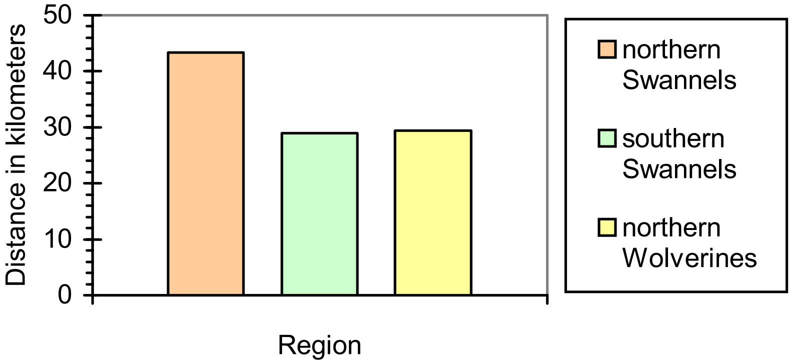

Figure 11: Distance of transect performed in each region of the Northern Wolverine Project study area. Less transect was performed in southern Swannel and northern Wolverine Ranges due to difficulty of travel in steeper terrain.

I developed burrow density estimates for all vegetation, slope, and aspect classes. Burrow densities were similar in all aspect classes with overlap in all confidence intervals (Figure 12). Burrow density estimates did show differences among slope classes (Figure 13). Estimates of 1.0 burrow/km^2 were calculated for slope classes below 40 degrees, and estimates near zero were calculated for slope classes above 40 degrees. Stratification by vegetation class indicated higher burrow density estimates in Alpine Tundra than all other vegetation types (Figure 14)

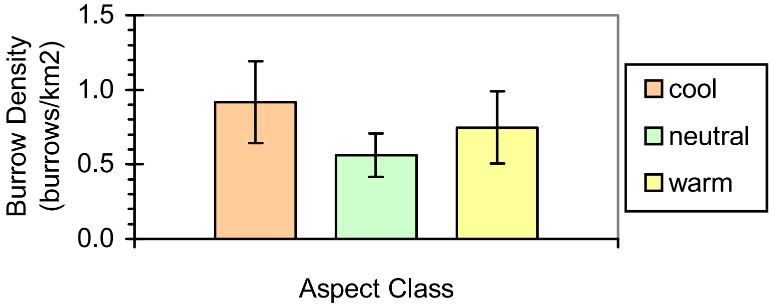

Figure 12: Burrow density estimates for each aspect class in Northern Wolverine Project study area with 95% confidence intervals. All aspect classes have similar burrow density estimates.

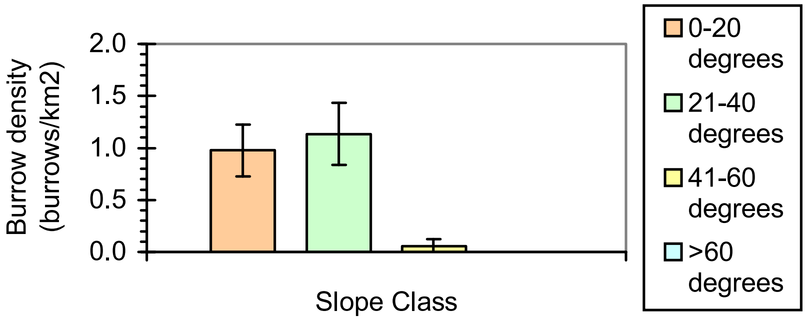

Figure 13: Burrow density estimates for each slope class in Northern Wolverine Project study area with 95% confidence intervals. Higher burrow density estimates were obtained for slopes less than 40 degrees.

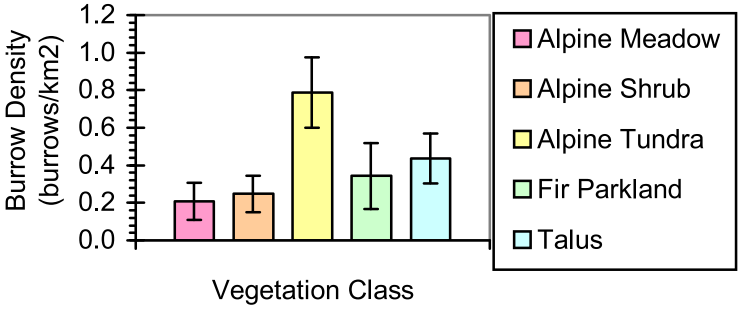

Figure 14: Burrow density estimates for each vegetation class in Northern Wolverine Project study area with 95% confidence intervals. All vegetation types have similar burrow density estimates except Alpine Tundra, which has a higher burrow density than all other vegetation types.

I also stratified transect data by region which provided estimated burrow densities for comparison among study area regions (Figure 15). All estimates were similar among regions with overlap occurring among all confidence intervals.

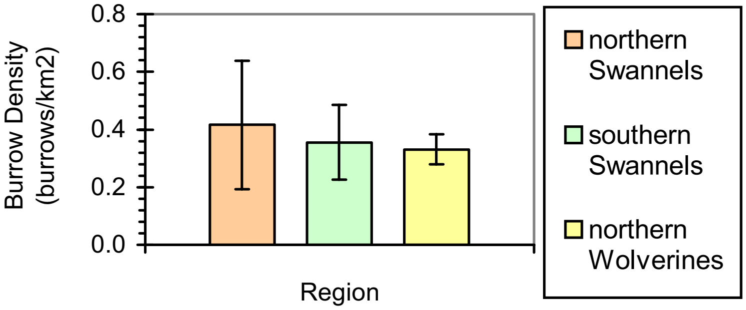

Figure 15: Burrow density estimates for each region in the Northern Wolverine Project study area with 95% confidence intervals. Similar burrow density estimates were obtained for each region of the Northern Wolverine Project study area.

4.4 Habitat Suitability Index (HSI) Models:

I developed 3 HSI models from my data. First, density and habitat data obtained from the direct observations at individual polygons were used to develop suitability curves. Although the results of the regression analyses provided some insight into the form a HSI model may take, I did not observe strong relationships among the marmot density and habitat variables (Appendix III). Therefore, I do not present HSI models relating density and habitat. I present only those hypotheses describing the possible relationship between habitat and density.

The first 2 HSI models incorporate only vegetation variables. The first model uses the geometric mean to combine variables. This model suggests that there is a compensatory relationship among all habitat variables. Variables with relatively small values influence the output to a greater degree than those variables with higher values (USFW 1981). Since the geometric mean will yield values of zero if any of the individual values are zero, I combined Alpine Shrub and Alpine Tundra variables into a single variable. Both of these vegetation types can provide suitable burrowing habitat and are not necessarily present in all areas.

$$HSI_2 = [SI_{AM} * SI_{FP} * SI_{TA} * ((SI_{AS} + SI_{AT})/2)]^{1/4}$$

where: HSI_2= the habitat suitability index value
SI_{AM} = index of proportion of Alpine Meadow available
SI_{AS} = index of the proportion of Alpine Shrub available
SI_{AT} = index of the proportion of Alpine Tundra available
SI_{FP} = index of the proportion of Fir Parkland available
SI_{TA} = index of the proportion of Talus available

I hypothesised a second model in which the limiting effects of Alpine Meadow are more strongly favoured because the Alpine Meadow is an important aspect of marmot habitat selection. The Alpine Meadow variable has a much larger influence on the index when removed from the geometric mean. Thus, the important role of Alpine Meadow in providing the primary food source is emphasised.

$$HSI_3= SI_{AM} +[SI_{FP}*SI_{TA}* ((SI_{AS}+SI_{AT})/2)]^{1/3}$$

where: HSI_3= the habitat suitability index value
SI_{AM} = index of proportion of Alpine Meadow available
SI_{AS} = index of the proportion of Alpine Shrub available
SI_{AT} = index of the proportion of Alpine Tundra available
SI_{FP} = index of the proportion of Fir Parkland available
SI_{TA} = index of the proportion of Talus available

The proportion of slope and aspect classes occurring in an area may also have some influence on the relative abundance of marmots. I developed an additional model that incorporated slope and aspect classes into the HSI. Slope class 3 (41-60 degrees) and western aspects appear to have the greatest influence on density:

$$HSI_4= [SI_{AM}*SI_{FP}*SI_{TA}*((SI_{AS}+SI_{AT})/2)*SI_{west}*SI_3]^{1/6}$$

where: HSI_{14}= the habitat suitability index value
SI_{AM} = index of proportion of Alpine Meadow available
SI_{AS} = index of the proportion of Alpine Shrub available
SI_{AT} = index of the proportion of Alpine Tundra available
SI_{FP} = index of the proportion of Fir Parkland available
SI_{TA} = index of the proportion of Talus available
SI_{west} = index of the proportion of western aspects available
SI_3 = index of proportion of slope class 3 available

Again, the relationships I observed between marmot density and the habitat variables are not strong enough to describe the suitability indexes required to obtain HSI values. However, I have developed a series of models that may provide adequate descriptions of the relationships among marmot density and environmental variables when more precise data are obtained.

5.0 Discussion:

Wildlife-habitat models are a tool widely used by wildlife managers. These models can provide useful, although not always precise, information in a cost-effective manner. However, model assumptions, the level of model verification, and the level of model testing should be clearly stated by modellers to enable an accurate assessment of a model's usefulness.

My HSI models have highlighted a number of the concerns regarding model development and application. No strong relationships were observed among marmot density and any of the environmental variables that I identified. Two factors may have affected the validity of the assumption that density is an indicator of marmot fitness. First, density may not adequately reflect the influence of each habitat variable on marmot survival and reproductive success (Van Horne 1983). Density may also not provide an adequate measure of marmot fitness unless examined at appropriate scales. Direct observations relate marmot density to habitat variables at the scale of individual colonies. Thus, measuring the relationship between habitat and density at the colony scale reduces social interaction and behavioural effects on density estimation. However, burrow density may not be an appropriate indicator of marmot fitness. Marmots burrow only in habitat types that are suitable for burrowing. Therefore, the importance of other variables in meeting marmot life history requirements, namely food availability, may be underestimated. Additionally, marmots need a range of habitat types to meet all of their life-history requisites. Habitats must be arranged in such a way that resources they provide are all available to the colony they support. Examining the relationship between density and habitat at the colony scale accounts for this spatial influence on fitness. Burrow transects examine this relationship at a landscape scale and the spatial arrangement of habitats is unaccounted for at this level.

The second reason that density may not be an effective indicator of marmot fitness relates to the regulation of marmot density. Morrison (1998) suggests that environmental variables commonly account for a maximum of 50% of the variation observed in population numbers. Other population regulation mechanisms, such as inter- and intra-specific competition, predation, and environmental stochasticity, account for the rest of the variation in population numbers. Density information must, therefore, be collected over time scales greater than 3 years for an annually reproducing organism, and populations must be highly regulated by habitat (Van Horne 1983, Bender 1996, Roloff 1999). The longer time frame of data collection can account both for changes in density due to environmental stochasticity and population cycling. Additionally, if populations are not highly regulated by habitat availability correlations between density and habitat may not be detectable.

In marmots, regional populations have not been observed to exhibit strong population cycles or fluctuations (Barash 1989). Although individual colonies may fluctuate in size, these fluctuations generally do not synchronise across larger spatial scales, and the result is that regional populations remain relatively stable. Additionally, marmot populations are not generally regulated by predation (Barash 1989). Although predation does occur, the predominant mortality factor for marmots is over-winter starvation during hibernation

(Barash 1989, Armitage 1991). Most researchers believe that marmots are food limited (Barash 1989).

Along with defining habitat variables pertinent to the organism of interest, the spatial arrangement of habitat variables must also be considered. I related habitat variables to marmot abundance using 2 methods: direct counts of marmots and counts of burrows. Direct observations occurred in defined polygons. Habitat data were collected and related to marmot abundance in these polygons. Therefore, the relative proportion of habitats combined to determine marmot abundance. Transect data determined the relative abundance of marmots in a relatively independent fashion. The number of burrows in each habitat type were determined and combined across the entire study area in an attempt to develop a model. It appears that very different answers are obtained depending on the method used to estimate abundance. Specific life-history requirements for an organism must occur in a spatial orientation that enables access to the appropriate habitats at specific times. For marmots, this means that the vegetation variables identified must occur in the home range of a particular colony. Since polygons roughly encompass the home range of a marmot colony in my study area, the polygons were sensitive to the spatial context of habitats; transects are not sensitive because they estimated density based on independent and widely dispersed habitats.

Marmots require an abundant and rich herbaceous food source to obtain enough nourishment to survive winter hibernation. They also require suitable burrow sites both during summer feeding seasons and hibernation. My results suggest that the Alpine Meadow vegetation type only occurs in low proportions in each region (Figure 4). This vegetation type provides the majority of rich food plants required by marmots. Hence, the ability to distinguish differences in the relative abundance of this vegetation type among the regions may be essential in determining the carrying capacity of each area. Of all the habitat variables, the Alpine Meadow vegetation type was correlated most strongly with marmot abundance (Appendix II).

I had hoped that the habitat classification using the data from polygon observations would provide sufficient resolution to see these differences in abundance among regions. It did not. Alpine Meadow only occurs in small proportions in all regions and polygons. Data may not have been collected at a scale fine enough to detect up the effects of abundance of Alpine Meadow on density. Predicted densities developed using these data may not be in my desired levels of error. Additionally, validating a model with data used in the creation of that model is invalid. Further work should be performed to adequately describe the habitat characteristics of these mountains. A satellite image analysis using remote sensing data may be appropriate and should provide resolution that is fine enough to detect differences in vegetation and topography.

In other study areas, marmots may occur in much larger colonies than I observed (Karels 2001). For example, near Kluane National Park, Yukon Territory, marmots were observed to live in large, multi-family colonies of 2-30 individuals in a mixed tundra-talus vegetation type. Kluane has large areas of similar vegetation types that are able to support a large number of marmots. Colonies are rarely isolated by steep mountain topography. Although similar environments to Kluane do occur in my study area, the steep and broken nature of the topography provides only small, discrete units suitable for marmots. Colony size may be limited by the restricted size of areas that provide all life-history requirements. Additionally, if the spatial arrangement of habitat variables is not taken into account, regions defined as highly suitable to marmots may have the habitat variables widely dispersed and, therefore, may be unsuitable. Holmes (1979) described the distribution and abundance of hoary marmots in Alaska. His study area was located in a large U-shaped valley, and 6 colonies in this valley were studied intensively. The local topography and the distribution of vegetation did not appear to be limiting marmot site selection. Marmots could easily move among sites, and the single valley was not highly broken by elevational and slope changes (Holmes 1979). Therefore, future model development should occur in other portions of the hoary marmot range to obtain support for hypotheses regarding marmot habitat selection.

The predictive ability of a multiple regression equation increases as the range of data used to create the equation increases (Lewis-Beck 1980). Since only a small range of abundances were observed, the predictive ability of my model is limited. Much of the abundance data were collected during the summer of 2001, and the weather patterns during this summer were unusual for the area. Substantial amounts of snow persisted until the middle of July and temperatures $<10^{o}$C occurred throughout July and early August. These conditions have had substantial effects on marmot activity patterns (Barash 1989). I attempted to time observations with periods of peak marmot activity, but due to the persistence of cool temperatures, no daily time period produced high marmot activity. Although plots of cumulative marmot observations over time produce asymptotic increases (Appendix I), very few juvenile and yearling marmots were observed in 2001.

Transect data suggest some selection by marmots of lower slope classes. Few steep slope classes over 40 degrees occur in my study area (Figure 5). However, a significant difference was observed between the abundance of burrows in the lower slope classes (<40 degrees) and the steeper classes (Figure 13). This suggests that marmots prefer the lower slope classes. These results coincide with incidental marmot observations. Marmots were most often observed close to shallow slopes. Burrows most often occurred on shallow slopes, and the Alpine Meadow vegetation types generally occurred in areas with the slower drainage of water, associated with shallow slopes. However, stepwise regression did not identify shallow slopes as predictors of marmot abundance. This most likely results from the requirement of marmots to be close to escape terrain. Each polygon where marmots occurred had some steep slopes. These slopes not only provide bluffs with abundant cavities for marmots to escape predators and high temperatures, but steep slopes produce talus fields and large erratics that provide escape terrain and burrow sites close to shallow slope feeding sites. Although burrows occur primarily on shallow slopes, marmots require a more complex habitat including shallow and steep slopes.

Results of the stepwise regression and incidental observations enabled me to propose a number of HSI models from which further verification and validation can be performed. These models incorporate variables thought to be important indicators of marmot habitat suitability. However, this is only the first step in a multi-step model-building process. A number of studies describe the process of development, verification, validation, and testing of wildlife-habitat models (Cook 1985, Thomasma 1991, Breininger 1998, Jorgensen 1998). These studies effectively outline procedures used in the selection and testing of appropriate environmental variables and the relation to organism fitness. The authors clearly outline the model components evaluated, input data variability and classification systems, the validity of statistical methods, the comparative tests used, the spatial and temporal scales addressed, and the geographic and environmental ranges over which the model is applicable. These criteria for evaluating habitat models are all identified by (Roloff 1999) as important criteria in validating HSI models. However, model testing is also extremely important (Thomasma 1991). Models should be verified and validated, and they should be applied to new areas to ensure their proper functioning. The multi-stage process of model development, verification, and testing should be documented at each step to ensure the model best describes the system of interest (Brooks 1997).

Brooks (1997) outlines the stages of HSI model building as development, calibration, verification, and validation. Unfortunately, these steps are not always distinct. My study fulfils a number of these steps. Development and calibration stages have been completed with identification of important habitat variables and an estimation of the relation of each to a measure of fitness. Model calibration involves the determination of the effect size of the measures of fitness, as this effect size relates to changes in the habitat suitability indices. Although I have identified a series of key environmental variables and estimated the relative effect of each of these variables on marmot density, the data lack the resolution to provide quantitative descriptions of suitability indices. Calibration can only occur following quantitative description of the relation between environmental variables and fitness. Calibration is site specific involving the resetting of model parameters in each new study area. Model verification involves the independent ranking of the habitat values in the area of interests to ensure the proper identification among environmental variables and density or other measure of fitness. The multivariate equation that I developed provides an indication of the relation of environmental variables to density and suggests the relative importance of each of these variables to marmots. Finally, the validation and testing stage is completed with the application of the model to single or multiple regions to ensure predictive ability of the model. Transect estimates provide an independent measure of relative abundance. Although transect estimates are unable to confirm the relationship among marmot densities and environmental variables; these estimates provide an independent assessment of the validity of abundance estimates.

Brooks (1997) outlines the relationship among the risks associated with the use of HSI models and the level of development or testing that has been performed. The 2 factors are inversely related. By completing each successive stage of the testing process, the risk incurred by wildlife managers in inferring information from a HSI model decreases. However, due to a lack of information, many models are used before risk levels fall to optimal levels. The proper description of assumptions, verification, and validation procedures by the developers of a model is essential at each stage of development to ensure the proper application of the model and to aid in future model development, verification, and validation.

6.0 Conclusion:

Hoary marmots have been identified as an important food source for adult female wolverines during period of lactation and weaning. An assessment of the relative abundance of marmots across the Northern Wolverine Project study area may provide insight into differences in female wolverine home ranges. To estimate marmot abundances over large areas, I developed a series of wildlife-habitat models to estimate abundances at regional scales.

I identified a series of environmental variables that I hypothesised would have some influence on hoary marmot abundance. I examined the relationship of each of these variables to marmot densities though the development of a multivariate statistical model. This model helped me to identify key environmental variables and to determine the relative influence of these key variables on marmot density. Additionally, I examined the individual relationships between each variable and marmot density to develop suitability indices and a habitat suitability index (HSI) model. Although I observed no strong relationships among density and environmental variables, I did hypothesise HSI models from results obtained in the multivariate model development. I also identified a number of problems with habitat data collection. These problems include the lack of an independent and fine-scaled identification of vegetation types. When re-solved, the data should provide an indication of the relationship among density and habitat variables. The use of remote sensing techniques to identify and classify habitat variables should provide better resolution than the methods used in my study.

The development and use of wildlife-habitat models is a complex multi-step process that requires an understanding of organism biology, sampling methodologies, and model assumptions. Environmental variables should be identified so that the variables are relevant to the biology of the organism and are readily identifiable and measurable. Sampling methods should measure the impact of the availability of environmental variables on fitness. Sampling methods also should determine the sensitivity of sampling methods to the spatial orientation of environmental variables and to the selection of appropriate scales of measurements to account for the range and distribution of organisms. These considerations should occur during model development and application. The model should be applied at spatial and temporal scales consistent with the assumptions made in development and sampling. Scaling up the application of suitability indices to aid in large-scale habitat assessment may result in the violation of spatial assumptions. The proper documentation, verification and validation of wildlife-habitat models are essential in determining the usefulness of the models predictions.

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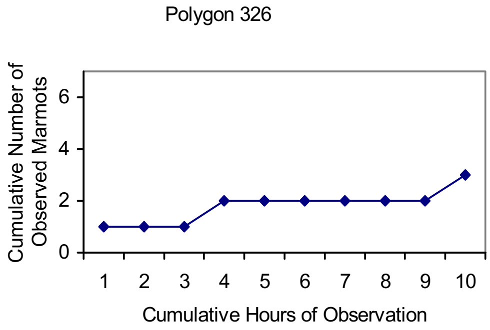
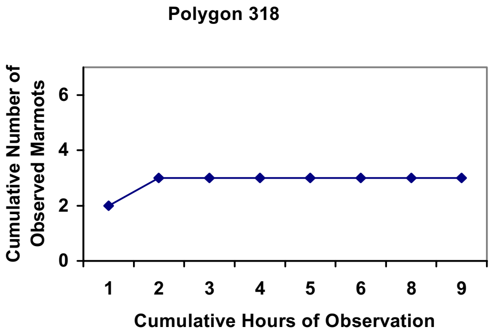
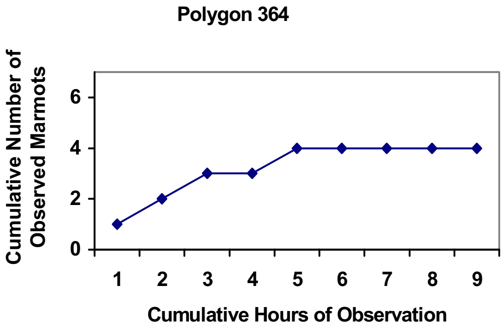
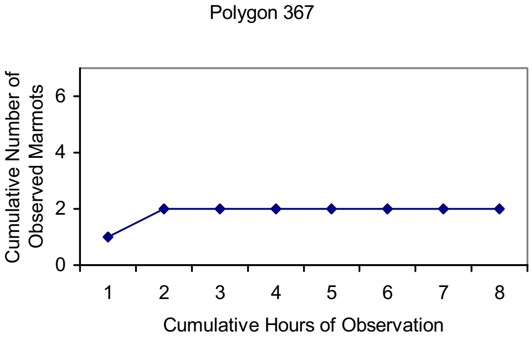
Appendix I:

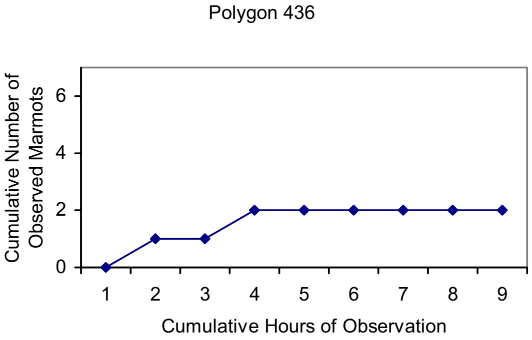
Cumulative Abundance vs. Cumulative Time Plots for Polygons Containing Hoary Marmots

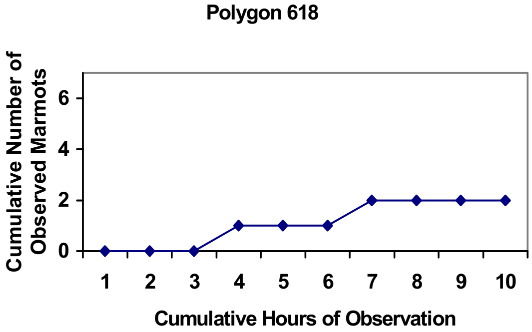


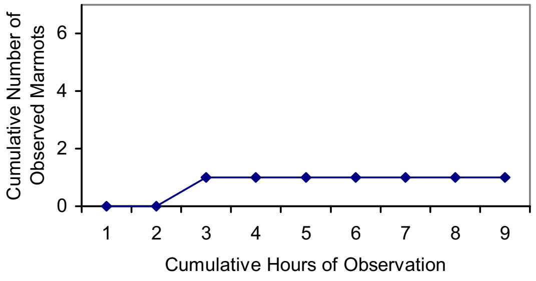


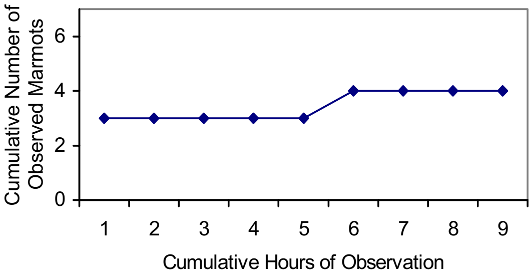









Polygon 623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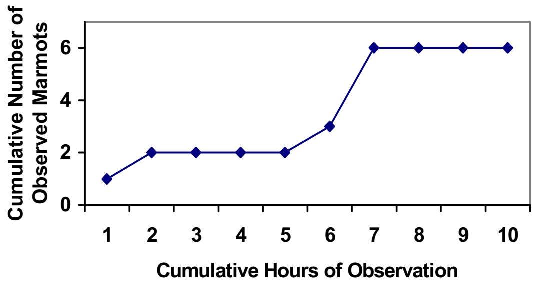
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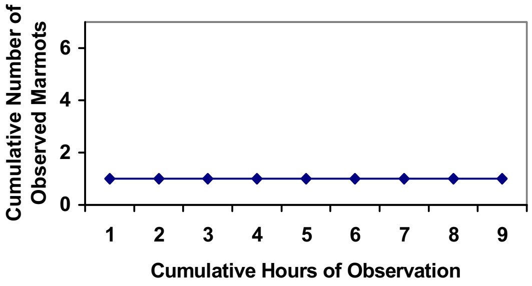
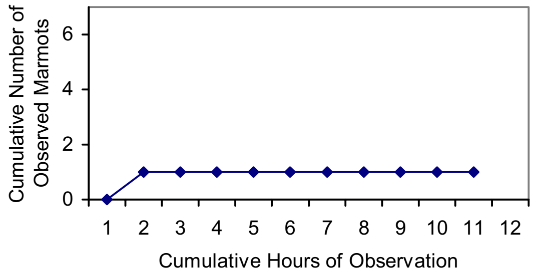
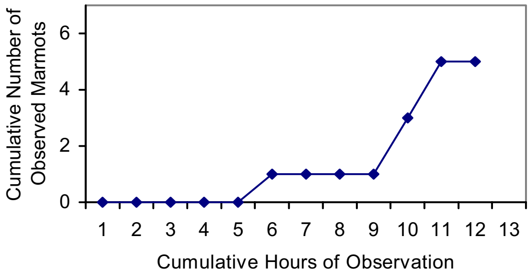

Polygon 720


Polygon 77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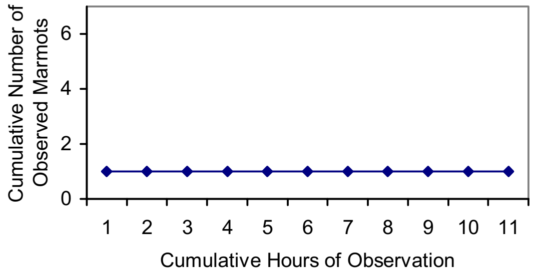
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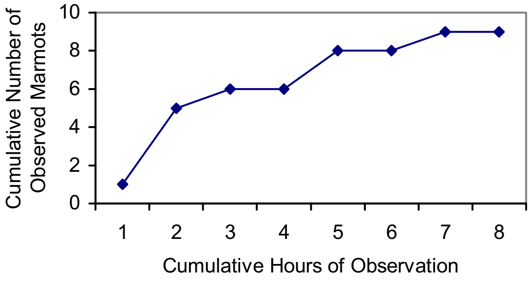
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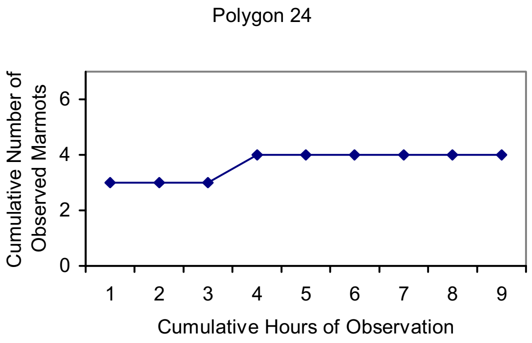
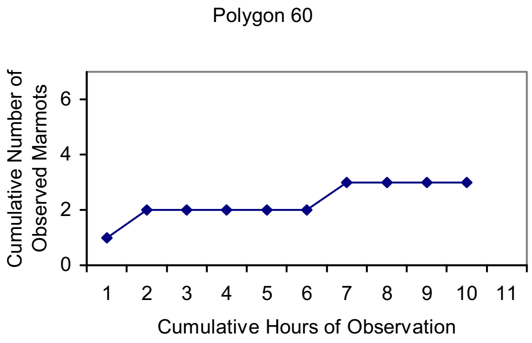

Polygon 24
Cumulative Number of Observed Marmots
0
2
4
6
1
2
3
4
5
6
7
8
9
Cumulative Hours of Observation


Polygon 60
Cumulative Number of Observed Marmots
0
2
4
6
1
2
3
4
5
6
7
8
9
10
11
Cumulative Hours of Observation

Appendix II:

Correlation Matrix of Environmental Variables

Spearman Correlations Section (Pair-Wise Deletion)

	Alpine_Meadow	Alpine_Shrub	Alpine_Tundra	Fir_Parkland	Talus	112.5-247.5
Alpine_Meadow	1.000000	-0.093462	-0.163775	0.026908	0.091498	-0.260157
Alpine_Shrub	-0.093462	1.000000	-0.173036	-0.101151	-0.333019	-0.064910
Alpine_Tundra	-0.163775	-0.173036	1.000000	-0.091774	-0.648273	0.270920
Fir_Parkland	0.026908	-0.101151	-0.091774	1.000000	-0.384937	0.435853
Talus	0.091498	-0.333019	-0.648273	-0.384937	1.000000	-0.411845
112.5-247.5	-0.260157	-0.064910	0.270920	0.435853	-0.411845	1.000000
247.5-292.5	-0.160346	0.194396	0.171288	0.063895	-0.340095	0.125505
292.5-67.5	0.135354	0.120397	-0.369031	-0.410000	0.506251	-0.840162
67.5-112.5	0.027315	-0.081010	0.183547	-0.371538	0.054436	-0.261204
0-20_degrees	0.052592	0.439068	0.310559	0.063846	-0.511694	0.004232
21-40_degrees	-0.014269	-0.319119	0.036787	0.103846	0.077765	0.208117
41-60_degrees	-0.056305	-0.091823	-0.625471	-0.414165	0.844401	-0.469682
>60_degrees	-0.112603	-0.213954	-0.321678	-0.259854	0.474179	-0.096442
Density	0.555244	-0.213438	-0.264689	-0.228524	0.286070	-0.460316

Spearman Correlations Section (Pair-Wise Deletion)

	247.5-292.5	292.5-67.5	67.5-112.5	0-20_degrees	21-40_degrees	41-60_degrees
Alpine_Meadow	-0.160346	0.135354	0.027315	0.052592	-0.014269	-0.056305
Alpine_Shrub	0.194396	0.120397	-0.081010	0.439068	-0.319119	-0.091823
Alpine_Tundra	0.171288	-0.369031	0.183547	0.310559	0.036787	-0.625471
Fir_Parkland	0.063895	-0.410000	-0.371538	0.063846	0.103846	-0.414165
Talus	-0.340095	0.506251	0.054436	-0.511694	0.077765	0.844401
112.5-247.5	0.125505	-0.840162	-0.261204	0.004232	0.208117	-0.469682
247.5-292.5	1.000000	-0.178599	-0.416474	0.304080	-0.163972	-0.221880
292.5-67.5	-0.178599	1.000000	0.105385	0.069231	-0.340769	0.608160
67.5-112.5	-0.416474	0.105385	1.000000	0.066923	-0.161538	-0.023865
0-20_degrees	0.304080	0.069231	0.066923	1.000000	-0.799231	-0.371055
21-40_degrees	-0.163972	-0.340769	-0.161538	-0.799231	1.000000	-0.106236
41-60_degrees	-0.221880	0.608160	-0.023865	-0.371055	-0.106236	1.000000
>60_degrees	0.027805	0.282734	0.026149	-0.148721	-0.328495	0.471041
Density	-0.324953	0.156986	0.362856	-0.205870	0.072730	0.275633

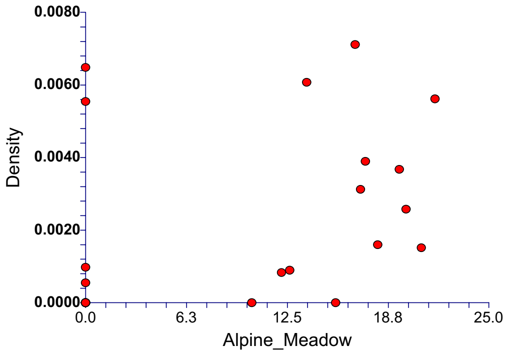
Spearman Correlations Section (Pair-Wise Deletion)

	>60_degrees	Density
Alpine_Meadow	-0.112603	0.555244
Alpine_Shrub	-0.213954	-0.213438
Alpine_Tundra	-0.321678	-0.264689
Fir_Parkland	-0.259854	-0.228524
Talus	0.474179	0.286070
112.5-247.5	-0.096442	-0.460316
247.5-292.5	0.027805	-0.324953
292.5-67.5	0.282734	0.156986
67.5-112.5	0.026149	0.362856
0-20_degrees	-0.148721	-0.205870
21-40_degrees	-0.328495	0.072730
41-60_degrees	0.471041	0.275633
>60_degrees	1.000000	-0.062484
Density	-0.062484	1.000000

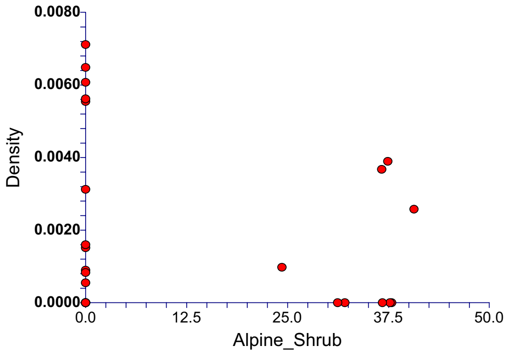
Appendix III:

Density Relationships to Polygon Habitat Variables

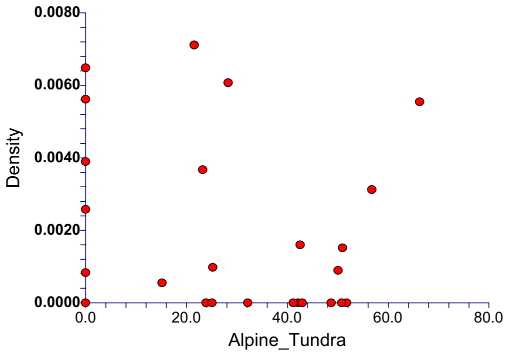
Density vs Alpine_Meadow



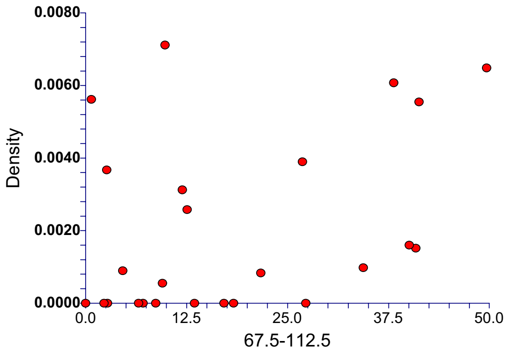
Density vs Alpine_Shrub



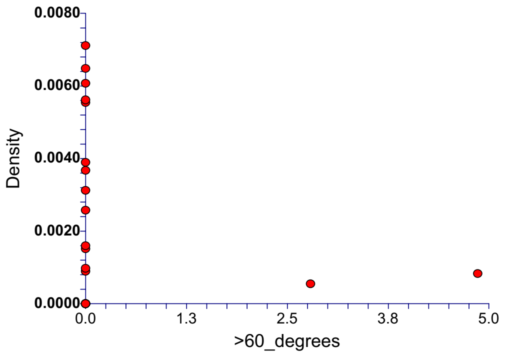
Density vs Alpine_Tundra



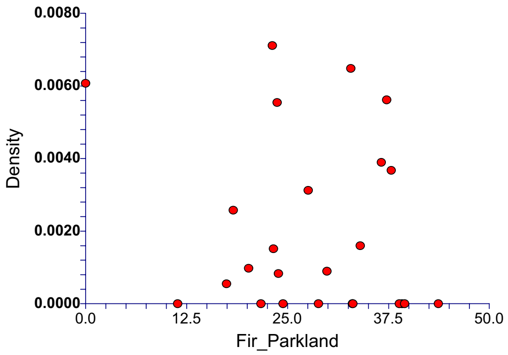
Density vs 67.5-112.5



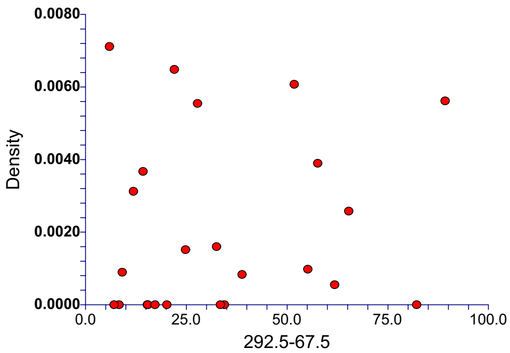
Density vs >60_degrees



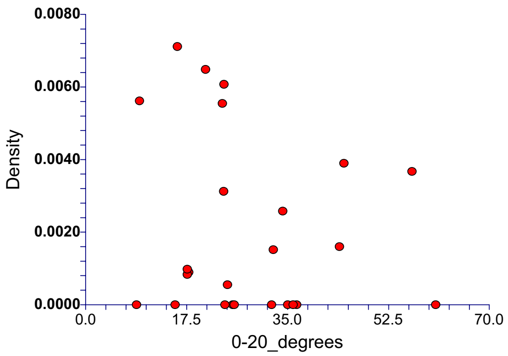
Density vs Fir_Parkland

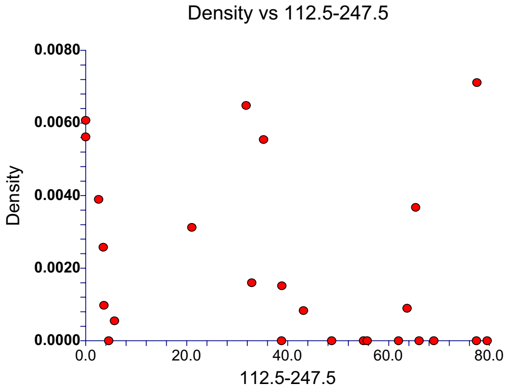


Density vs 292.5-67.5

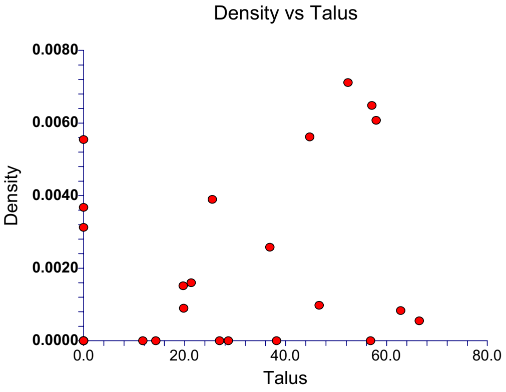


Density vs 0-20_degrees

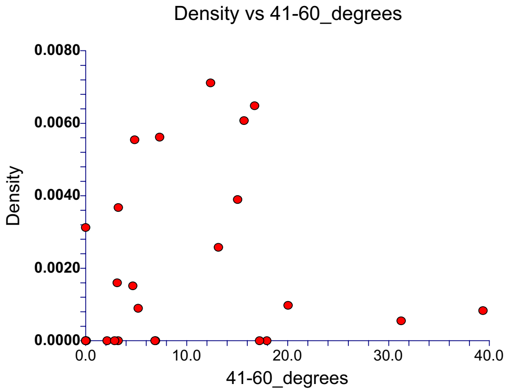




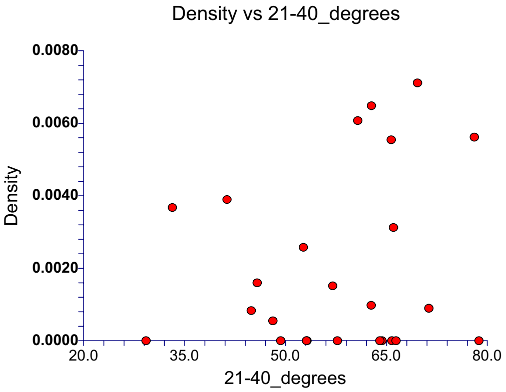
Density vs 112.5-247.5



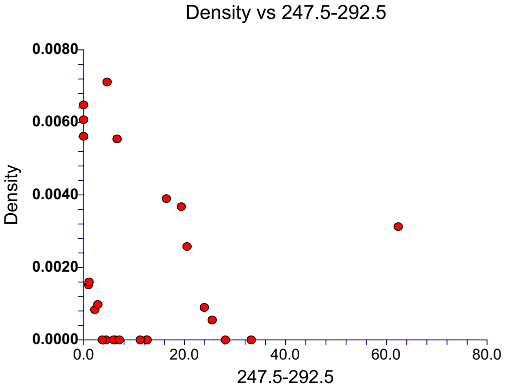
Density vs Talus



Density vs 41-60_degrees



Density vs 21-40_degrees



Density vs 247.5-292.5