

**Pattern, composition and resource selection of terrestrial vertebrates across
the Yukon forest to tundra transition**

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ABSTRACT

Ecotones are gradients of change between expanses of similar species composition. These regions often mark co-occurring range limits for several species, and thus are ideal for elucidating ecological and biogeographical phenomena. The forest to tundra transition (FTT) is one of the world's most prominent ecotones, but remains poorly studied especially with regard to vertebrate species occurrence. Vertebrate diversity, ecological structure and resource selection were characterized across the Yukon FTT using diversity metrics, ordination, hierarchical clustering, and resource modeling. The FTT represents an abrupt drop in vertebrate species richness within the more gradual, continental scale diversity gradient. Despite the patchiness and complexity in vegetative structure over this ecotone, the terrestrial vertebrate community is divisible into boreal, taiga, and tundra compartments. Most species conform to resource associations reported closer to the core of their range, generating remarkably consistent habitat and species associations despite a complex patchwork of contrasting habitat types.

RÉSUMÉ

Les écotones constituent des gradients entre régions dont les compositions d'espèces sont similaires. Les écotones représentent souvent la limite de distribution de plusieurs espèces et ils sont donc idéaux pour élucider les phénomènes écologiques et biogéographiques. La transition entre la forêt et la toundra (TFT) est l'un des écotones les plus importants mais demeure peu étudiée, surtout en ce qui concerne la présence de vertébrés. Nous avons caractérisé la diversité des vertébrés, la structure écologique et la sélection des ressources dans la TFT du Yukon en utilisant des métriques de diversité, des ordinations, des classifications hiérarchiques et des modélisations de l'utilisation des ressources. La TFT représente une chute soudaine dans la richesse des espèces vertébrées lorsque l'on se place dans le gradient de diversité à l'échelle du continent. Malgré la structure agrégée et complexe de la végétation dans cet écotone, la communauté des vertébrés terrestres peut être divisée en trois compartiments : boréal, taïga et toundra. La plupart des espèces se conforment aux associations de ressources déjà décrites plus près du centre de leurs distributions malgré la mosaïque complexe d'habitats différents que représente cet écotone.

PREFACE

Contribution of authors

This thesis consists of two manuscripts prepared and formatted for submission to the *Journal of Global Ecology and Biogeography* and *Oikos*, respectively. This project started as the idea of my supervisor Murray M. Humphries who asked me three years ago if I would take on a project to sample the mammal community across the forest to tundra transition (FTT) somewhere in Canada. With Murray's initial idea, I selected a field site, found and modified the necessary sampling protocols, and organized and managed the data collection phase, including collecting the bulk of the data. This involved the expansion of the project from the original focus on mammals to a broader focus on terrestrial vertebrates, including terrestrial grouse which occur across the FTT. I also conducted the associated community outreach and obtained the necessary permits and permissions.

Chapter one is coauthored by Murray M. Humphries. Murray provided the initial research idea, logistical and methodological support, thorough editorial comments, as well as guidance along the way. I contributed the conceptual focus of this chapter, sought out, learned and applied the necessary statistical methods and wrote the manuscript.

Chapter two is coauthored by Murray M. Humphries, Stan Boutin and Tom Jung. As with chapter one, Murray provided the initial research idea, logistical and methodological support, thorough editorial comments, as well as guidance along the way. Stan provided additional logistical support and pushed me toward the statistical methodology, as well as providing comments on the final draft. Tom Jung provided logistical support, ideas regarding small mammal sampling, assisted with identifying captured small mammals, and provided comments on the final draft. I contributed the conceptual focus of this chapter, researched and applied the necessary statistical techniques and wrote the manuscript.

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First and foremost, I thank my supervisor Murray M. Humphries for electing me to run with an embryonic/fantastical idea with utmost trust and freedom. I hope I have done him and this project justice. I thank my pseudo co-supervisor Stan Boutin for his academic and logistical support. My thanks to the Wildlife Energetics and Ecology lab at McGill for helping me complete and greatly improve this Thesis. I also appreciate the statistical expertise of Chris Buddle and the GIS expertise of Charlene Nielson.

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I thank my family for finally (I hope) understanding what it means to write a thesis, why I am not “going to class” and why I am still a student at 26 years old. I thank Mai-Linh for always being “there”- no matter where “there” is or even if “there” is the same for the both of us- she is the best.

I dedicate this thesis to her

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GENERAL INTRODUCTION

This thesis examines the constituent vertebrates of the forest to tundra transition (FTT), including many aspects of their ecology. The goal herein was to thoroughly describe the terrestrial vertebrate community occurring across the FTT. Specifically, I examined the vertebrate species assemblage with regard to:

- 1) the patterned assortment (diversity and ecological structure) of species, including the pattern of species complement by sample site and the co-occurrence of ecologically linked species across all sites, as well as the environmental predictors of these patterns.
- 2) resource selection by several of the most numerous species.

This thesis greatly expands our rudimentary knowledge of the vertebrate species occurring across this vast ecotone, and with this knowledge, I hope to make a meaningful contribution to our understanding of ecology.

Literature review

Assemblage of Species in Space

Determining the reason why species occur where, in the combinations, densities, and diversity they do, is one of the central tenants of ecology (Boyce and McDonald 1999; Willig *et al.* 2003; Holt and Keitt 2005; Holt *et al.* 2005; Parmesan *et al.* 2005). There is strong unevenness in biodiversity across the earth, including a consistent, broad scale trend of decreasing biodiversity from the tropics to the poles (Fischer 1960; Pianka 1966; Badgely and Fox 2000; Willig *et al.* 2003). This trend is evident across many taxa (Hilliebrand 2004) and many hypotheses have been proposed to describe this trend, but its true causation remains unknown (Whittaker *et al.* 2001; Willig *et al.* 2003; Zapata *et al.* 2003; Scheiner and Wilig 2005).

At smaller scales there is, however, much variability in this trend, with the large scale latitudinal trend being composed of many smaller plateaus and abrupt transitions (Gosz 1993; Whittaker *et al.* 2001). These plateaus correspond to patches of internally similar communities resulting from species clustering in space (Peters *et al.* 2006). The largest scale patches are biomes, separating earth's

biota into regions of largely consistent species composition and functional groups (Prentice *et al.* 1992). These biomes can be divided into infinitely smaller and smaller patches with increasingly similar species composition and ecological function (Gosz 1993; Bevers and Flather 1999). Patches often coincide with underlying abiotic factors such as lakes and mountain tops (Prentice *et al.* 1992), but the persistence of the patch often involves a complex interplay with biotic factors (Peters *et al.* 2006). This is exemplified by tree patches within a tundra matrix being maintained by microclimate created by the higher albedo of trees vs. snow covered tundra (Harding *et al.* 2002). Patches are subject to edge effects, whereby the internal homogeneity is perturbed along its periphery (Ries *et al.* 2004). These edge effects often result in gradients known as ecotones, between the more internally consistent core areas of each neighboring patch (Risser 1995; Baker *et al.* 2002; Cadenasso *et al.* 2003; Ries *et al.* 2004).

Ecotones

As gradients of transition between patches of similar species composition, ecotones mark abrupt shifts in whole animal communities and determine the ecological connectedness of these communities (Risser 1995; Baker *et al.* 2002; Cadenasso *et al.* 2003; Ries *et al.* 2004). The interaction between biodiversity and ecosystem function is enhanced at ecotones where there is markedly higher species turnover than in surrounding biomes (Gosz 1993; Risser 1995; Walker *et al.* 2003; Rodriguez and Arita 2004; Mena and Vazquez-Dominguez 2005). Thus, within ecotones, changes in diversity and community composition across space are steeper and more variable than in surrounding areas (Hillebrand 2004; Rodriguez and Arita 2004).

Ecotones often generate coincident range limits of several species (Risser 1995; Baker *et al.* 2002; Walker *et al.* 2003). This pattern seems unlikely since a suite of different niche requirements limits each species (Hutchinson 1957; Brown 1984). The relative abruptness of change and congruence among species at ecotones suggest some underlying threshold of habitat suitability (Risser 1995; Baker *et al.* 2002; Ries *et al.* 2004). Indeed ecotones are often marked by highly perceivable changes in architecture of abiotic (e.g. aquatic vs. terrestrial) or biotic

variables (e.g. forest vs. prairie), and abrupt changes in physiognomy are known to strongly affect edge permeability (Risser 1995; Ries *et al.* 2004; Cadenasso *et al.* 2003).

Although the importance of boundaries to species patterning is well established (Baker *et al.* 2002; Cadenasso *et al.* 2003; Ries *et al.* 2004; Peters *et al.* 2006), studies of ecotones have been largely left to realm of vegetation ecologists (Peters *et al.* 2006), and most studies of habitat edges have focused on the fitness and/or abundance of single species, or small groups of closely related taxa, at a local scale (Ries *et al.* 2004). Edges effects are highly variable between and within taxa and our ability to scale-up observed phenomena to the community- biome level has been limited (Baker *et al.* 2002; Ries *et al.* 2004; Peters *et al.* 2006). Ecotones can have positive, negative or neutral effect on species presence/abundance and the effect is scale dependant because ecotones are themselves complex mosaics of many smaller ecotones (Baker *et al.* 2002; Ries *et al.* 2004). Revealing general ecotone properties and corresponding mechanisms is therefore difficult (Risser 1995; Baker *et al.* 2002; Ries *et al.* 2004; Peters *et al.* 2006).

Ecotones can be simple gradations between two adjoining patches or represent a unique structure not present in either patch (Walker *et al.* 2003; Ries *et al.* 2004). Ecotones can be marked by high diversity if they contain species from two adjacent patches, or low diversity if species from neighboring ecosystems find the transition unsuitable (Ries *et al.* 2004; Peters *et al.* 2006). Moreover, ecotones can have increased diversity if there are ecotonal species that specialize in the unique conditions found in the overlap of two patches (Risser 1995; Baker *et al.* 2002; Walker *et al.* 2003; Peters *et al.* 2006). The generality of these potential ecotonal effects on diversity remain to be established (Walker *et al.* 2003; Ries *et al.* 2004).

Ecotones are complex transitions, where much insight into the pattern and processes of community structure and global diversity patterns can be made (Risser 1995; Spector 2002). Furthermore, these biogeographic crossroads may be essential to the evolution of new species and the maintenance of existing biodiversity (Spector 2002). Understanding patterns of diversity and ecological structuring across major global ecotones and exposing the relationship between

pattern and environment will thus be fruitful in our quest for general theories on ecological patterning (Spector 2002). Recent emphasis on large scale pattern and heavy reliance on readily-available coarse-grained survey data (e.g., mammal species' ranges, breeding bird surveys), has caused the ecotones between most of the world's major biomes to be overlooked. Understanding the ecological processes determining diversity changes across these critically important regions requires new, multi-species data, collected at scales intermediate to continental diversity patterns and local habitat use.

The Forest to Tundra Transition

The FTT is the largest, most striking ecotone in Canada, marking the transition between the boreal forest and the arctic tundra (Payette *et al.* 2001; Callaghan *et al.* 2002; Sveinbjörnsson *et al.* 2002). The FTT exemplifies the complexity of ecotones, being not a distinct boundary but a mosaic of lessening tree abundance and changing forest structure across vast landscapes into strikingly dissimilar tundra communities (Lavoie and Payette 1994; Payette *et al.* 2001; Callaghan *et al.* 2002; Sveinbjörnsson *et al.* 2002). Fine scale habitat structure across the FTT cannot be explained by synoptic climate alone and is largely influenced by local geology, topography and disturbance history (Timoney *et al.* 1992; Sveinbjörnsson *et al.* 2002).

The FTT presumably comprises the co-occurring southern range boundary of several arctic mammal species and northern range boundary for several boreal forest species (Hagemeier 1966; Wilson and Ruff 1999). The FTT probably accounts for a great deal of the reduction of biodiversity north of 55° N, representing a constriction in the latitudinal species filter. This pattern suggests some definitive factors limiting species occurrence within the FTT. The abrupt shift in vegetative physiognomy and composition at the FTT (Sveinbjörnsson *et al.* 2002) is the type of change that has deterministic influence on species occurrence (Fisher and Wilkinson 2005). However, exactly where and why boreal species fallout over the FTT is largely unknown, especially for vertebrates (Callaghan *et al.* 2002). Several authors have explicitly studied the pattern and inferred the mechanisms behind vegetation physiognomy and composition across

the FTT (Payette *et al.* 2001; Callaghan *et al.* 2002; Payette *et al.* 2002; Sveinbjörnsson *et al.* 2002). However, there have been very few vertebrate diversity surveys across the FTT (Ste-Georges *et al.* 1995; Johnson *et al.* 2005; Olofsson *et al.* 2004) and of these none have explicitly considered the community structure over this gradient. Knowing how vertebrate species sort or associate across this boundary and inferring environmental drivers would greatly improve our understanding of the functioning of large scale ecotones and why species and ecosystems have borders.

Pattern and Process

Species interactions are among the foremost ascribed mechanisms for where species occur and how they are assembled (Whittaker *et al.* 2001; Willig *et al.* 2003; Scheiner and Wilig 2005; but see Zapata *et al.* 2003). Therefore, ecological structure, the patterned arrangement of species corresponding to an underlying ecological mechanism (Legendre and Legendre 1998), should be apparent in most naturally occurring systems. Compartmentation is a specific type of ecological structure where species cluster in space and time based on the intensity of ecological interaction (Krause *et al.* 2003; McCann *et al.* 2005; Proulx *et al.* 2005). Species cluster into spatial compartments through several mechanisms including similar habitat preferences and strong trophic interactions (Bever and Flather 1999; Krause *et al.* 2003; McCann *et al.* 2005; Proulx *et al.* 2005). At ecotones, species from bordering patches should exhibit parallel resource preferences and have more ecological interactions with sympatric species than with parapatric species (McCann *et al.* 2005), resulting in rapid shifts of whole communities across short distances (Walker *et al.* 2003; Lopez-Gonzalez 2004; Mena and Vazquez-Dominquez 2005). Ecological structure should therefore be especially conspicuous at ecotones (Ricklefs 2004).

Species occurrence and abundance in space is largely determined by how well their resource requirements are met (Hutchinson 1957; Boyce and McDonald 1999), notwithstanding top-down regulation (Menge 2000). In turn, species occurrence and densities should reflect the availability of these resources (Manly *et al.* 2002). This effect is perhaps exacerbated at ecotones such as the FTT with

relatively low diversity (Wilson and Ruff 1999) and abrupt changes in habitat physiognomy and vegetative composition (Walker *et al.* 2003; Ries *et al.* 2004; Cadenasso *et al.* 2003). The composition of these communities is not always predictable since species exhibit unique habitat associations in suboptimal conditions often coincident with range boundaries (Brown 1984; Swihart *et al.* 2003; Case *et al.* 2005; Holt *et al.* 2005).

Scale

At large spatial and temporal scales, species composition arises from historical processes of colonization and diversification (Risser 1995; Ricklefs 2004). At more local scales, species sorting arises from indirect influence of factors such as climate or direct influence of habitat selection or ecological linkages among species (Risser 1995; Ricklefs 2004). At the continental scale, species diversity and individual species abundances are often more closely correlated to measures of climate than to resource availability (Whittaker *et al.* 2001; Willis and Whittaker 2002; Pearson and Dawson 2003). Although it is possible that observed patterns are a result of direct climate effects (eg. Post and Forchhammer 2002; Humphries *et al.* 2004), species presence and abundance is likely more often determined by resources than climate (Hutchinson 1957; Brown 1984; Manly *et al.* 2002). If this paradox of superior predictive power of climate across large scale despite presumed mechanistic primacy of resources at local scales is a byproduct of the scale of analysis, decreasing the scale across which abundance is measured should enhance the predictive power of habitat and weaken the predictive power of climate (Whittaker *et al.* 2001; Fig. 5: Pearson and Dawson 2003). This has important implications for climate and resource-based approaches to predicting the distribution and abundance of species.

Environmental Change

Climate models predict more pronounced warming in the arctic than any other region, with increases as high as 10°C in winter over the next 80 years (Maxwell 1997; Intergovernmental Panel on Climate Change 2001). Changes are already apparent, as most arctic regions have experienced milder winters in the past

several decades (Callaghan *et al.* 2002; Intergovernmental Panel on Climate Change 2001). As the southern limit of the arctic, the FTT is expected to undergo similar extents of climate change (Callaghan *et al.* 2002; IPCC). Thus, the FTT will experience more severe climate change sooner than more southerly ecotones, and can thus be used as a model for the type of changes that will happen elsewhere. Climate change will most likely alter the location and structure of the FTT, as has occurred in past warming bouts (Payette *et al.* 2001; Skre *et al.* 2002) and corresponding shifts in the range of associated animal species are expected (Parmesan *et al.* 1999; Humphries *et al.* 2004; Parmesan and Yohe 2003; Thomas *et al.* 2004). Climate warming has already altered the behavior, phenology, community structure and distributions of animals and their habitats (Payette 1986; Parmesan *et al.* 1999; Post *et al.* 1999; Hughes 2000; Payette *et al.* 2001; Post and Forchhammer 2002; Parmesan and Yohe 2003; Root *et al.* 2003; Berteaux *et al.* 2004).

The range shifts and abundance changes imposed by climate change are likely to vary from species to species since different aspects of climate are predicted to change in discordant fashion (Intergovernmental Panel on Climate Change 2001) and species vary in their sensitivity and adaptability to specific components of climate (Berteaux *et al.* 2004). Species adapt to climate change through dispersal, evolution, and phenotypic plasticity (Berteaux *et al.* 2004). Species can be limited directly by climate variables, if some aspect of temperature or precipitation acts directly on a species bioenergetics and/or phenology (Post and Forchhammer 2002; Berteaux *et al.* 2004; Humphries *et al.* 2004) or indirectly if climate mediated interactions among species direct patterns of diversity through food web dynamics (Risser 1995; Skre *et al.* 2002; Ives and Cardinale 2004). Time-lags in the ecological sorting process (Burns *et al.* 2003) and an increasing importance of habitat heterogeneity as climate warms (Kerr and Packer 1997) will result in emergent ecosystems with no current analog (Hughes 2000; Walker *et al.* 2003). These new communities will be composed of invading southern species as much as by evading northern species (Hughes 2000; Humphries *et al.* 2004; Thomas *et al.* 2004).

The FTT is also susceptible to direct industrial alteration. The FTT is experiencing accelerating industrial development both in Asia (Vlassova 2002) and North America (Johnson *et al.* 2005). Mineral and petroleum acquisition are the most prevalent types of disturbance, and there is huge increase in both activities across the FTT (Vlassova 2002; Johnson *et al.* 2005). Many recent shifts in species ranges are associated with anthropomorphic environmental modification and species are thus expected to continue to be affected by such perturbations (Channell and Lomolino 2000; Case *et al.* 2005).

Documenting the distribution, ecological patterning and resource selection of species in areas under threat of change is imperative to conservation. The persistence of species is often most limited and threatened at range peripheries, and extirpation and colonization usually results from range shifts (Channell and Lomolino 2000). Resource utilization varies across a species range (Swihart *et al.* 2003), making it difficult to extrapolate models developed in the core of the range to range peripheries (Parmesan *et al.* 2005). However, few classifications of vertebrate species patterning or resource selection have been conducted at range boundaries, such as the FTT (Ste-Georges *et al.* 1995; Johnson *et al.* 2005). Documenting current species habitat associations at the FTT is essential to building predictions and as a baseline to compare with future states. Chapter 1 of this thesis addresses the pattern of species diversity and ecological patterning of terrestrial vertebrates across the FTT, while chapter 2 examines the resource use of individual species at this juncture coincident with their range boundaries. Thus this thesis fulfills the need for good baseline data from which I infer ecological significance.

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CHAPTER 1: DIVERSITY AND ECOLOGICAL STRUCTURE OF TERRESTRIAL VERTEBRATES ACROSS THE FOREST TO TUNDRA TRANSITION.

Abstract

Ecotones are gradients of composition that represent important foci for the study of habitat partitioning and coexistence of species. However, change in vertebrate species composition across many of the ecotones that separate biomes remains uncharacterized. Herein we provide the first characterization of the pattern and environmental predictors of terrestrial vertebrate diversity and ecological structure over the Yukon Forest to Tundra Transition (FTT). We sampled terrestrial vertebrates at 66 sites over a 390km gradient spanning the FTT, using snow tracking (winter) and small mammal trapping (summer). We used diversity metrics, indirect gradient analyses (Nonmetric Multidimensional Scaling), indicator species analyses, and hierarchical clustering to characterize the diversity and ecological structuring of species assemblages. We then used an information theoretic approach (Akaike's Information Criterion) to test the relative plausibility of general linear models predicting vertebrate diversity and structure based on environmental variables. Finally, we decomposed the variation explained by climate and vegetation in mixed models using partial regression. The FTT is characterized by a sharp drop in diversity and strong ecological structure. Terrestrial vertebrates present in the transition are sorted into four discrete assemblages that are strongly affiliated with boreal, taiga, or tundra habitats. The habitat affinities of the different assemblages maintain strong ecological structure across a mosaic of adjacent, contrasting habitat types, such that there is little overlap of boreal, taiga, and tundra species at any given site. The strongest predictors of species richness and assemblages are, in order of importance, vegetation type, seasonality, growing season temperature and precipitation. Although the taiga species assemblage can be considered ecotone specialists, fine-scale species richness is not higher within the ecotone because habitat affinities of the three major assemblages reduces site co-occurrence.

Introduction

There is a strong biodiversity gradient across the earth, with decreasing diversity observed from the tropics to the poles (Fischer 1960; Pianka 1966; Willig *et al.* 2003; Hillebrand 2004). Much work has been dedicated to describing and inferring mechanisms behind this major biogeographical paradigm (reviewed in Whittaker *et al.* 2001 and Willig *et al.* 2003). A central component of our understanding of this gradient is the importance of spatial scale; diversity gradients observed across continental scales may be generated by a variable array of gradients and processes operating at more regional scales (Gosz 1993; Whittaker *et al.* 2001). Thus, the large-grained, species occurrence approaches that predominate the literature (Currie 1991; Badgley and Fox 2000; Willig *et al.* 2003; Hillebrand 2004; Rodriguez *et al.* 2006) may obscure a frequent pattern of relatively constant diversity across large spatial extents interspersed by hotspots of change across small spatial extents (Gosz 1993; Risser 1995a; Walker *et al.* 2003; Ricklefs 2004; Rodriguez and Arita 2004; Mena and Vazquez-Dominguez 2005).

Landscapes are scale variant mosaics of habitat patches separated by boundaries (Gosz 1993; Cadenasso *et al.* 2003; Peters *et al.* 2006). Edge effects operating at these boundaries create ecological gradients called ecotones (Risser 1995a; Baker *et al.* 2002; Cadenasso *et al.* 2003; Ries *et al.* 2004). The largest scale terrestrial patches are biomes, distinct regions defined by similar vegetation, soil, and climate (Prentice *et al.* 1992), separated by expansive ecotones (Risser 1995a). Since the ecological importance of boundaries was emphasized over 100 years ago (Clements 1905), many have studied patterns of biodiversity (Willig *et al.* 2003; Hillebrand 2004), edge effects (Baker *et al.* 2002; Ries *et al.* 2004; Peters *et al.* 2006), and ecological structure (Krause *et al.* 2003; Proulx *et al.* 2005; Walker *et al.* 2003) at ecotones. However, these studies rarely focused at the spatial scales required to assess community composition patterns across the boundaries separating the world's biomes, particularly for vertebrates. Given that vertebrates are frequent subjects of continental scale diversity studies, research on vertebrate communities composition across biome boundaries is a critical missing link

between ecotone studies conducted at the habitat scale and diversity gradient studies conducted at the continental scale.

The forest to tundra transition (FTT), the largest ecotone in Canada, is a mosaic of lessening tree abundance marking the transition between the boreal forest and the arctic tundra biomes (Payette *et al.* 2001; Callaghan *et al.* 2002). In the broadest sense, this is the transition from forest to tundra (Payette *et al.* 2001). However, this transition can be further divided into boreal, taiga, and tundra, where boreal is characterized by dense coniferous and mixed forests, taiga is characterized by sparse, stunted coniferous forests growing on permafrost, and tundra is characterized by permafrost and the absence of trees (Callaghan *et al.* 2002). We chose to characterize the terrestrial vertebrate community across this ecotone, because the FTT coincides with a major boundary in the distributions of North American mammals (Hagmeier 1966) and is a region of relatively low diversity allowing the relative abundance of most major species to be sampled.

In the present study, we quantify how the relative abundance of terrestrial mammals and birds detected through winter snow tracking and summer snap trapping varies across more than 60 sampling sites spanning the FTT in north-western Canada. In particular, we sought to evaluate:

1. The pattern of diversity to determine a) if the gradient in diversity across the FTT ecotone corresponds to the continental gradient in diversity, b) if diversity is higher in the ecotone than the surrounding areas, and c) what environmental factors best predict diversity.
2. The pattern of ecological structure to determine a) if there is a strong ecological sorting of species across the FTT gradient, b) if species assemblages in the ecotone correspond to boreal and tundra species assemblages or represent a new combination of ecotonal species, and c) what environmental factors best predict the ecological structure.

Methods

Study Area

Our study area was located in the northern continental Yukon and Northwest Territories, Canada, consisting of the region immediately adjacent to the Southern 500km of the Dempster highway and immediately adjacent to the Klondike highway 25 km east and west of the junction of the Klondike and Dempster highways. This transect spans 63°55' N, 138°30' W to 67°11' N, 135°41' W, covering a straight line distance of *ca.* 390km from contiguous boreal forest to contiguous arctic tundra. Along this gradient, we sampled 78 randomly selected sites for medium and large vertebrates via snow tracking in winter and a subset of 66 sites for small mammals using snap trapping in summer.

Species Composition

Large Vertebrates- Snow Tracking

In winter, between 8 February and 21 April 2005, we surveyed one triangular snow tracking transect at each of the 78 sites (1 km per side = 3 km total; Fig. 1; similar to Pellikka *et al.* 2005). Transects were situated at least 100m from the highway to minimize road disturbance effects, while retaining accessibility. Surveys, conducted on foot, consisted of recording all mammal track crossings, at least 24 hours after snowfall, to allow for the accumulation of tracks. We haphazardly mixed the sampling order across the gradient over time, to avoid confounding time of year with habitat type. More than 95% of all triangles were surveyed by TP for consistency and all questionable tracks were measured, photographed and verified by TP. The smallest mammal for which snow track data were collected was the least weasel (*Mustela nivalis*). Most mammals smaller than 200g are primarily subnivean (Pruitt and Lucier 1958) and, when moving on the snow surface, leave tracks too small to identify with certainty (Elbroch 2003).

We use track density as an index of relative abundance for each mammal present. Although track number is highly correlated to animal abundance

(Thompson *et al.* 1989) we seek only to compare relative abundance within species across sites and make no assumptions about absolute abundance.

Small Mammals- Trapping

In summer, between 8 July and 17 August 2005, we trapped small mammals at 66 of the 78 winter triangle transect sites. Two 250 m trap-lines, with 25 trap stations each, were sampled coincident with two closest triangle axes to the road, 10 meters from the apex (Fig.1). Trap stations consisted of 1 Museum Special™ and 1 Victor™ snap trap baited with a mixture of rolled oats, peanut butter and powdered milk. All traps were checked in the morning and the day after setting/resetting, for three consecutive trap nights. Specimens were immediately frozen and transported to Whitehorse, YT, where they were identified to species by Yukon Government Biologists and Dave Nagorsen (Mammalia Biological Consulting) using keys in Nagorsen (2002) and van Zyll de Jong (1983). We converted trapping data to capture per unit effort (CPUE) by dividing captures by trap nights (the number of trap sets minus half the number of disturbed traps without captures).

Although trapping indices are proportional to absolute abundance, the relationship between the two vary depending on time of year and study location and calibration is necessarily study specific (Hopkins and Kennedy 2004). Small mammal abundance in seasonal environments generally increases from spring to autumn as populations rebound from winter mortality (Norrdahl and Korpimäki 2002; Hopkins and Kennedy 2004). To minimize the effect of time of year on our estimates of relative abundance, we did not commence trapping until 30 days after snow melt and we staggered the temporal order of our small mammal sampling. Moreover, we make comparisons of relative abundance within species across sites only and make no assumptions regarding absolute abundance.

Compilation

Data for small and large mammals was compiled into a single community composition matrix (C) for all sites at which both snow tracking and trapping

were conducted (n=66). To make track number and CPUE comparable, data was relativized to a measure of relative abundance for each species, using:

$$b_{ij} = x_{ij} / x \max_j$$

where rows (*i*) represent sites and columns (*j*) represent species in C, and $x \max_j$ is the largest abundance value for species (*j*) across all sites (*i*=1-66). This relativization equalizes the weight of rare and common species. We subsequently normalized C using the arcsine squareroot transformation (Zar 1999).

Environmental Variables

Landcover

Landcover data were extracted from thematic mapped orthorectified images based on Landsat 7 Enhanced Thematic Mapper (ETM+) 25 x 25m pixel images (Wulder and Nelson 2001; Wulder *et al.* 2002), created by the Canadian Forest Service and Canadian Space Agency joint project, Earth Observation for Sustainable Development of Forests (EOSD). We reclassified images into six cover classes: conifer, deciduous, herbaceous, shrub, rock and water. The proportion of these cover types within 575m circle radius encompassing each sampling triangle was calculated using raster calculator functions in ArcGIS® (Environmental Systems Research Institute 2002), and the resultant neighborhood statistics were collected for each triangle centroid using Hawth's Analysis® Point Intersect tool (Beyer 2004).

Climate

Climate data was extracted from PRISM (Parameter-elevation Regressions on Independent Slopes Model) datasets, including average monthly and annual temperature and precipitation for 1969-1990, created for the Yukon Territory (Daly *et al.* 1994; Daly *et al.* 2002; Simpson *et al.* 2005). Climate variables were extracted for each site by intersecting winter triangle centroid point data through the PRISM layers using Point Intersect tool, Hawth's Analysis® tools extension (Beyer 2004), in ArcGIS® (Environmental Systems Research Institute 2002). Our five most northerly sites lie outside the available climate data spatial extent. For

these sites, climate was sampled at the nearest available pixel having the same aspect and elevation ($\pm 10\text{m}$) as the site location (average distance 7.6 km; range 2.6-11.6 km). We selected a subset of climate variables corresponding to our *a priori* hypotheses that species would be influenced by both annual and seasonal climate: annual, growing season (June-August, inclusive; average temperature ≥ 0 degrees and most precipitation was rain) and winter (October-April, inclusive; average temperature ≤ 5 degrees below freezing, most precipitation was snow) average temperature, cumulative precipitation, and seasonality (July minus January temperature).

Compilation

Environmental data were combined into a single matrix, E, for the 66 mammal community sites. To make temperature, precipitation and landcover data comparable we relativized E by the standard deviate:

$$b_{ij} = (x_{ij} - \bar{x}_j) / s_j$$

where s_j is the standard deviation within each column (j) of matrix E.

Spatial variables

In addition to the mammal and environment variables, each site was classified according to latitude, longitude and elevation. We extracted the elevation for each site as the centroid elevation of each triangle using the Point Intersect tool, Hawth's Analysis[®] tools extension (Beyer 2004) in ArcGIS[®] (Environmental Systems Research Institute 2002).

Pattern Characterization

Diversity

We characterized the pattern of alpha diversity over the FTT as species richness (S) and beta diversity as spatial turnover (β_{sim} ; Lennon *et al.* 2001) and as the 'number of distinct communities' (β_w ; Whittaker 1972). Spatial turnover is the most accurate representation of the average change in species composition between a site and neighboring sites (Lennon *et al.* 2001). For the present

analyses, the neighboring sites considered were the nearest site to the north and south.

To investigate potential predictors of species richness over the FTT we created a series of general linear models of species richness regressed on vegetation and climate variables, which we hypothesized to be biologically important. One site for which we had no cover type data was removed (n=65 sites). We first created a series of univariate regression models to determine the top environmental variables describing species richness. We then created a series of multivariable models by combining selected variables ($r^2 > 0.10$, $P < 0.05$) into biologically meaningful combinations. To avoid multicollinearity amongst variables, only models with variable tolerance values > 0.80 were retained. These models were then ranked for plausibility and parsimony using an information theoretic approach, Akaike's Information Criterion (AIC; Burnham and Anderson 2002). We also regressed spatial variables, latitude, and elevation to assess the purely geographical and spatially autocorrelated aspects of richness.

We examined the relative importance of climate and land cover variables using partial regression analysis of the best bivariate species richness model containing terms of both types. We decomposed the variation in species richness into that a) described exclusively by climate, b) described equally well by climate and land cover, and c) described exclusively by cover (Legendre and Legendre 1998).

Ecological Structure

To describe the ecological structure of species occurrence across the FTT we used indirect gradient analysis, ordinating sites in species space using Nonmetric Multidimensional Scaling (NMS). NMS is the best suited ordination technique for community data, requiring no inherent assumptions regarding the data structure (e.g., linear relationships amongst species, few zeros; Clarke 1993). All ordinations and related analysis were performed using PC-ORD software (McCune and Mefford 1999; NMS algorithms: Kruskal 1964; Mather 1976). To reduce the noise and improve the interpretability, we first removed rare species, occurring at less than 4.5% of sites from Matrix C. We then conducted a series of NMS ordinations [Sorensen (Bray & Curtis) distance measure, 50 runs with real

data, with 6 axes initially and sequential step downs in dimensionality with each ordination] with a predetermined starting configuration [Detrended Correspondence Analysis (DCA) ordination; PC-ORD defaults; 26 segments], to chose the optimal number of axes (dimensions; k) that minimizes stress (a measure of the NMS distances relative to the original distances in n dimensional space), while maintaining interpretability. We then calculated a final ordination in k dimensional space, using the same predetermined start configuration, and assessed the likelihood of attaining similar stress by chance using Monte Carlo test (50 runs with randomized data). Finally, to maximize interpretability, we Varimax rotated the decisive ordination (Legendre and Legendre 1998).

To visualize the correspondence between environmental attributes and ecological structure we overlayed categorical environmental clusters on the ordination. To group sites by environmental attributes we used hierarchical clustering [relative euclidean distance and Ward's linkage method (Orloci 1967)]. We determined the most ecologically meaningful level of clustering to overlay using indicator species analysis by selecting the number of clusters where a) the maximum number of species were significant indicators and b) the summed indicator species significance was minimized (Dufrene and Legendre 1997). We then used a multivariate nonparametric method, Multiple Response Permutation Procedure [MRPP: Sorensen (Bray-Curtis) distance (Mielke and Berry 2001)], to compare the environmental attributes of these site clusters.

We determined the relative importance of individual species abundances and the ability of environmental variables to describe the ordination by calculating the cumulative variance of the original distances in k dimensional space explained by each species/variable:

$$P(\text{original}\sigma^2) = \sum_{i=1}^k \frac{r^2 \text{variable}_a \times r^2 \text{Axis}_i}{r^2 \text{Axis}_i / \text{original}\sigma^2}$$

where $r^2 \text{variable}_a \times r^2 \text{Axis}_i$ is the amount of variance in Axis i described by variable a , and $r^2 \text{Axis}_i / \text{original}\sigma^2$ is the original variance accounted for by Axis i . We then divided $P(\text{original}\sigma^2)$ by $\text{original}\sigma^2$ for a measure of ordination variance explained.

To further characterize ecological structure across this gradient we grouped species with corresponding and proportional patterns of abundance into spatial compartments. Using hierarchical clustering we created a dendrogram of species clustered by their numerical and distributional overlap [relative euclidean distance, Ward's linkage method (Orloci 1967), and Wishart's objective function (Wishart 1969)]. We then chose a clustering level that broke species into ecologically meaningful groups while retaining much of the original information. At this level, we combined the relative abundance data of species within each cluster for each site. We transformed these compartment abundance values, using a modified log transformation:

$$b_{ij} = \log[x_{ij} + \log^{-1}(\text{int}(\log(\min_j)))] - \text{int}(\log(x\min_j))$$

We regressed each compartment's abundance by k ordination axes to determine if the delineated level of compartmentation maintained the original ecological structure. We then used the same model building and selection techniques used for describing the pattern of species richness (see *Diversity*) to determine the best fit and most plausible and parsimonious model describing abundance within compartments. We included a model containing the same parameters as the model that best described species richness in each compartment model set. Finally, as with diversity, we conducted partial regression analysis to decompose the importance of climatic and vegetative variables (see *Diversity*).

Results

Diversity

We detected 22 terrestrial vertebrate species across 66 sample sites (Table 1). Of these, 20 were terrestrial mammals representing a large proportion of the 34 species thought to occur in this region (Banfield 1981). Species richness (α diversity, S) declined significantly with a loss of 0.7 species per degree of latitude ($y = -0.69x + 49.91$; $F_{1,63} = 8.683$, $P = 0.004$; Fig. 1), but the relationship had low explanatory power ($r^2 = 0.12$) and residuals were non-uniform. Introducing elevation into the model, in addition to latitude, substantially improved the explanatory power ($r^2 = 0.37$, $F_{2,62} = 19.471$, $P < 0.005$). Species richness at each

sampling site was not consistently higher in the midst of the ecotone than at the southern and northern periphery of the gradient, but total species richness was only slightly higher in the 9 most southerly sites (16 species) and lower in the 9 most northerly sites (9 species) than in 9 intervening sites, centered on the middle of the FTT at 65.5° N (15 species; Fig. 1). Global β diversity (β_w) was 4.55, and there was no relationship between spatial turnover (β_{sim}) and latitude ($r^2 = 0.00$, $F_{1,63} = 0.058$, $P = 0.811$; Fig. 1).

Several environmental variables were reasonably strong univariate predictors of species richness, with herbaceous vegetation cover being the strongest (Table 2). However, the two most likely models both included herbaceous vegetation and seasonality (Table 2). The relative likelihood of both models is very strong compared to the 11 others we evaluated and both have much more explanatory power than the latitude plus elevation model. Coefficient signs indicate species richness increases with decreasing herbaceous vegetation, increasing seasonality, and increasing growing season precipitation (Table 2).

Partial regression analysis of model 2 (Table 2) indicates 22, 13, and 10 % of variation in species richness was explained by, respectively, herbaceous vegetation alone, seasonality alone, and herbaceous vegetation and seasonality in combination.

Ecological Structure

Gradient Analyses

Our final ordination optimized to three dimensions indicates strong ecological structure among terrestrial vertebrates across the FTT (Fig. 3). Axis one, two, three and the cumulative 3 dimensional ordination explain, respectively, 34, 26, 18, and 78 % of the original variance (measured as the r^2 between the distance in ordination space and original n dimensional space). The relationship between individual species abundance and the 3 dimensional ordination varies from r^2 of 0.25 to <0.005 (Table 1). Abundance of fox, marten, red-backed vole, red squirrel and snowshoe hare was most correlated to the ordination space (Table 1). The

NMS Ordination axes describe 64 % of the variation in species richness ($S = -0.31 \times \text{Axis1} - 0.66 \times \text{Axis2} + 0.03 \times \text{Axis 3}$; $r^2 = 0.644$, $F_{3,61} = 36.812$, $P < 0.005$).

Indicator species analysis revealed that sites cluster by environmental variables most indicatively at two levels: 1) at the three cluster level, where 14/18 species are significant indicators and 2) at the seven cluster level, with a summed significance for indicator species of $P = 0.076$ (Fig. 3). At both cluster levels there was a significant difference in the environmental variables between clusters (MRPP: 3 clusters: $A = 0.32$, $P < 0.005$, 7 clusters: $A = 0.74$, $P < 0.005$). At both levels, clusters correspond closely to dominant cover classes and are categorized and named accordingly (Table 3). The largest environmental difference between site categories is a trend of decreasing coniferous and increasing herbaceous cover from boreal to tundra (Table 3). Site categories are clumped in ordination space and there is an overall gradient in 3 dimensions from *Tundra* (*northern tundra*, *southern tundra*, *valley taiga*) through *Taiga* (*northern taiga*, *open taiga*, *middle taiga*) to *Boreal* (*core boreal*; Fig. 3). There is clear separation between *Tundra*, *Taiga* and *Boreal* sites with the exception of some *valley taiga* (*Tundra*) sites in the space of *Taiga* and *Boreal*, some *middle taiga* (*Taiga*) sites in the space of *Boreal* and some *northern taiga* (*Taiga*) sites in the space of *Tundra* (Fig. 3). The presence of *valley taiga* (*Tundra*) sites in *core boreal* (*Boreal*) space likely results from a misclassification of *valley taiga* sites into *Tundra* due to sampling grain. *Valley taiga* consists of a narrow band of taiga between mountains and thus climate variables, sampled at 2km^2 , are indicative of the surrounding mountains and not of the valley (Table 3). Biplot vectors are parallel to the major gradient from core boreal to northern tundra sites (Fig. 3).

Environmental variables vary widely in their ability to describe the three dimensional ordination space, although the overall trends are consistent with the site habitat groupings (Table 4). Coniferous and herbaceous vegetation, seasonality, annual and winter precipitation and growing season temperature best describe the ordination (Table 4). There is a trend in average species richness (S) with 6.7 ± 0.7 , 5.2 ± 0.4 and 3.9 ± 0.4 for *Boreal*, *Taiga* and *Tundra* habitat categories respectively (Fig. 5). Average spatial turnover (β_{sim}) is quite similar

across habitat categories with 0.71 ± 0.02 , 0.71 ± 0.04 , and 0.70 ± 0.04 for *Boreal*, *Taiga* and *Tundra* habitat categories respectively (Fig. 5).

Spatial Compartmentation

We cut the species clustering dendrogram into four groups corresponding to a balance between information retained (~ 55%, 60%, 45%, 40% retained) and meaningful ecological species groupings based on previous known affiliations (*Boreal*, *Taiga*, *Tundra*, and *Vagrant* species; Fig. 4, Table 1). The NMS Ordination axes describe 69, 84, 67, and 36 % of the *Boreal*, *Taiga*, *Tundra*, and *Vagrant* within compartment summed species abundance (*Boreal* = $-0.24 \times \text{Axis1} - 0.72 \times \text{Axis2} - 0.08 \times \text{Axis3}$; $F_{3,61} = 45.329$, $P < 0.005$; *Taiga* = $-0.76 \times \text{Axis1} - 0.30 \times \text{Axis2} + 0.41 \times \text{Axis3}$; $F_{3,61} = 106.174$, $P < 0.005$; *Tundra* = $0.59 \times \text{Axis1} + 0.22 \times \text{Axis2} + 0.34 \times \text{Axis3}$; $F_{3,61} = 41.784$, $P < 0.005$; *Vagrant* = $-0.06 \times \text{Axis1} - 0.16 \times \text{Axis2} - 0.55 \times \text{Axis3}$; $F_{3,61} = 11.590$, $P < 0.005$).

We were able to describe a substantial amount of the grouped species abundances with several environmental variables for all but the *Vagrant* compartment (Table 5). As for species richness, AIC shows that the model containing herbaceous vegetation, seasonality and growing season precipitation were the closest approximation to reality describing abundance in the *Boreal* and *Taiga* compartments. AIC shows that the model containing herbaceous vegetation and winter precipitation best described abundance in the *Tundra* compartment (Table 5). Herbaceous vegetation, seasonality, and growing season temperature were the best overall descriptors of compartment abundance (Table 5).

The bivariate model containing seasonality and herbaceous vegetation cover was highly ranked by AIC and described a substantial amount of the *Boreal*, *Taiga* and *Tundra* grouped species abundances (5th, 3rd and 2nd rank; 45, 44, and 43 % respectively) and was thus decomposed using partial regression. There was ~ 10 % overlap in variation explained by the climate and vegetative variable for all groups (Fig. 2).

Of the four compartments, 3 correspond closely to environmental clusters delineated at the 3 cluster level (Fig. 5). There is a strong consistency between

individual species abundance, compartment delineation and environmental clusters (Fig. 5).

Discussion

This study provides the first systematic examination of diversity and ecological structure of vertebrate fauna along the FTT. There is strong consensus between the various analytical techniques we used to characterize the FTT suggesting a clear emerging pattern and that our characterization is a good approximation of reality. The ordination axes explained more than 60 % of the observed richness gradient and compartmental abundance (with the exception of the Vagrant compartment which remains unexplained). The species that were most correlated to the ordination axes represented all spatial species compartments (Table 1; Fig. 5). The observed global beta diversity indicates a high level of complexity, suggesting several distinct communities, corresponding to compartmentation. Compartments in turn correspond to the environmental site clusters we overlayed on the ordination (Fig. 5). Environmental correlates of the diversity gradient, ordination axes, compartment habitat models and environmental site clustering suggest that herbaceous and coniferous vegetation, seasonality, growing season temperature and precipitation are important (Fig. 3; Fig. 5). Predictors related to the vegetation were the best overall descriptors of this pattern implying that faunal species flux at this boundary is mediated by mechanisms directly related to plant regime. Marginal overlap (~ 10 %) between the variation explained by vegetation and climate further suggests vegetation is the major driver of terrestrial vertebrate patterning. The emerging pattern is that terrestrial vertebrate fauna is limited by the vegetative regime into compartments which vary in space to create a diversity gradient. This matches our preconceived notion of the importance of abrupt shifts in plant regimes, which are widely implicated in modifying ecological flows and are often used to define ecotones (Risser 1995a; Cadenasso *et al.* 2003; Walker *et al.* 2003; Ries *et al.* 2004).

In the remainder of the discussion, we will examine diversity and ecological structure in detail, discuss the importance of scale to our results, and then synthesize this into a model of vertebrate fauna at the FTT in our conclusion.

Diversity

Species richness patterns across the FTT are consistent with the continental trend of decreasing diversity with increasing latitude (Willig *et al.* 2003; Hillebrand 2004), and with the dominant paradigm of ecotones as sharp gradients in the midst of less abrupt regional trends (Gosz 1993; Risser 1995a). The loss of 0.7 species per degree of latitude suggested by the linear model translates to a flux of 2.8 species across 3.25° of latitude spanning the Yukon FTT. Correspondingly, the nine core boreal sites at the southern extreme of our gradient have, on average, about 3 more species (average \pm SE species richness = 6.7 ± 0.7) than the 13 northern tundra sites at the northern extreme of our gradient (species richness = 3.6 ± 0.3). This represents a 46 % decline in species richness across the FTT, which far exceeds the continental scale relationship that predicts a 7.4% decline in mammal species density over the latitudinal extent of our gradient. Thus across the FTT there is an increased change in diversity relative to the continental trend, as documented for birds (Baker *et al.* 2002), mammals (Mena and Vazquez-Dominquez 2005) and plants (Walker *et al.* 2003) for a variety of other ecotones.

Contrary to our expectations, we observed no consistent trend of elevated species richness at sites within the midst of the FTT, relative to boreal and tundra sites at the periphery of the FTT. Ecotones should be hotspots for species diversity because of a) overlapping ranges of species from adjacent ecosystems and b) novel environmental conditions found within the ecotone providing habitat for ecotone specialists (Risser 1995a; Ries *et al.* 2004). However, studies have shown this not to be the case for some birds (Baker *et al.* 2002), mammals (Stevens and Husband 1998), and plants (Walker *et al.* 2003). We did identify an assemblage of ecotone specialists (*Taiga*, Fig 4; Fig. 5), but this did not translate into higher diversity at ecotonal sites because a) sites where taiga species were present were largely devoid of boreal or tundra species and b) the taiga cluster was not more speciose than the boreal and tundra groups. Thus, the pronounced habitat partitioning of boreal, taiga, and tundra species across the forest tundra transition, despite the juxtaposition of habitat types across the gradient, meant that there was little overlap of species from adjacent ecosystems at any given site. If,

however we compare the gamma diversity present across nine sites in the interior of the gradient that include a mixture of habitat types (15 species) to that present across the nine core boreal sites at the southern periphery of the gradient (16 species) and the nine tundra sites at the northern periphery of the gradient (9 species), we can see that at a coarser scale there is almost as high diversity in the midst of the ecotone than in the adjacent contiguous forest and tundra. This suggests that when the scale of analysis is broad enough to include different habitat classes in each grain or long enough to capture temporally shifting boundaries, can species richness peak over ecotones (Gosz 1993; Risser 1995a; Peters *et al.* 2006).

We expected beta diversity to peak over the FTT relative to the boreal or tundra (Spector 2002) and to decline with increasing latitude (Willig *et al.* 2003). However, beta diversity did not adhere clearly to either pattern. The observed Global β diversity (β_w) value is indicative of at least 4 distinct communities suggesting a medium to high level of complexity, likely resulting from the patchiness of the FTT itself being composed of many smaller patch ecotones (Gosz 1993).

Although species richness does decline with latitude, there is a lot of residual variation that can be reasonably well explained by land cover and climate. AIC rankings suggest herbaceous vegetation, seasonality and growing season precipitation are the most important variables, (Table 2). Diversity across the FTT increases with increasing forest structure, increasing seasonality, and decreasing summer precipitation (Table 2). We expected to observe an increase in diversity with increasing forest structure because boreal forests host more species of terrestrial vertebrates than arctic tundra, likely in part because forests are vertically structured environments that offer more niche space and higher plant diversity than tundra environments (Diaz and Cabido 2001). However, the relationship between diversity and climatic variables is less intuitive. Higher environmental stability, temperature and precipitation are usually associated with higher species richness (Hawkins *et al.* 2003; Willig *et al.* 2003) but we found increased diversity at sites with increased seasonality and reduced precipitation.

Identifying potential mechanisms that could generate these correlations will require better, fine-scale climate data (due to the regions sparse instrumental record and topographic complexity) and more detailed ecological research focused on the complex inter-relationships between climate, vegetation and vertebrate abundance.

Ecological Structure

Ecological structure is the patterned, non random assortment of organisms associated with underlying ecological sorting. Our analyses show there is strong ecological structure across the FTT. Close correspondence between the ecological structure of the community based on species abundances (NMS ordination) and environmental characteristics (cluster analyses), suggests ecological structure at the FTT is strongly linked to species habitat preferences. This conforms to our expectation that despite the complexity, sites along the FTT should be classifiable by species configurations. The only exceptions to this order include some overlap between habitat groupings in ordination space. The overlap among groups is a byproduct of the species similarity among sites in neighboring areas (spatial autocorrelation), whereby *Taiga* sites are intermediate in species composition between the *Boreal* and *Tundra*, consisting of species representative of both neighboring habitat types (Fig. 5).

Correlations between environmental variables and the three dimensional ordination space suggest that at one extreme, increasing conifer cover, seasonality and growing season temperature correspond to *Boreal* sites and that at the other, increasing amounts of herbaceous vegetation and precipitation correspond to *Tundra* sites. *Taiga* sites correspond to the middle ground between these two extremes with some tendency toward *Boreal* space. In a broad sense, the taiga represents a transitional biome across the FTT. This type of unique transitional community composed of an intermediate mix of species has been demonstrated at smaller scale ecotones for birds (Baker *et al.* 2002), and plants (Walker *et al.* 2003), supporting the idea of the ecotone itself being composed of many finer ecotones. Correlations between the axes and vegetation are strongest, while

seasonality and precipitation are close seconds (Table 4), again reinforcing the importance of the vegetation regime.

Compartmentation is a particular kind of ecological structure where species co-occur and are characterized by strong ecological interactions (McCann *et al.* 2005). Based on range maps we anticipated nearly coincident boundaries of many species at the FTT (Hagmeier 1966). However, range boundaries do not represent the spatial heterogeneity of distribution and abundance within those boundaries (Brown 1984). Demonstrating that several species occur in proportional equivalence at their range boundaries suggests that they cluster into ecologically meaningful groups (Krause *et al.* 2003; Proulx *et al.* 2005). We have strong evidence for such clustering, and three of four species clusters, *Boreal*, *Taiga*, and *Tundra*, correspond closely to our *a priori* conjecture, based on habitat associations and trophic linkages, and reflect much of the ecological structure represented by our ordination.

Overall, the species composition of each compartment matches the habitat separation along both climatic and vegetative grounds (Table 3). *Boreal* compartment habitat is characterized by coniferous forests, warm dry summers, and cold winters and the compartment is composed of species commonly associated with the boreal forest (e.g., lynx, hare and moose, Wilson and Ruff 1999). The *Taiga* compartment habitat is characterized by similar vegetative characteristics, wetter summers, and colder winters relative to the *Boreal* compartment (Table 5). This compartment is composed of species that although present over much of the boreal and tundra ecosystems are most abundant at their interface in the taiga (e.g., caribou and wolverine, Fig. 5), forming an ecotonal grouping (Ries *et al.* 2004; Mena and Vazquez-Dominguez 2005). Woodland caribou are present in the taiga region of the Yukon FTT year round but barren ground caribou vastly outnumber them during the winter migratory stopover (Griffith *et al.* 2002). These in turn provide winter food for wolverine, through the carcasses left from wolf and human caribou kills (Johnson *et al.* 2005). The inclusion of the American marten, taiga and red-backed vole group in the *Taiga* compartment is less intuitive and contradicts previous studies categorizing marten

as an old growth forest species (Wilson and Ruff 1999). *Tundra* compartment habitat is characterized as cold, stable, treeless and covered by low-lying herbaceous vegetation, indicative of tundra. Species within this compartment include two well known tundra species the ptarmigan and collared lemming as well as one which is ubiquitous throughout North America having replaced the arctic fox in many tundra areas (Hersteinsson and Macdonald 1992; Wilson and Ruff 1999; Dalen *et al.* 2004).

We were not able to characterize the *Vagrant* compartments preferred habitat. The *Vagrant* grouping is composed of species which are seemingly spread haphazardly across the gradient (Fig. 5). A lack of consistent pattern is suggested by smaller amount of clustering information retained in delineating this species group and the reduced ecological structure maintained relative to the other three (5% less information and $NMSr^2$ 0.31 less than that of the next least coherent group- *Tundra*). This could result from these species being generalists, compartmental integrators (Krause *et al.* 2003; McCann *et al.* 2005; Proulx *et al.* 2005) or our inability to sample them reliably due to, for example, their subnivean tendencies (Pruitt and Lucier 1958).

Species cluster into spatial compartments through several mechanisms (Krause *et al.* 2003; McCann *et al.* 2005; Proulx *et al.* 2005). Amongst the foremost of these mechanisms are similar habitat preferences and strong trophic interactions (McCann *et al.* 2005). The importance of similar habitat preferences is obvious at a region with abrupt changes of physiognomy (Walker *et al.* 2003; Ries *et al.* 2004; Cadenasso *et al.* 2003), such as the FTT (Payette *et al.* 2001). Our analyses show that compartmental habitat selection is occurring. However, we have not calculated energy flows and food web linkages and thus are limited to occupancy as a proxy measure of spatial compartments. Species aligning themselves at ecotones with familiar counterparts from adjoining ecosystems to form clearly defined assemblages is well documented for several taxa (Walker *et al.* 2003; Lopez-Gonzalez 2004; Mena and Vazquez-Dominquez 2005).

Limitations

Important caveats of our characterization of the FTT are the limitations of our approach, as they relate to scale and process. Methodologically, we were limited to sampling species in only one season and were not able to sample some species at all. Barren ground caribou undergo large seasonal migrations (Griffith *et al.* 2002), and moose undergo smaller seasonal migrations (Ball *et al.* 2001), to exploit seasonally available resources. The seasonality of our study design precludes knowledge of the whereabouts for these species during the summer season. Several other species present in the region were not detected with our surveys, because a) the species was too patchily distributed to be detected by our sampling [e.g. dall's sheep (*Ovis dalli*), water shrew (*Sorex palustris*)] b) the species was beyond the scope of our methodology [e.g. grizzly bears (*Ursus arctos*), arctic ground squirrels (*Spermophilus parryii*)], or c) the species is highly mobile and highly grouped so our sampling scheme missed them by chance [e.g. wolf (*Canis lupus*)]. Accordingly, we must be cautious in our interpretations of linkages between species detected in different seasons and those missed altogether. Although more visits per site within a year and across multiple years would provide more and better data, our success in elucidating a consistent pattern of diversity and ecological structure based on one session per site indicates that much insight can be gained with single visit systematic surveys.

The observed pattern is scale dependant because constraints limiting species at ecotones are important at different scales of analyses (Gosz 1993). The importance and predictive ability of various factors form a hierarchy from climate at macro scales to biotic interactions at micro scales (Whittaker *et al.* 2001; Willis and Whittaker 2002; Pearson and Dawson 2003). At broad scales, there will be much predictive overlap between climate and vegetation while at finer scales there will be little (Pearson and Dawson 2003). When we sample at fine scales, we can describe the specific system well but risk missing broad scale generalities, and when we sample at broad scales we risk missing important details (Cadenasso *et al.* 2003). The only “correct” scale is the scale at which one can address the question at hand (Gosz 1993; Pearson and Dawson 2003). We chose an extent

which encompasses an entire ecotone between two major biomes, and a grain size at which the FTT is distinguishable. Our questions were addressed with specific reference to this scale.

Finally, given the correlational nature of this study, it is possible that the predictors of diversity and structure we have identified are spurious, even if they are the likeliest of the variables we considered (Burnham and Anderson 2002; Ricklefs 2004). The consistency with which the same fundamental variables emerged from multiple independent analysis and model selection technique makes us hopeful that we have successfully identified mechanistic drivers of vertebrate diversity across the FTT (Burnham and Anderson 2002). But ultimately, pattern derived hypotheses such as those generated above must be evaluated with process-oriented research.

Conclusion

Looking for biologically relevant drivers of species patterning at the scale of ecotones is important because so many species share coincident range boundaries. Understanding the linking mechanisms for these patterns is undoubtedly important to understanding ecological processes causing range boundaries (Whittaker *et al.* 2001; Burnham and Anderson 2002). Here we confirm that the Yukon's forest to tundra transition marks a boundary between boreal and arctic terrestrial vertebrates. Vertebrates present in the transition are sorted into four rather discrete assemblages, three of which are strongly affiliated with boreal, taiga, or tundra habitats. Due primarily to topography, habitats belonging to each of these categories are juxtaposed along the latitudinal gradient, creating a mosaic of adjacent, contrasting habitat types. However, the habitat affinities of the different assemblages maintain strong ecological structure across this mosaic, such that there is little overlap of boreal, taiga, and tundra species at any given site. As a result, species richness is not higher at sites within the ecotone than in southern boreal and northern tundra sites. Instead, diversity generally declines across the transition zone, corresponding to the lower diversity of arctic vertebrates relative to boreal vertebrates.

The FTT varies widely in topography, plant species composition and width around the world (Timoney 1992; Callaghan *et al.* 2002; Payette *et al.* 2001), and thus the patterns we have identified in this study may not generalize to other FTT's or to ecotones in general (Walker *et al.* 2003). Risser (1995b) stated 10 years ago that ecotones should be on the forefront of research examining the link between biodiversity and ecosystem process but most of the world's major ecotones remain undescribed, especially with regard to animals. Describing and understanding the complexity at these boundaries should be a goal of ecologists seeking to understand diversity gradients and community structure, particularly in times of rapid environmental change.

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Table 1. Species, the number of sites at which each species was detected, species compartment assignment by hierarchical clustering, the r^2 between species abundances and the original distance in multi dimensional space (r^2 OD) and the r^2 between species abundances and three dimensional ordination axes (r^2 NMS). Species occurring at less than three sample sites were removed from analyses except that of diversity.

Species Detected	No. Sites	Compartment	r^2 OD	r^2 NMS
Snowshoe Hare (<i>Lepus americanus</i>),	28	Boreal	0.12	0.16
American Red Squirrel (<i>Tamiasciurus hudsonicus</i>)	26	Boreal	0.14	0.18
Spruce Grouse (<i>Falcapennis canadensis</i>)	8	Boreal	0.09	0.12
Moose (<i>Alces alces</i>)	7	Boreal	0.07	0.09
Canadian Lynx (<i>Lynx canadensis</i>)	6	Boreal	0.04	0.06
North American Deermouse (<i>Peromyscus maniculatus</i>)	3	Boreal	0.05	0.06
Northern Red-backed Vole (<i>Clethrionomys gapperi</i>)	57	Taiga	0.19	0.25
American Marten (<i>Martes americana</i>)	34	Taiga	0.19	0.25
Wolverine (<i>Gulo gulo</i>)	16	Taiga	0.06	0.08
Taiga Vole (<i>Microtus xanthognathus</i>)	13	Taiga	0.09	0.12
Caribou (<i>Rangifer tarandus</i>)	8	Taiga	0.03	0.04
Ptarmigan (<i>Lagopus spp.</i>)	32	Tundra	0.10	0.13
Red Fox (<i>Vulpes vulpes</i>)	27	Tundra	0.19	0.25
Northern Collared Lemming (<i>Dicrostonyx groenlandicus</i>)	3	Tundra	0.06	0.07
Ermine (<i>Mustela erminea</i>)	21	Vagrant	0.10	0.13
Least Weasel (<i>Mustela nivalis</i>)	8	Vagrant	0.04	0.05
Masked Shrew (<i>Sorex cinereus</i>)	8	Vagrant	0.00	0.01
Tundra Vole (<i>Microtus oeconomus</i>)	7	Vagrant	0.02	0.03
Brown Lemming (<i>Lemmus trimucronatus</i>)	2	—	—	—
Long-tailed Vole (<i>Microtus longicaudus</i>)	2	—	—	—
Meadow Vole (<i>Microtus pennsylvanicus</i>)	2	—	—	—
Northern Bog Lemming (<i>Synaptomys borealis</i>)	1	—	—	—

Table 2. Category (type), Fit (r^2), number of estimatable parameters (K), second order Akaike's Information Criterion (AICc), Δ AICc, and Akiake weights (w_i) for linear regression models of species richness (S) regressed on environmental variables. Models are ranked according to Akiake weights (w_i).

Rank	Model	Type	r^2	K	AICc	Δ AICc	w_i
1	Herbaceous (-), Seasonality (+), Grow. S. Precip (-)	Mixed	0.48	5	70.6977	0.0000	0.567
2	Herbaceous (-), Seasonality (+)	Mixed	0.45	4	71.5582	0.8605	0.369
3	Herbaceous (-), Ann. Precip. (-)	Mixed	0.41	4	76.0794	5.3816	0.038
4	Herbaceous (-), Winter Precip. (-)	Mixed	0.39	4	77.8925	7.1948	0.016
5	Herbaceous (-), Grow. S. Precip (-)	Mixed	0.37	4	80.2901	9.5924	0.005
6	Coniferous (+), Seasonality (+), Grow. S. Precip (-)	Mixed	0.39	5	80.6918	9.9941	0.004
7	Herbaceous (-)	Vegetation	0.32	3	83.2876	12.5898	0.001
8	Coniferous (+), Seasonality (+)	Mixed	0.32	4	85.0789	14.3812	0.000
9	Seasonality (+)	Climate	0.23	3	90.7706	20.0729	0.000
10	Ann. Precip. (-)	Climate	0.22	3	91.7271	21.0294	0.000
11	Coniferous (+)	Vegetation	0.22	3	92.3278	21.6301	0.000
12	Winter Precip. (-)	Climate	0.15	3	97.2987	26.6009	0.000
13	Grow. S. Precip. (-)	Climate	0.15	3	97.9870	27.2893	0.000

Table 3. Number of species detected, climate and vegetation cover for site groupings chosen using indicator species analysis on hierarchical clusters of sites based on environmental attributes [mean \pm SE (n)]. Only variables which described significant amount of variance in analyses are included.

Group	Ann. Temp. (°C)	Grow. S. Temp. (°C)	Winter Temp. (°C)	Ann. Precip. (mm)	Grow. S. Precip. (mm)	Winter Precip. (mm)	Seasonality (°C)	Coniferous (Prop.)	Herbaceous (Prop.)
<i>3 Clusters</i>									
Boreal	-5.0 \pm 0.0 (9)	12.6 \pm 0.2 (9)	-15.3 \pm 0.2 (9)	343.4 \pm 5.0 (9)	132.8 \pm 1.8 (9)	149.9 \pm 3.2 (9)	39.8 \pm 0.5 (9)	40.9 \pm 6.3 (9)	4.3 \pm 1.9 (9)
Taiga	-7.0 \pm 0.2 (28)	11.8 \pm 0.1 (28)	-18.0 \pm 0.3 (28)	419.3 \pm 8.3 (28)	200.0 \pm 4.0 (28)	155.1 \pm 3.3 (28)	39.1 \pm 0.4 (28)	27.2 \pm 4.9 (28)	18.4 \pm 4.0 (28)
Tundra	-6.5 \pm 0.1 (29)	10.0 \pm 0.2 (29)	-16.2 \pm 0.2 (29)	459.6 \pm 10.0 (29)	187.4 \pm 5.5 (29)	203.0 \pm 5.4 (29)	35.5 \pm 0.3 (29)	5.3 \pm 2.3 (28)	47.4 \pm 5.7 (28)
<i>7 Clusters</i>									
Core Boreal	-5.0 \pm 0.0 (9)	12.7 \pm 0.2 (9)	-15.3 \pm 0.1 (9)	343.4 \pm 5.0 (9)	132.8 \pm 1.8 (9)	149.9 \pm 3.2 (9)	39.8 \pm 0.5 (9)	40.9 \pm 6.3 (9)	4.3 \pm 1.9 (9)
Southern Taiga	-8.4 \pm 0.2 (8)	11.6 \pm 0.2 (8)	-20.2 \pm 0.2 (8)	368.5 \pm 12.1 (8)	177.4 \pm 5.7 (8)	132.6 \pm 4.7 (8)	42.1 \pm 0.4 (8)	15.4 \pm 6.9 (8)	30.4 \pm 8.5 (8)
Middle Taiga	-7.0 \pm 0.0 (5)	11.8 \pm 0.2 (5)	-17.6 \pm 0.2 (5)	482.8 \pm 3.6 (5)	233.2 \pm 2.1 (5)	176.0 \pm 1.0 (5)	38.6 \pm 0.7 (5)	61.1 \pm 7.6 (5)	1.1 \pm 0.7 (5)
Northern Taiga	-6.3 \pm 0.1 (15)	11.8 \pm 0.1 (15)	-17.0 \pm 0.0 (15)	425.2 \pm 3.3 (15)	201.0 \pm 1.7 (15)	160.2 \pm 1.3 (15)	37.7 \pm 0.2 (15)	22.2 \pm 5.9 (15)	17.8 \pm 4.9 (15)
Valley Taiga	-6.0 \pm 0.0 (5)	10.0 \pm 0.0 (5)	-16.0 \pm 0.0 (5)	380.0 \pm 8.7 (5)	141.0 \pm 3.1 (5)	185.2 \pm 5.4 (5)	35.6 \pm 0.4 (5)	27.0 \pm 7.7 (5)	3.5 \pm 1.3 (5)
Southern Tundra	-6.4 \pm 0.2 (11)	9.1 \pm 0.3 (11)	-15.5 \pm 0.2 (11)	487.3 \pm 15.5 (11)	188.8 \pm 5.2 (11)	229.6 \pm 8.9 (11)	33.7 \pm 0.3 (11)	0.7 \pm 0.5 (11)	37.4 \pm 4.4 (11)
Northern Tundra	-6.8 \pm 0.2 (13)	10.8 \pm 0.2 (13)	-17.0 \pm 0.2 (13)	466.8 \pm 8.8 (13)	204.2 \pm 6.6 (13)	187.4 \pm 3.5 (13)	37.0 \pm 0.3 (13)	0.4 \pm 0.2 (12)	74.9 \pm 4.6 (12)

Table 4. Relationship of spatial and environmental variables to the original distance in multi dimensional space (r^2 OD) and to three dimensional Nonmetric Multidimensional Scaling (NMS) ordination axes (r^2 NMS), measured as the r^2 between the variable and the cumulative axes.

Attribute	r2 Oda	r2 NMSb
<i>Spatial</i>		
Elevation	0.11	0.15
Latitude	0.06	0.08
Longitude	0.06	0.07
<i>Environmental</i>		
Coniferous	0.19	0.25
Herbaceous	0.17	0.23
Seasonality	0.16	0.20
Ann Precip.	0.15	0.19
Winter Precip.	0.14	0.18
Growing S. Temp.	0.14	0.18
Growing S. Precip.	0.07	0.09
Deciduous	0.04	0.06
Water	0.03	0.04
Shrub	0.03	0.03
Winter Temp.	0.02	0.03
Rock	0.02	0.02
Annual Temp.	0.01	0.01

Table 5. Category (type), Fit (r^2), number of estimatable parameters (K), second order Akaike's Information Criterion (AICc), Δ AICc, and Akiake weights (w_i) for linear regression models of summed species abundance within compartment (Boreal, Taiga, Tundra, and Vagrant), delineated using hierarchical clustering. Models for each group are ranked according to Akiake weights (w_i).

Rank	Model	Type	r^2	K	AICc	$\Delta AICc$	w_i
<i>Boreal</i>							
1	Herbaceous (-), Seasonality (+), Grow. S. Precip (-)	Mixed	0.54	5	-139.6893	0.0000	0.808
2	Coniferous (+), Seasonality (+), Grow. S. Precip (-)	Mixed	0.52	5	-136.4391	3.2502	0.159
3	Herbaceous (-), Ann. Precip. (-)	Mixed	0.46	4	-131.4317	8.2576	0.013
4	Herbaceous (-), Grow. S. Temp. (+), Grow. S. Precip. (-)	Mixed	0.48	5	-131.1153	8.5740	0.011
5	Herbaceous (-), Seasonality (+)	Mixed	0.45	4	-129.7028	9.9865	0.005
6	Seasonality (+), Grow. S. Precip (-)	Climate	0.43	4	-127.5211	12.1683	0.002
7	Herbaceous (-), Grow. S. Precip. (-)	Mixed	0.43	4	-127.4155	12.2738	0.002
8	Coniferous (+), Seasonality (+)	Mixed	0.36	4	-120.3346	19.3547	0.000
9	Grow. S. Temp. (+), Grow. S. Precip. (-)	Climate	0.36	4	-120.1094	19.5799	0.000
10	Herbaceous (-), Grow. S. Temp. (+)	Mixed	0.36	4	-119.7767	19.9126	0.000
11	Ann. Precip. (-)	Climate	0.33	3	-119.5242	20.1651	0.000
12	Herbaceous (-)	Vegetation	0.28	3	-115.0401	24.6492	0.000
13	Seasonality (+)	Climate	0.27	3	-113.8783	25.8110	0.000
14	Grow. S. Precip. (-)	Climate	0.26	3	-113.4850	26.2043	0.000
15	Coniferous (+)	Vegetation	0.24	3	-111.0949	28.5944	0.000
16	Winter Precip. (-)	Climate	0.17	3	-105.8565	33.8328	0.000
17	Grow. S. Temp. (+)	Climate	0.16	3	-104.7194	34.9699	0.000
<i>Taiga</i>							
1	Herbaceous (-), Seasonality (+), Grow. S. Precip (+)	Mixed	0.48	5	-150.9676	0.0000	0.439
2	Herbaceous (-), Winter Temp. (-)	Mixed	0.45	4	-149.8583	1.1094	0.252
3	Herbaceous (-), Seasonality (+)	Mixed	0.44	4	-148.6098	2.3579	0.135
4	Coniferous (+), Winter Temp. (-)	Mixed	0.44	4	-147.8831	3.0845	0.094
5	Herbaceous (-), Seasonality (+), Grow. S. Temp. (+)	Mixed	0.44	5	-145.7221	5.2455	0.032
6	Herbaceous (-), Winter Precip. (-)	Mixed	0.41	4	-144.5780	6.3897	0.018
7	Coniferous (+), Seasonality (+)	Mixed	0.40	4	-143.7069	7.2607	0.012
8	Herbaceous (-), Grow. S. Temp. (+)	Mixed	0.39	4	-142.7959	8.1717	0.007
9	Coniferous (+), Seasonality (+), Grow. S. Precip (+)	Mixed	0.41	5	-142.5879	8.3797	0.007
10	Coniferous (+), Seasonality (+), Grow. S. Temp. (-)	Mixed	0.40	5	-141.4923	9.4754	0.004
11	Coniferous (+)	Vegetation	0.31	3	-137.0794	13.8882	0.000
12	Herbaceous (-)	Vegetation	0.29	3	-135.4190	15.5486	0.000
13	Seasonality (+)	Climate	0.25	3	-131.8249	19.1427	0.000
14	Winter Precip. (-)	Climate	0.20	3	-127.5105	23.4571	0.000
15	Grow. S. Temp. (+)	Climate	0.19	3	-127.0415	23.9262	0.000
16	Winter Temp. (-)	Climate	0.13	3	-122.2740	28.6937	0.000
<i>Tundra</i>							
1	Herbaceous (+), Winter Precip. (+)	Mixed	0.43	4	-144.6626	0.0000	0.326
2	Herbaceous (+), Seasonality (-)	Mixed	0.43	4	-144.3775	0.2850	0.283
3	Herbaceous (+), Ann. Precip. (+)	Mixed	0.42	4	-143.3845	1.2780	0.172
4	Herbaceous (-), Seasonality (-), Grow. S. Precip (+)	Mixed	0.44	5	-142.6623	2.0002	0.120
5	Herbaceous (+), Grow. S. Temp. (-)	Mixed	0.41	4	-141.7153	2.9473	0.075
6	Coniferous (-), Seasonality (-), Grow. S. Precip (+)	Mixed	0.39	5	-137.2464	7.4162	0.008
7	Coniferous (-), Winter Precip. (+)	Mixed	0.36	4	-136.8376	7.8249	0.007
8	Herbaceous (+)	Vegetation	0.33	3	-136.4282	8.2344	0.005
9	Coniferous (-), Seasonality (-)	Mixed	0.35	4	-135.7771	8.8855	0.004
10	Coniferous (-)	Vegetation	0.29	3	-132.6434	12.0192	0.001
11	Ann. Precip. (+)	Climate	0.22	3	-126.3595	18.3030	0.000
12	Seasonality (-)	Climate	0.19	3	-123.8345	20.8281	0.000
13	Winter Precip. (+)	Climate	0.19	3	-123.6050	21.0575	0.000
14	Grow. S. Temp. (-)	Climate	0.17	3	-122.0355	22.6270	0.000
<i>Vagrant</i>							
1	Grow. S. Precip. (-)	Climate	0.18	3	-122.8922	0.0000	0.723
2	Herbaceous (-), Seasonality (-), Grow. S. Precip (-)	Mixed	0.19	5	-119.0037	3.8885	0.104
3	Ann. Precip. (-)	Climate	0.12	3	-118.6762	4.2160	0.088
4	Coniferous (+), Seasonality (-), Grow. S. Precip (-)	Mixed	0.18	5	-118.6131	4.2791	0.085

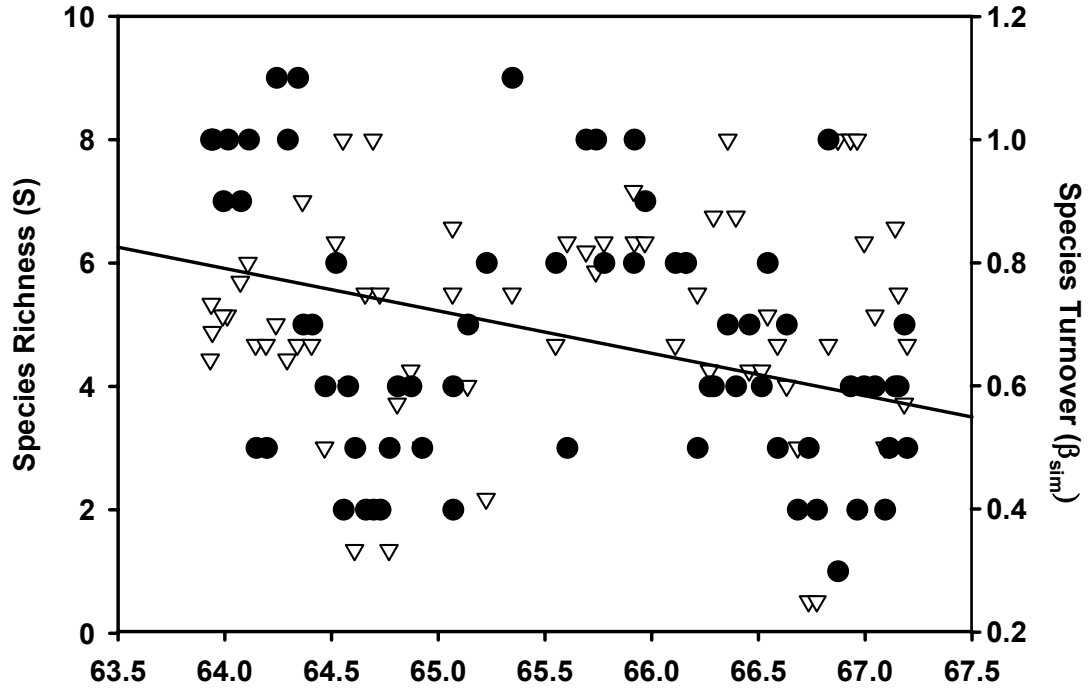


Figure 1. Latitudinal pattern of terrestrial vertebrate diversity sampled over the forest to tundra ecotone in the Yukon Territory, Canada. Closed circles indicate species richness (S) and open triangles indicate species turnover (β_{sim}). Regression line shows relationship between species richness and latitude ($r^2 = 0.12$, $F_{1,63} = 8.683$, $P = 0.004$).

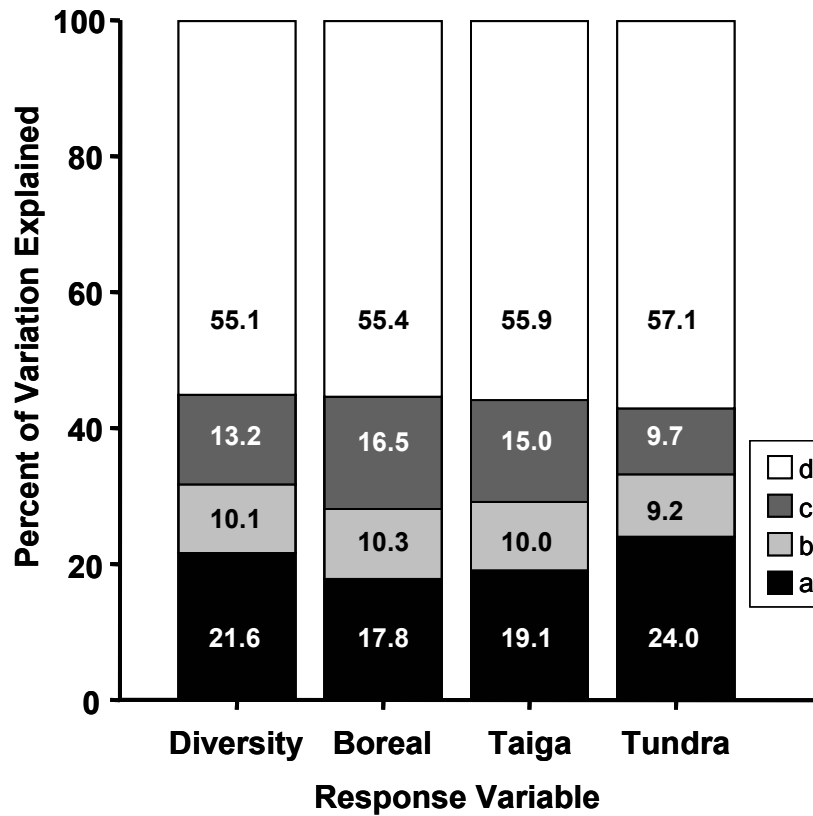


Figure 2. Partial regression results of the relative importance and overlap between climatic and vegetative variables in explaining species richness and boreal, taiga, and tundra grouped species abundances at the forest to tundra ecotone in the Yukon Territory, Canada. Variation is explained a) independently by vegetation-herbaceous cover, b) by joint effects of vegetation and climate, c) independently by climate- seasonality, and d) remains unexplained.

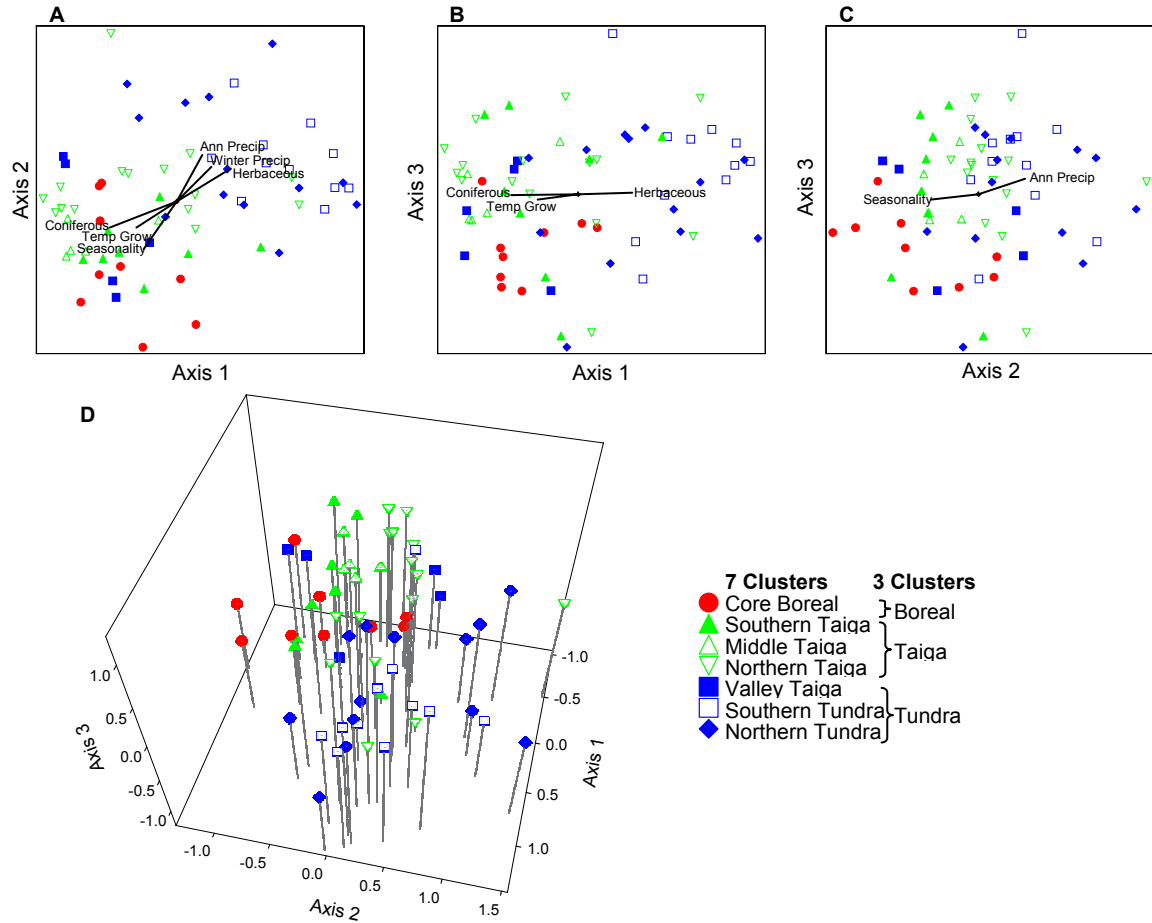


Figure 3. Nonmetric Multidimensional Scaling (NMS) ordination of terrestrial vertebrate assemblage sampled across 66 sites spanning the forest to tundra ecotone in Yukon Territory, Canada. [Initial starting configuration from DCA; Sorenson (Bray & Curtis) distance; no species weighting; final stress = 15.89; final stability = 0.00001; number of iterations = 221; Monte Carlo Simulation $P = 0.02$]. Sites were categorized and overlaid by color and shape using hierarchical clustering optimized at three and seven environmental cluster levels using indicator species analysis. A, B, and C are two dimensional biplots of all environmental variables $r^2 > 0.25$ with ordination axes. D shows the complete 3 dimensional ordination.

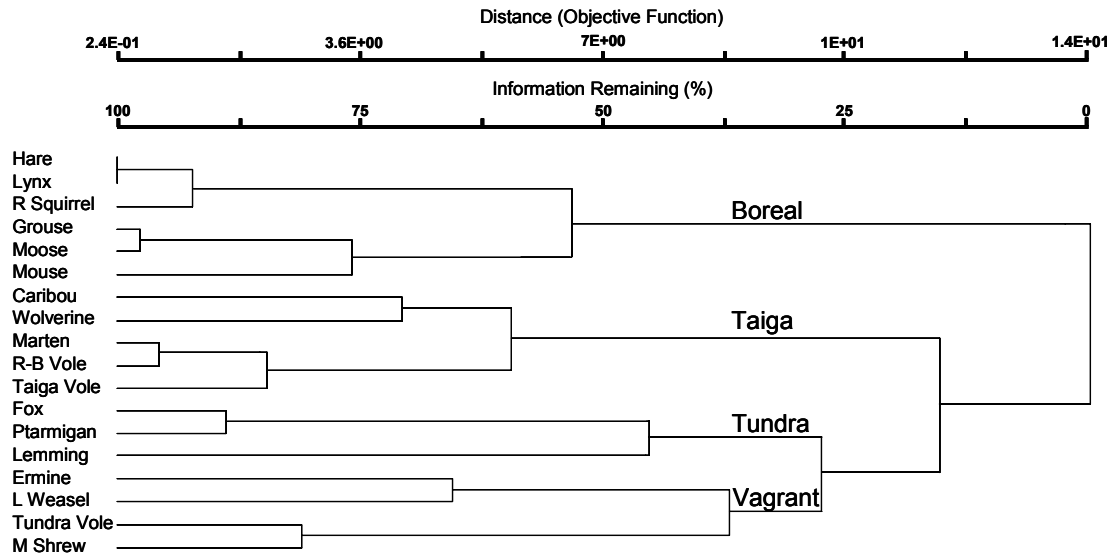


Figure 4. Dendrogram from hierarchical cluster analyses of terrestrial vertebrate species across a gradient spanning the forest to tundra ecotone, Yukon Territory, Canada (Euclidean distance measure; Wards linkage method; scaled by Wishart's objective function). Boreal, Taiga, Tundra, and Vagrant show pruning points which cluster species into ecologically meaningful, spatially compartmented groups.

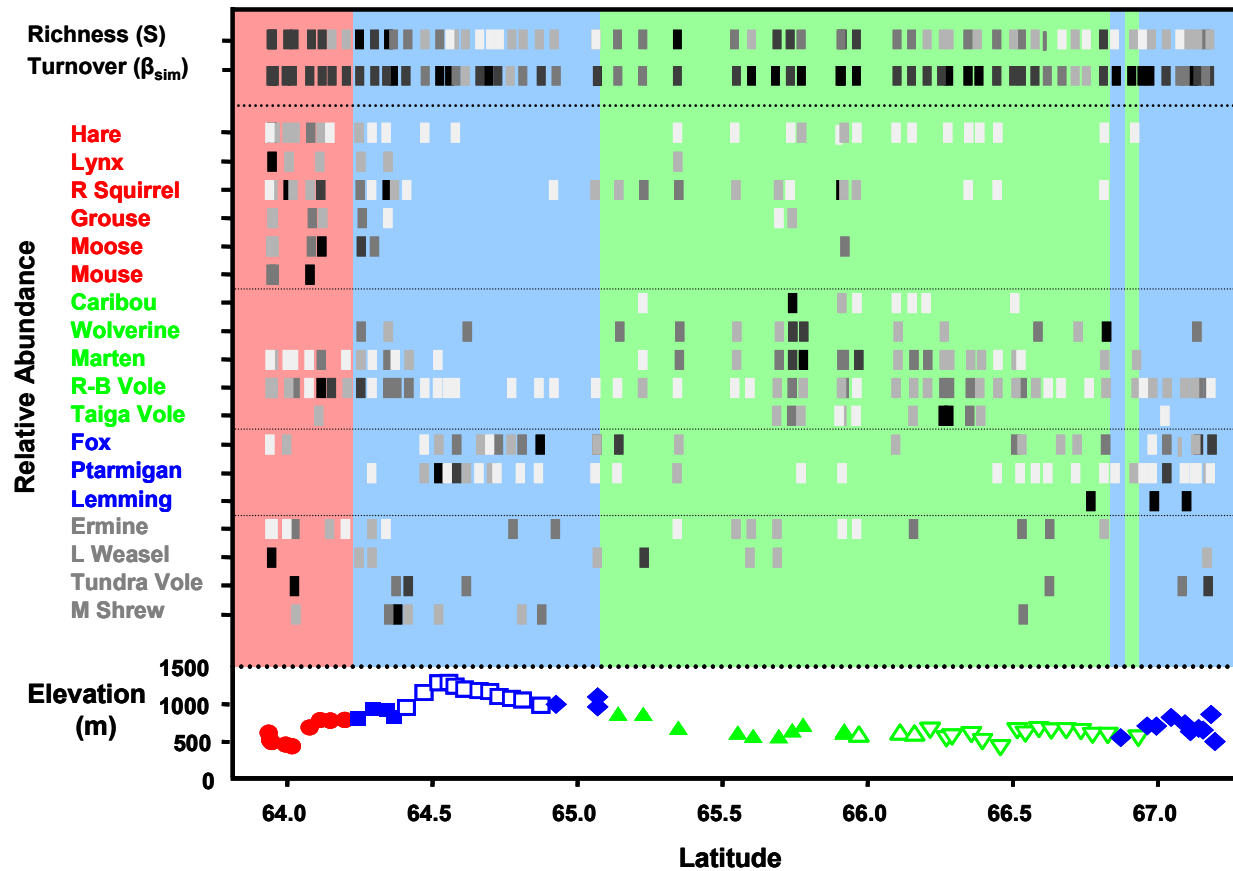


Figure 5. Pattern of relative species richness (S), spatial turnover (β_{sim}), and abundance across sites spanning the Yukon Forest Tundra Transition, with respect to latitude, elevation and site habitat category. Habitat categories are *Boreal* (red), *Taiga* (green), and *Tundra* (blue) separated into 7 subclasses (see Fig. 3 legend for details). Lighter and darker bars indicate smaller and larger values, respectively and were delineated by partitioning each index into five equal categories. Missing bars indicates a value of zero for that measure. Species are grouped according to spatial compartments and colour coded with colours of the best corresponding habitat category. Five sites shown as solid blue squares are thought to be misclassified by this analysis and to more closely correspond to the *Taiga* category (see text for details).

CONNECTING STATEMENT

Chapter 1 characterized the ecological structure of the terrestrial vertebrate assemblage at the forest to tundra transition (FTT). This examination explicitly considered the overall diversity and community composition, as well as the environmental predictors of the observed patterns. Chapter 2 complements this general multi-species analysis with a detailed examination of the resource selection of eight terrestrial vertebrate species occurring across the FTT.

CHAPTER 2: LESSONS FROM THE EDGE: OCCURRENCE AND RESOURCE SELECTION OF TERRESTRIAL VERTEBRATES ACROSS THE FOREST-TUNDRA TRANSITION

Abstract

Determining the factors limiting species at range margins is central to many questions in ecology and biogeography. Fulfilling resource requirements in marginal environments may force individuals to occupy atypical habitats and consume unusual prey. Thus, resource selection near range boundaries should reflect niche plasticity, but this has not been evaluated for most species. Ecotones represent the coincident range limits of several species and are therefore ideal foci for studies of resource selection at range boundaries. We characterized resource selection of eight terrestrial vertebrates across the forest to tundra transition, using Resource Selection Functions (RSF) and Akaike's Information Criteria (AIC) model selection. Resource selection of herbivores was described primarily by vegetative variables while resource selection of carnivores was described primarily by the distribution of herbivores, generating strong patterns of co-occurrence of predator-prey combinations sorted by habitat types. Species generally followed resource selection patterns reported from nearer the core of their range, with the exception of American Marten (*Martes americana*), which, contrary to common conviction, preferentially utilized open taiga areas, rather than boreal forest, and was positively associated with small mammal biomass.

Introduction

Understanding the underlying factors restricting species ranges is fundamental to many questions in ecology, ranging from gene flow to community structure (Holt and Keitt 2005; Holt *et al.* 2005; Parmesan *et al.* 2005). Assuming a declining gradient of habitat quality from range centers to edges (Brown 1984; Swihart *et al.* 2003), species are likely to encounter suboptimal habitat conditions at range boundaries. These suboptimal conditions should exert strong selective pressure (Case *et al.* 2005) favouring species with large niche breadth (Pulliam 2000; Swihart *et al.* 2003). Local adaptation may result in unique habitat associations at range peripheries that differ from the core of the range where species experience higher productivity, more competitors, higher densities, etc. (Brown 1984; Swihart *et al.* 2003; Case *et al.* 2005; Holt *et al.* 2005). Range limits are the clearest focal points to determine the factors limiting an organism, and thus are prime areas at which to define resource selection (Holt and Keitt 2005). A particularly strong resource selection approach involves characterizing areas where a species is present and adjacent areas where that species is absent (Manly *et al.* 2002), such as range boundaries, where populations reach their existence thresholds (Swihart *et al.* 2003; Holt and Keitt 2005). However, characterizations of species resource selection typically focus on range interiors, where species are more abundant and therefore easier to sample and are then extrapolated across species ranges (Manly *et al.* 2002; Boyce and McDonald 1999).

Resource selection is a scale-dependant process in terms of both the scale at which a species select resources and the scale at which the limiting resources operate (Manly *et al.* 2002; Meyer and Thuiller 2006). The predictive ability of broad scale abiotic resource attributes such as climate is often high at coarse scales with increasing importance of vegetation and trophic interactions at finer scales (Whittaker *et al.* 2001; Willis and Whittaker 2002; Pearson and Dawson 2003). Species can be limited directly by climate variables, if some aspect of temperature or precipitation acts directly on their bioenergetics or phenology (Post and Forchhammer 2002; Humphries *et al.* 2004), or by habitat structure

which often varies in response to climate variables (Skre *et al.* 2002). Most species are ultimately limited by food resources, which, within terrestrial food webs characterized primarily by three trophic levels, should result in herbivore abundance being dictated by vegetation and carnivore abundance being dictated by herbivores. Trophic position should also influence the spatial scale at which selection operates because predators tend to integrate across larger spatial scales than most herbivores (Moore *et al.* 2003; Ives and Cardinale 2004; Rooney *et al.* 2006).

Species range limits are often coincident with ecotones due to dispersal barriers, interspecific competition and species co-evolution (Risser 1995; Case *et al.* 2005), making ecotones ideal foci for studying resource selection. Moreover, ecotones often represent abrupt vegetative and climatic gradients (Sveinbjörnsson *et al.* 2002), enabling evaluation of the relative importance of these factors. The transition from boreal forest to arctic tundra represents one of the largest ecotones in the northern hemisphere (Timoney 1992; Payette *et al.* 2001). Despite its size and importance (Spector 2002), we know little of the ecology of organisms occupying this ecotone, especially in regards to terrestrial vertebrates (Callaghan *et al.* 2002). The forest to tundra transition (FTT) is delineated by a strong climate gradient and an abrupt change in vegetative structure and composition (Fisher and Wilkinson 2005). Based on coarse-grained species range maps, the FTT coincides with the northern range boundary of many boreal vertebrates and the southern range boundary of many arctic vertebrates (Hagmeier 1966). However, systematic surveys of vertebrate distributions across the FTT are extremely scarce, an omission that is especially critical given the consensus expectation of pronounced climatic warming and species range shifts centered on this ecotone. (Payette *et al.* 2001; Hughes 2000; Thomas *et al.* 2004).

Herein we quantify resource selection of eight terrestrial vertebrate species across the FTT, providing the first explicit examination of resource selection by these species at their FTT range limits. Because we have multi-species survey data, we are able to evaluate resource selection functions that include prey abundance as well as vegetative and climate variables. We predict:

- 1) The occurrence of herbivores will be best predicted by habitat variables and the occurrence of carnivores will be best predicted by the distribution of herbivores.
- 2) Species will generally conform to resource selection patterns identified previously nearer the core of their range.
- 3) Vegetation and prey generalists will be more ubiquitous across the FTT than vegetation and prey specialists.

Methods

Study Region

The study region consisted of the area adjacent to the southern 500 km of the Dempster highway, and 50 km of the adjoining Klondike highway, Yukon Territory, Canada. These roads provided year-round access to areas of boreal forest, arctic tundra and the forest to tundra transition (FTT). Qualitatively, from south to north, our study area is defined by contiguous boreal forest, southern tundra, northern lichen woodland (taiga) and finally contiguous arctic tundra.

Species

We sampled and characterized the resource selection of eight species across the FTT: snowshoe hare (*Lepus americanus*), American red squirrel (*Tamiasciurus hudsonicus*), ptarmigan (*Lagopus spp.*), northern red-backed vole (*Clethrionomys rutilus*), taiga vole (*Microtus xanthognathus*), Canadian lynx (*Lynx canadensis*), American marten (*Martes americana*), and red fox (*Vulpes vulpes*). Occurrence and relative abundance data of vertebrates' active in winter, on top of the snow, were collected at 78 randomly selected sites by snow tracking between 8 February and 21 April, 2005. All identifiable tracks were recorded on 3 km long equilateral triangular transects, removed at least 100m from the road, and spaced at least 5 km apart. Tracking was done at least 24 hours after the last track obliterating snowfall to allow for track accumulation. Occurrence and relative abundance data of small mammals (< 200 g) were collected at 66 of the 78 aforementioned sites by snap trapping between July 8 and 17 August, 2005. Sites consisted of two 250 m long trap-lines, 25 traps per line situated along the triangular transect sides, 10

m from the apex. Sites were trapped for 3 consecutive nights and data were converted to capture per unit effort (CPUE). Thus we obtained a measure of presence/absence and relative abundance for each species.

We calculated the total biomass of 11 species of small mammal prey for each site, j , to factor in the large variance of prey sizes:

$$Biomass_j = \sum_{i=1}^k \frac{N_j}{N_{max}} \times c_{ij} \times x_i$$

where c is the number of captures for species i at site j , x is the average mass of species i , and N is the number of trap-nights for site j and max .

Habitat

Vegetation was characterized at 2 grain sizes for each site. Fine grained vegetation data were collected in June 2005 at three randomly chosen sites along each small mammal trap-line. Each sample site consisted of three, 2 m diameter subplots, nested within a 0.01 ha plot, nested within a 0.04 ha plot. We recorded trees in three size categories: small (< 7.5 cm DBH), medium (7.5-20 cm DBH), and large (> 20 cm DBH). Trees < 20 cm were recorded at the 0.01 ha level; while trees > 20 cm and snags were recorded at the 0.04 ha plot level. From subplot centers we estimated canopy cover as anything over 3m in height within a 5m radius circle. Within subplots, we recorded proportion occupied by moss, lichen, litter and shrubs. Shrub cover was recorded in three height classes: short (< 20 cm), medium (20-50 cm), and tall (> 50 cm). We recorded and ranked the four most abundant shrub species within a subplot. We estimated berry availability at each site by summing the ranks of all berry-producing shrubs (4 representing berry shrubs that were most abundant and 1 indicating shrubs that were least abundant). Coarse woody debris (CWD) was quantified at each site from the diameter of all debris crossing 2 perpendicular 25m transects (Van Wagner 1968). Fine grained vegetation data were averaged between sample points for each site.

Broad grain vegetation was extracted from thematic mapped orthorectified images based on Landsat 7 Enhanced Thematic Mapper (ETM+) 25 x 25m pixel images (Wulder and Nelson 2001; Wulder *et al.* 2002). These maps were

subsequently reclassified into 6 cover classes: conifer, deciduous, herbaceous, shrub, rock and water. We sampled the proportion of coverage for each of these categories within a 575m radius circle, using raster calculator functions in ArcGIS® (Environmental Systems Research Institute 2002), and calculated the neighborhood statistics for each triangle centroid using the Point Intersect tool, Hawth's Analysis® tools extension (Beyer 2004).

Climate was sampled at a larger spatial resolution of 2 km² from PRISM (Parameter-elevation Regressions on Independent Slopes Model) datasets created for average monthly and annual temperature and precipitation for 1969-1990 in the Yukon Territory (Daly *et al.* 1994; Simpson *et al.* 2005) by intersecting winter triangle centroid point data with the PRISM layers using Hawth's Analysis® tools extension (Beyer 2004), in ArcGIS® (Environmental Systems Research Institute 2002). Climate variables, including annual, growing season (June-August, inclusive) and winter (October-April, inclusive) average temperature and cumulative precipitation, as well as seasonality (July minus January temperature), were calculated from PRISM data.

A more detailed account of data collection methods is provided in Chapter 1.

Modeling

We created resource selection functions (RSF) for our species using logistic regression (Manly *et al.* 2002) and selected the best of competing RSF models using Akaike's Information Criteria (AIC: Burnham and Anderson 2002; Greaves *et al.* 2006). AIC model selection is based on the premise that only a small number of models created *a priori*, with specific reference to the known natural history of the organism, are considered (Burnham and Anderson 2002; Greaves *et al.* 2006). Therefore we constructed a short series of plausible logistic regression models predicting presence/absence for each species based on previously documented habitat and trophic associations. Models were built upon as many site observations as data were available. For snow-tracked species hypothesized to require small mammal prey, we were restricted to data from 65 sites. For all other snow-tracked species we used data from the 77 sites for which we had vegetation

data. The fit of all models was assessed with Nagelkerke r^2 (Nagelkerke 1991). In order to avoid over-fitting our models with collinear variables we restricted our models to have no two variables with Pearson's correlation coefficient > 0.6 . Models at least one third as likely as the top ranked model according to AIC weights were considered plausible (Burnham and Anderson 2002) and compose the candidate set used to infer resource selection. Resource selection studies are susceptible to misclassifications and spurious correlations (Manly *et al.* 2002). Although our model selection approach (Burnham and Anderson 2002) provides support to our conclusions, we cannot conclusively determine whether structure is overriding prey availability because we may not have measured some important food source or structural habitat attribute.

We measured the performance (reclassification accuracy) of habitat models using Cohen's Kappa statistic (Fielding and Bell 1997, Manel *et al.* 2001) and the area under receiver operating characteristic (ROC) curves (AUC: Fielding and Bell 1997; Pearce and Ferrier 2000). Cohen's Kappa statistic measures the reclassification accuracy at some probability cutoff; we used 0.5 (Fielding and Bell 1997, Manel *et al.* 2001). Kappa values 0.4-0.6, 0.6-0.8 and 0.8-1.0 indicate moderate, substantial and almost perfect model performance respectively (Manel *et al.* 2001). Although Cohen's Kappa is a good measure for optimizing prediction models, its value is threshold dependant (Manel *et al.* 2001). AUC constitutes a threshold independent measure of reclassification accuracy (Fielding and Bell 1997; Pearce and Ferrier 2000; Greaves *et al.* 2006). AUC of the ROC curve is an unbiased measure of the overall reclassification accuracy across all thresholds (Fielding and Bell 1997; Pearce and Ferrier 2000). Models with AUC 0.7-0.8 are considered acceptable/useful, models with AUC 0.8-0.9 are considered excellent and models with AUC > 0.9 are considered highly accurate/outstanding (Hosmer and Lemeshow 2000; Manel *et al.* 2001).

Implicit in our analyses are the assumptions that 1) we have correctly determined species occurrence and relative abundance based on a single site visit in winter and a three day trap session in summer and 2) that winter and summer occurrences are correlated, such that we can model the occurrence of predators

detected in winter based on small mammal abundance detected the following summer. We assume that we have either correctly assigned either presence or absence of each species at each site and that their detection probabilities were the same (Mackenzie 2006). Although we cannot calculate detection probabilities without multiple surveys (MacKenzie 2006), misclassifications should be rare since we surveyed large areas at each site under optimal conditions (similar to Pellikka *et al.* 2005). Contrary to our second assumption, fox and marten can make small seasonal migrations (Larivière and Pasitschniak-Arts 1996; Poole *et al.* 2004) and small mammal abundance is known to fluctuate however both seasonally and annually (Hopkins and Kennedy 2004). We rely on temporal autocorrelation to minimize this error. Even though the same individual may not occupy a triangle in winter and summer, and there are undoubtedly fewer small mammals in the winter than summer, it is unlikely that species will be present in one season and vacant in another and the number of individuals present in the summer should reflect the size of the surviving population (Hopkins and Kennedy 2004).

Results

There was strong multicollinearity amongst vegetation and climatic variables along the FTT gradient. Herbaceous cover was negatively correlated to shrub cover ($r = -0.62$), coniferous cover ($r = -0.68$), and seasonality ($r = -0.23$). Seasonality was positively correlated to growing season temperature ($r = 0.79$), and coniferous cover ($r = 0.39$), and negatively correlated to winter temperature ($r = -0.66$). Precipitation was negatively correlated to coniferous cover ($r = -0.28$) and positively correlated to herbaceous cover ($r = 0.33$). Correlations among vegetative variables correspond to the replacement of conifer by increasing shrub and herbaceous cover from forest to tundra that is associated with a corresponding decline in growing season temperature, reduced seasonality and increased precipitation.

The abundance patterns for species followed the same general trend as the occurrence patterns with species being most abundant where their occurrence was widespread (Fig. 1). The best resource models for each species' occurrence, based

on AIC, described much of the variance in occurrence for all species (> 50 % for all species except red fox: ~ 40 %) and demonstrated good performance (AUC and Kappa moderate to excellent: Table 1; Table 2).

Herbivore resource selection was primarily related to vegetative cover and secondarily to climatic variables (Table 1), and these species were correspondingly most abundant in areas where vegetative cover best suited their preferences (Fig. 1). Hare were most abundant in the contiguous boreal, existing at low levels in areas of tundra and taiga. Hare selected for coniferous and deciduous trees, shrubs and seasonality and avoided herbaceous vegetation. Red squirrels were most abundant in the south and were restricted to areas of coniferous forest, avoiding herbaceous vegetation, precipitation and selecting for seasonality. Ptarmigan were restricted to the tundra and correspondingly selected herbaceous vegetation and deciduous trees while avoiding coniferous forest, shrubs and seasonality. Red backed voles were present across all vegetation types, but were most abundant in southern forested areas, selecting for shrubs and trees while avoiding moss. Taiga voles were mostly restricted to taiga, selecting for warm growing seasons, high precipitation, lichen, moss and shrubs, and avoiding forest cover.

Carnivore resource selection was mostly related to prey (herbivore) abundance, with secondary importance of structural vegetative characteristics (Table 2). Carnivores were most abundant where their prey was most abundant (Fig. 1). Lynx occupancy was limited to the southern boreal and two southern taiga sites. Lynx selected for prey species abundance, primarily hare and red squirrels. Marten were most abundant in the northern taiga regions and selected for seasonality and small mammal biomass while avoiding herbaceous vegetation and winter precipitation. Fox were the most widespread of the three predators analyzed, occurring most abundantly in tundra areas. Fox occurred across the FTT with much more prevalence in tundra areas, selecting for abundance of ptarmigan and tundra vegetation.

Discussion

The FTT provides the opportunity to assess the habitat selection of a variety of species at their range limits (Hagmeier 1966) over an abrupt climatic and vegetative gradient (Timoney 1992; Payette *et al.* 2001; Sveinbjörnsson *et al.* 2002). This combination is ideal for examining the importance of limiting factors to organisms, and to look for unique resource selection patterns endemic to range peripheries (Swihart *et al.* 2003; Holt and Keitt 2005) where habitat specialization and adaptive potential of species should be most apparent (Spector 2002; Swihart *et al.* 2003; Holt *et al.* 2005). In accordance with our hypotheses species selected resources in accordance with trophic linkages, and level of specialization, and departures from stereotypical resource use were proportional to niche breadth.

Herbivore resource selection was primarily described by vegetation and carnivore resource selection was primarily described by prey abundance, which is consistent with trophic (Ries *et al.* 2004) and biogeographical (Case *et al.* 2005) expectations. Negative vegetative and climatic parameters were also important, suggesting avoidance of vegetation types and unaccounted for biotic determinants correlated to climate variables (Skre *et al.* 2002) or direct climate limitation (Post and Forchhammer 2002; Humphries *et al.* 2004). However, high ranked models may indicate precedence for highly collinear proxy variables if we sampled those variables more accurately than the mechanistically linked variables. This is evident in many of our resource selection functions. We believe herbaceous cover and climate are more indicative of the lack of forest than conifer cover is indicative of forest, as a by-product of our vegetation sampling grain. Thus, in our interpretation we considered selection of negatively collinear variables as a distinct possibility, *i.e.* an aversion to one extreme of our gradient could also represent selection for the other extreme. Notwithstanding this caveat, the persistence of trophic relationships in the resource selection models demonstrates the importance of ecological linkages in determining the occurrence and range of species across this complex gradient.

Our ability to model carnivore occurrence based on herbivore abundance varied according to the degree of predator specialization, with models for more

generalist species containing more vegetative and climatic parameters. Lynx prey specificity is extreme as they consume mostly snowshoe hare with few alternative prey items (e.g. red squirrels; Tumilson 1987; Poole 2003). Accordingly, lynx occurrence was well predicted by snowshoe hares and the distribution of dense patches of regenerating forest (20-30 years post disturbance) preferred by snowshoe hares (Tumilson 1987; Murray *et al.* 1994; O' Donoghue *et al.* 1998; Mowat and Slough 2003; Poole 2003). Marten are much more omnivorous, eating primarily small mammals, but also large quantities of seed, berries and larger vertebrate prey such as snowshoe hare (Thompson and Colgan 1990). Marten are an arboreal species, requiring tree cover for traveling, nesting and for subnivean access points to access prey in the winter (Clark *et al.* 1987; Thompson and Curran 1995), which accounts for their avoidance of tundra vegetation. Fox are the most omnivorous species we examined, eating a huge variety of animal and plant prey across their extensive geographical range (Larivière and Pasitschniak-Arts 1996). We were least able to characterize fox resource selection and were able to describe their occurrence equally well with a variety of herbivore, vegetation and climate variables. The weak positive association with herbaceous vegetation may occur because fox are restricted by the same hunting inefficiencies in thick understory as other canids and lynx (Small and Keith 1992), and correspondingly select more open habitat along the FTT.

There is an overall tendency for species to follow their previously described resource selection patterns across the FTT despite the patchiness and supposed unique conditions at their range peripheries. The occurrence and abundance of all species except for marten are consistent with initial predictions based on previous studies. Hare select for forest and shrub cover and avoid tundra corresponding to dense overstory vegetation, providing thermal refuge, adequate food and cover from predators (Livaitis *et al.* 1985; Fisher and Wilkinson 2005). Red squirrels are most abundant in core forest areas corresponding to food availability (Fisher and Wilkinson 2005) and the inverse relationship between spruce island colonization and patch distance (Etienne 2004). Ptarmigan occur in the tundra and select tundra vegetation and precipitation corresponding to food availability (Ste-

Georges *et al.* 1995). Red-backed voles occur across the FTT and are most abundant in forest selecting for trees, moss and shrubby vegetation corresponding to food abundance (Bangs 1984; Fisher and Wilkinson 2005), cover and nesting sites (Fisher and Wilkinson 2005). Taiga voles select for shrubby, moss and lichen covered environments and avoid trees, and are most abundant in the northern forest, or taiga, utilizing moss and lichen tunnels and runways in lieu of woody material utilized by many vole species for cover and nesting sites (Wolff and Lidicker 1980; Cook 1999). Lynx are restricted to core forest areas selecting for prey abundance (Tumlison 1987; Poole 2003), and open enough environments in which to hunt (O' Donoghue *et al.* 1998). Fox occur across the FTT selecting for prey abundance and openness, corresponding to food availability and habitat plasticity (Larivière and Pasitschniak-Arts 1996; Kurki *et al.* 1998; Tannerfeldt *et al.* 2002). Although these patterns of resource selection are consistent with the well-described, basic ecology of the species examined, collectively they provide a remarkable indication of the strong habitat fidelity displayed by groups of interacting species at the periphery of their range and across a mosaic of contrasting habitat types. Thus, an isolated patch of remnant boreal forest at the northern fringe of the FTT shares a very similar complement of vertebrate species, selecting for similar resources, as contiguous boreal forest at the southern margins of the FTT.

American marten provided the only prominent exception to the stereotypical resource selection exhibited observed for most species. Marten were most abundant in open taiga, near their range periphery, with no association to CWD, contrary to many previous studies (Clark *et al.* 1987; Potvin *et al.* 2000; Payer and Harrison 2003; Poole *et al.* 2004; Fisher and Wilkinson 2005). Marten in other regions avoid open areas, and areas with small trees, requiring adequate amounts of downed woody debris and complex over-story structure such as that found in mature coniferous habitat forest (Clark *et al.* 1987; Potvin *et al.* 2000; Payer and Harrison 2003; Poole *et al.* 2004; Fisher and Wilkinson 2005). Preferential use of structurally complex environments by martens may arise from a requirement for protected nesting sites and access points to subnivean prey in winter and/or an

increase in small mammal prey associated with large amounts of low level vegetation and CWD (Clark *et al.* 1987; Thompson and Curran 1995; Potvin *et al.* 2000). Martens have been widely implicated as major predators to small mammals (Thompson and Colgan 1990; Fryxell *et al.* 1999) including taiga and red-backed (*Clethrionomys*) voles (Wolff and Lidicker 1980; Douglass *et al.* 1983) and the importance of small mammals in the marten diet likely increases when diet choice is small (Thompson and Colgan 1990), as it is at the FTT. At the northern forested region of our study site, there is an abundance of small mammal prey, which marten selected for, very sparse trees and virtually no CWD. This represents a decoupling of the structural complexity/prey requirements for this species providing a unique opportunity to identify the fundamental importance of these factors to martens. Much of our small mammal biomass, especially in our most densely populated marten areas can probably be attributed to taiga voles, which are more than double the average mass of red-backed voles and likely represent a proportionately larger energy return to martens. Our data support the hypothesis of higher marten numbers in response to small mammal biomass (Fryxell *et al.* 1999) and not CWD (Potvin *et al.* 2000). Although taiga elements are sometimes quite old, growth is slow and trees are sparse and stunted resulting in the lack of old growth structures such as snags and CWD (Payette *et al.* 2001). The inclusion of vegetation parameters in our candidate set suggests marten (being arboreal) require trees but that taiga serves equally well to old growth boreal forest in this regard.

Why are we surprised by marten resource selection at the FTT and not equally surprised by red fox, which are even more generalist, inhabiting boreal, taiga and tundra? Both species are generalists, and are thus able to adapt to unusual circumstances at range peripheries (Pulliam 2000; Swihart *et al.* 2003). However, red fox have long been considered generalists (Larivière and Pasitschniak-Arts 1996), and thus their widespread utilization of FTT was expected (Ste-Georges *et al.* 1995), whereas marten were dogmatically considered habitat specialists requiring complex woody environments irrespective of prey base (Clark *et al.*

1987; Potvin *et al.* 2000). These results highlight the importance of considering niche plasticity explicitly when making resource extrapolations.

We have identified previously unknown patterns of abundance and resource selection of terrestrial vertebrates across the FTT, which coincides with the approximate, coarse-grained range limits of many boreal and tundra species. Our results show that these approximately coincident range limits are comprised, at a much finer scale, of coincident patterns of habitat occupancy and resource selection across a mosaic of contrasting habitat types. Thus, moving across the FTT from contiguous forest in the south to contiguous tundra in the north, one encounters patches of boreal vertebrates occupying patches of boreal habitat immediately adjacent to patches of tundra vertebrates occupying patches of tundra habitat. For the most part, patterns of resource selection within this ecotonal periphery of species ranges was remarkably consistent with patterns of resource selection described previously nearer to the core of the range. However, marten were an important exception in this regard, and serve to illustrate how studies of resource selection studies at the range peripheries can elucidate the importance of structural habitat elements versus prey abundance. These results generally endorse the extrapolation of resource selection functions from core to peripheral regions of a species range, however they also advocate caution in the extrapolating these models for generalist species, whether or not we realize they are generalist.

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Table 1. Summary of habitat models for medium sized prey species across the forest to tundra transition ranked by Akaike Information Criteria (AIC). Logistic regression models for snowshoe hare, red squirrel, ptarmigan, red-backed and taiga voles occurrence. Data were collected using winter snow tracking data from n=77 sites summer snap trapping data from n=65 sites for herbivores other than the voles and voles respectively. Model type, Fit (measured as Nagelkerke r^2), number of parameters (K), AIC for small sample size (AIC_C), Relative AIC_C (ΔAIC_C), AIC weight (w_i) of each model. Measure of model performance including area under ROC curves (AUC) and Cohen's Kappa Statistic for 0.5 cut-off (Kappa) are shown for candidate set models.

Rank	Model	Type	Nr^2	K	AIC_C	ΔAIC_C	w_i	AUC	Kappa
<i>Hare</i>									
1	Herbaceous (-), Deciduous (+), Seasonality (+)	Mixed	0.59	4	70.57	0.00	0.22	0.90	0.63
2	Herbaceous (-), Seasonality (+)	Mixed	0.56	3	70.83	0.26	0.20	0.89	0.61
3	Coniferous (+), Shrub (+), Seasonality (+)	Mixed	0.58	4	71.07	0.50	0.17	0.90	0.63
4	Coniferous (+), Shrub (+), Deciduous (+), Seasonality (+)	Mixed	0.60	5	71.44	0.87	0.14	0.90	0.69
5	Coniferous (+), Shrub (+), Deciduous (+)	Vegetation	0.57	4	72.41	1.84	0.09	0.90	0.58
6	Coniferous (+), Shrub (+)	Vegetation	0.54	3	72.59	2.02	0.08	—	—
7	Coniferous (+), Shrub (+), Winter Precip. (-)	Mixed	0.55	4	74.35	3.78	0.03	—	—
8	Herbaceous (-), Deciduous (+)	Vegetation	0.52	3	74.50	3.93	0.03	—	—
9	Herbaceous (-), Winter Precip. (-)	Mixed	0.50	3	76.21	5.64	0.01	—	—
10	Herbaceous (-)	Vegetation	0.48	2	76.65	6.08	0.01	—	—
11	Deciduous (+)	Vegetation	0.30	2	90.80	20.23	0.00	—	—
<i>R. Squirrel</i>									
1	Herbaceous (-), Winter Temp. (-), Ann. Precip. (-)	Mixed	0.57	4	69.73	0.00	0.51	0.84	0.59
2	Herbaceous (-), Seasonality (+), Ann. Precip. (-)	Mixed	0.56	4	70.54	0.81	0.34	0.89	0.59
3	Coniferous (+), Shrub (+), Seasonality (+), Ann. Precip. (-)	Mixed	0.57	5	72.24	2.51	0.15	—	—
4	Coniferous (+), Shrub (+), Grow. S. Temp. (-), Winter Precip. (-)	Mixed	0.48	5	80.09	10.36	0.00	—	—
5	Herbaceous (-), Seasonality (+), Winter Precip. (-)	Mixed	0.43	4	82.21	12.48	0.00	—	—
6	Coniferous (+), Shrub (+), Seasonality (+)	Mixed	0.42	4	83.24	13.51	0.00	—	—
7	Coniferous (+), Seasonality (+)	Mixed	0.30	3	90.40	20.67	0.00	—	—
8	Herbaceous (-)	Vegetation	0.19	2	95.37	25.64	0.00	—	—
9	Coniferous (+), Shrub (+)	Vegetation	0.22	3	95.73	26.00	0.00	—	—
10	Coniferous (+), Winter Temp. (-)	Mixed	0.16	3	99.62	29.89	0.00	—	—
11	Coniferous (+)	Vegetation	0.10	2	101.23	31.50	0.00	—	—
<i>Ptarmigan</i>									
1	Coniferous (-), Deciduous (+), Shrub (-), Seasonality (-)	Mixed	0.54	4	75.29	0.00	0.40	0.88	0.58
2	Herbaceous (+), Winter Precip. (+)	Mixed	0.50	3	76.55	1.26	0.21	0.85	0.51
3	Coniferous (-), Deciduous (+), Shrub (-), Ann. Precip. (+)	Mixed	0.55	5	76.66	1.37	0.20	0.89	0.64
4	Herbaceous (+), Winter Precip. (+), Grow. S. Temp. (-)	Mixed	0.51	4	78.48	3.19	0.08	—	—
5	Herbaceous (+), Seasonality (-)	Mixed	0.48	3	78.90	3.61	0.07	—	—
6	Herbaceous (+), Shrub (+), Seasonality (-)	Mixed	0.48	4	81.07	5.78	0.02	—	—
7	Coniferous (-), Deciduous (+), Shrub (-)	Vegetation	0.46	4	82.77	7.48	0.01	—	—
8	Coniferous (-), Shrub (-)	Vegetation	0.43	3	83.10	7.82	0.01	—	—
9	Herbaceous (+)	Vegetation	0.37	2	85.53	10.24	0.00	—	—
10	Herbaceous (+), Shrub (+)	Vegetation	0.38	3	86.88	11.60	0.00	—	—
<i>R-b. Vole</i>									
1		Vegetation	0.58	4	36.08	0.00	0.26	0.94	0.43
2	Moss (-), All Shrub (+), Small Trees (+)	Mixed	0.58	4	36.08	0.00	0.26	0.94	0.43
3	Moss (-), All Shrub (+), All Trees (+)	Vegetation	0.61	5	36.78	0.70	0.18	0.93	0.48
4	Med. Shrubs (+), Berry Shrubs (+), Moss (-), All Trees (+)	Vegetation	0.58	5	38.42	2.35	0.08	—	—
5	Moss (-), All Shrub (+), Small Trees (+), CWD (-)	Mixed	0.58	5	38.42	2.35	0.08	—	—
6	All Shrub (+), Lichen (+), Moss (-), All Trees (+)	Vegetation	0.50	4	39.91	3.83	0.04	—	—
7	Moss (-), Berry Shrubs (+), All Trees (+)	Vegetation	0.44	3	40.41	4.33	0.03	—	—
8	Berry Shrubs (+), All Trees (+)	Vegetation	0.44	3	40.77	4.69	0.03	—	—
9	All Shrub (+), All Trees (+)	Mixed	0.46	4	42.05	5.97	0.01	—	—
10	All Shrub (+), All Trees (+), Seasonality (+)	Mixed	0.45	4	42.57	6.50	0.01	—	—
11	All Shrub (+), Grow. S. Temp. (+), All Trees (+)	Vegetation	0.38	3	43.13	7.05	0.01	—	—
12	Med. Shrubs (+), Canopy (+)	Vegetation	0.34	4	47.29	11.21	0.00	—	—
13	Med. Shrubs (+), Berry Shrubs (+), Moss (-)	Mixed	0.28	3	47.88	11.80	0.00	—	—
14	All Shrub (+), Seasonality (+)	Vegetation	0.19	2	49.46	13.38	0.00	—	—
15	Berry Shrubs (+)	Mixed	0.24	3	49.55	13.47	0.00	—	—
16	Berry Shrubs (+), Winter Precip. (-)	Vegetation	0.21	3	50.71	14.63	0.00	—	—
<i>Taiga Vole</i>									
1	Moss (-), Berry Shrubs (+)	Vegetation	0.62	5	43.77	0.00	0.33	0.94	0.59
2	All Shrub (+), Lichen (+), Moss (+), All Trees (-)	Vegetation	0.62	5	43.96	0.18	0.30	0.94	0.63
3	Small Shrubs (+), Lichen (+), Moss (+), All Trees (-)	Mixed	0.62	6	45.82	2.05	0.12	0.90	0.65
4	All Shrub (+), Lichen (+), Moss (+), Grow. S. Temp. (+), All Trees (-)	Mixed	0.62	6	45.83	2.05	0.12	0.93	0.67
5	All Shrub (+), Lichen (+), Moss (+), All Trees (-), Ann. Precip. (+)	Mixed	0.62	6	45.83	2.06	0.12	0.94	0.59
6	All Shrub (+), Lichen (+), Moss (+), All Trees (-), CWD (-)	Mixed	0.52	5	50.24	6.47	0.01	—	—
7	All Shrub (+), Lichen (+), Moss (+), Seasonality (+)	Mixed	0.50	5	51.47	7.70	0.01	—	—
8	All Shrub (+), Lichen (+), Moss (+), Grow. S. Temp. (+)	Vegetation	0.42	4	53.88	10.11	0.00	—	—
9	All Shrub (-), Moss (+), All Trees (-)	Mixed	0.45	5	54.20	10.43	0.00	—	—
10	All Shrub (+), Lichen (+), Moss (+), Winter Precip. (-)	Vegetation	0.38	4	55.89	12.12	0.00	—	—
11	All Shrub (+), Lichen (+), Moss (+)	Vegetation	0.33	3	56.15	12.37	0.00	—	—
12	All Shrub (+), All Trees (-)	Vegetation	0.31	3	57.40	13.63	0.00	—	—
13	All Shrub (+), Lichen (+)	Vegetation	0.34	5	60.26	16.49	0.00	—	—

Table 2. Summary of habitat models for predator species across the forest to tundra transition ranked by Akaike Information Criteria (AIC). Logistic regression models of American Marten, Canada Lynx and Red Fox occurrence were created using winter snow tracking data from n=65, 77 and 65 sites respectfully. Model type, Fit (measured as Nagelkerke r^2), number of parameters (K), AIC for small sample size (AIC_C), Relative AIC_C (ΔAIC_C), AIC weight (w_i) of each model. Measure of model performance including area under ROC curves (AUC) and Cohen's Kappa Statistic for 0.5 cut-off (Kappa) are shown for candidate set models.

Rank	Model	Type	Nr^2	K	AIC_C	$\Delta_i AIC_C$	w_i	AUC	Kappa
<i>Lynx</i>									
1	S. Hare (+), R. Squirrel (+)	Trophic	0.54	3	34.38	0.00	0.72	0.95	0.58
2	S. Hare (+), R. Squirrel (+), Grouse (+)	Trophic	0.54	4	36.28	1.90	0.28	0.94	0.58
3	S. Hare (+)	Trophic	0.22	2	46.67	12.29	0.00	—	—
4	Herbaceous (-), S. Hare (+)	Mixed	0.23	3	48.41	14.03	0.00	—	—
5	Herbaceous (-), Winter Precip. (-), S. Hare (+)	Mixed	0.28	4	48.63	14.25	0.00	—	—
6	Herbaceous (-), Seasonality (+), S. Hare (+)	Mixed	0.26	4	49.36	14.98	0.00	—	—
7	Coniferous (+), Shrub (+), S. Hare (+)	Mixed	0.24	4	50.30	15.92	0.00	—	—
8	Herbaceous (-), Seasonality (+)	Mixed	0.14	3	52.35	17.97	0.00	—	—
9	Herbaceous (-)	Structural	0.06	2	53.08	18.70	0.00	—	—
10	Coniferous (+)	Structural	0.04	2	54.07	19.69	0.00	—	—
11	Coniferous (+), Shrub (+)	Structural	0.08	3	54.80	20.42	0.00	—	—
<i>Marten</i>									
1	Herbaceous (-), Seasonality (+)	Mixed	0.70	3	48.00	0.00	0.37	0.93	0.81
2	Herbaceous (-), Seasonality (+), Biomass (+)	Mixed	0.71	4	49.02	1.02	0.22	0.93	0.81
3	Herbaceous (-), Winter Precip. (-), Biomass (+)	Mixed	0.71	4	49.68	1.67	0.16	0.93	0.81
4	Herbaceous (-), CWD (+), Seasonality (+), Biomass (+)	Mixed	0.71	5	51.30	3.30	0.07	—	—
5	Herbaceous (-), CWD (+), Winter Precip. (-), Biomass (+)	Mixed	0.71	5	52.01	4.01	0.05	—	—
6	Coniferous (+), Shrub (+), Biomass (+)	Mixed	0.68	4	52.20	4.20	0.05	—	—
7	Herbaceous (-), Biomass (+)	Mixed	0.65	3	53.40	5.40	0.03	—	—
8	Coniferous (+), Shrub (+), CWD (+)	Structural	0.66	4	54.52	6.52	0.01	—	—
9	Herbaceous (-), Biomass (+), S. Hare (-)	Mixed	0.66	4	54.53	6.53	0.01	—	—
10	Herbaceous (-), CWD (+), Biomass (+)	Mixed	0.65	4	55.54	7.54	0.01	—	—
11	Herbaceous (-), CWD (+)	Structural	0.62	3	55.60	7.60	0.01	—	—
12	Herbaceous (-), CWD (+), Biomass (+), S. Hare (-)	Mixed	0.66	5	56.51	8.51	0.01	—	—
13	Coniferous (+), Biomass (+)	Mixed	0.57	3	60.31	12.30	0.00	—	—
14	Winter Precip. (-), Biomass (+)	Mixed	0.50	3	65.64	17.64	0.00	—	—
15	R-b. Vole (+), T. Vole (+), S. Hare (-), R. Squirrel (+)	Trophic	0.56	5	65.67	17.66	0.00	—	—
16	Biomass (+)	Trophic	0.37	2	72.98	24.97	0.00	—	—
17	Biomass (+), S. Hare (+)	Trophic	0.37	3	74.97	26.97	0.00	—	—
<i>Fox</i>									
1	Ptarmigan (+), R-b. Vole (-), T. Vole (-)	Trophic	0.38	4	74.66	0.00	0.21	0.80	0.40
2	Ptarmigan (+), Biomass (-)	Trophic	0.34	3	74.74	0.07	0.21	0.80	0.48
3	Herbaceous (+), Ptarmigan (+), Biomass (-)	Mixed	0.38	4	74.75	0.09	0.20	0.80	0.55
4	Herbaceous (+), Ptarmigan (+), R-b. Vole (-), T. Vole (-)	Mixed	0.41	5	74.90	0.24	0.19	0.81	0.49
5	Herbaceous (+), Seasonality (-), Ptarmigan (+), Biomass (-)	Mixed	0.39	5	76.66	2.00	0.08	0.81	0.52
6	Herbaceous (+), Seasonality (-)	Mixed	0.29	3	78.48	3.82	0.03	—	—
7	Herbaceous (+), Seasonality (-), Ptarmigan (+)	Mixed	0.31	4	78.99	4.33	0.02	—	—
8	Herbaceous (+), Winter Precip. (+)	Mixed	0.27	3	79.13	4.47	0.02	—	—
9	Herbaceous (+)	Structural	0.23	2	79.53	4.87	0.02	—	—
10	Coniferous (-), Shrub (-)	Structural	0.24	3	81.00	6.34	0.01	—	—
11	Ptarmigan (+)	Trophic	0.13	2	84.92	10.26	0.00	—	—

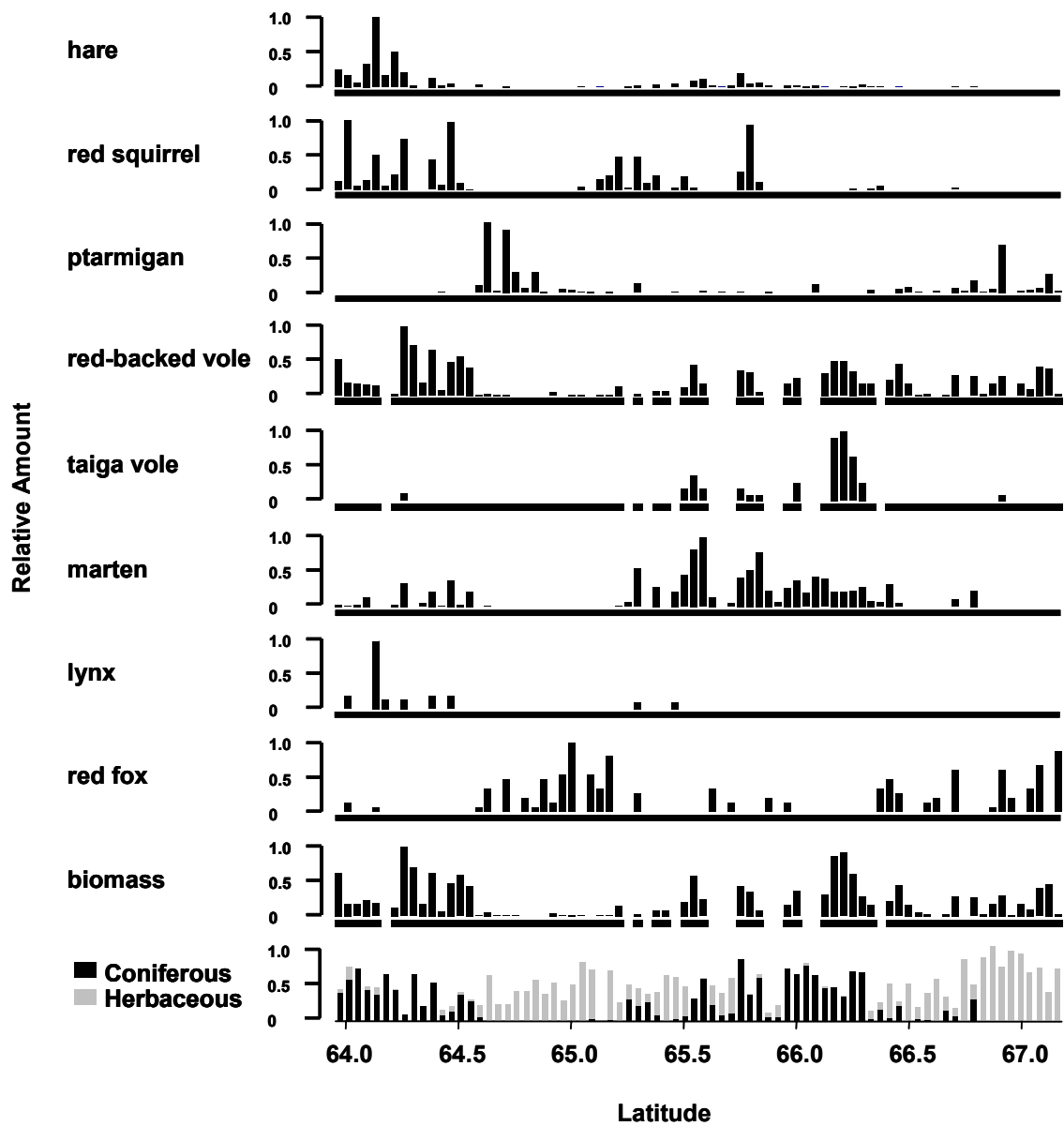


Figure 1. Relative abundance of snowshoe Hare (*Lepus americanus*), American red squirrel (*Tamiasciurus hudsonicus*), ptarmigan (*Lagopus spp.*), northern red-backed vole (*Clethrionomys rutilus*), taiga vole (*Microtus xanthognathus*), american marten (*Martes americana*), Canadian lynx (*Lynx canadensis*), and red fox (*Vulpes vulpes*), relative biomass of small mammals and major vegetation cover by latitude over the forest to tundra transition. Coniferous and herbaceous vegetation covers are indicative of forest and tundra, respectively. Vertical bars indicate relative amount and horizontal bars indicate sample coverage. Data used to build habitat models was limited to the minimum coverage of model components.

GENERAL CONCLUSION

The objective of this project was to thoroughly characterize the terrestrial vertebrate assemblage occurring over the forest to tundra transition (FTT). The underlying motivation for this characterization was to provide baseline data on a previously undescribed vertebrate community needed to 1) predict, detect, and potentially minimize impacts associated with future environmental change in the region and 2) evaluate ecological questions pertaining to species patterning and resource use across an ecosystem boundary.

Chapter 1 examines the broad scale patterns of the terrestrial vertebrate species assemblage across the FTT. There is a more rapid gradient of declining diversity across the FTT relative to core areas of boreal forest and arctic tundra, and diversity changes across this zone are better predicted by vegetative than climate variables. Species occurrence across the FTT is highly patterned, corresponding primarily to vegetation structure and composition, with assemblages of boreal, taiga, and tundra species displaying strong affinities to their respective habitat types.

Chapter 2 examines the fine scale resource selection of eight of the species from the assemblages described in Chapter 1. Herbivore occurrence was predicted primarily by vegetation and predator occurrence was predicted primarily by herbivore (prey) abundance. Most species followed resource associations typical of the core of their range, with the exception of marten (*Martes americana*). This outlier, as well as the predominance of red fox (*Vulpes vulpes*), may result from the wide niche breadth of these species that allows them to exploit novel habitats and prey species at range peripheries.

A strong consensus emerges from the wide array of species, analytical techniques and spatial scales considered in this thesis. Terrestrial vertebrates across the FTT are strongly sorted into distinct assemblages, characterized by strong habitat affinities and presumably strong trophic linkages. Broad scale patterns of diversity and community composition correspond most strongly to vegetation composition. Herbivores associate with appropriate vegetation and predators associate with appropriate prey, which results in distinct groups of

vertebrates occupying distinct habitats across the juxtaposition of contrasting habitat types that define the FTT (Ries *et al.* 2004). Ultimately, vegetative structure and composition across the FTT is determined by climate, geology, and disturbance events in a complex system of cascades and feedbacks (Harding *et al.* 2002; Sveinbjörnsson *et al.* 2002). Several authors are currently working to predict vegetative structure based on purely abiotic factors such as climate and geology (Payette *et al.* 2002; Skre *et al.* 2002). The results of this thesis show that, in turn, vertebrate species occurrence across the FTT can be reasonably predicted from well-defined vegetative structure.

This thesis unequivocally demonstrates the need for empirical investigation of species assemblage in undescribed regions. Only after we describe current patterns of species occurrence across the earth can we understand the ecological mechanisms creating the patterns and make predictions of how perturbations will modify these patterns.

Future Direction

This thesis provides a thorough baseline description of the FTT vertebrate community; the necessary groundwork to formulate informed hypotheses and select appropriate study methodologies and spatial extents on which much future work could be based. Potential areas to focus for this research include ecological monitoring and more targeted examination of the ecological processes driving the observed patterns.

The FTT is a region that will change in terms of both structure and function, due to both anthropomorphic and natural causes. With the initial survey work completed it would be feasible and desirable to set up a long term monitoring project along this gradient. This would likely entail periodic resampling of the vertebrate species occurrence and abundance at the same sites, and/or an intensification of sampling in subregions of specific interests. A less labor intensive plan could entail choosing a subsample of sites for long-term monitoring. This subsample should include sites that are 1) highly representative of the boreal, taiga, and tundra species assemblages and 2) transitional between these three habitat types and species assemblages.

The ecological questions examined in this thesis are just the beginning of what could be elucidated by more in depth research at this gradient. Fine scale patterns of species occurrence could be linked to landscape metrics such as fragmentation indices (Gustafson 1998). Trophic linkages could be examined via stable isotope or stomach content analyses among a subset of abundant species within each assemblage (Kelly 2000). Issues of ecological connectedness among the assemblages occurring in the juxtaposition of contrasting habitat types within the FTT could be assessed with analyses of population genetic structure (Williams *et al.* 2003).

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APPENDIX

Table 1. Location, elevation and anecdotal description of sites sampled for terrestrial vertebrates.

Site	Location		Elevation (m)	Anecdotal Description Terrain; Vegetation
	Latitude	Longitude		
2	64.015920	-144.806970	441	Mostly Flat; Small- Large Conifer and Deciduous, Lots of variation with very thick willow sections
3	63.994258	-144.703562	463	Flat; Medium Density Conifer with willow patches
4	63.940799	-144.643401	522	Medium upslope; varying spruce density with some aspen
5	63.946188	-144.582544	496	Flat with Medium steep hill on right side; Small- Large Conifer and Deciduous, Spruce bog
6	63.935725	-144.503785	619	Medium steep uphill from road; Thick Spruce with Tall Aspen and open patches
7	64.031742	-144.589056	555	Low Rolling; Small- Large Conifer and Deciduous, Lots of variation with very thick old burn section
8	64.076365	-144.535609	690	Upslope Rolling; Medium sized spruce and aspen with willow- some thick sections
9	64.112856	-144.549744	788	Medium Uphill climb; Medium to Dense Spruce and willow- some thick sections
10	64.147964	-144.565262	781	Low-Medium Rolling ; Large Spruce and Aspen with willow patches
11	64.197401	-144.575355	790	gentle upslope; Mostly medium density black spruce
12	64.243486	-144.535204	812	Upslope from road then rolling; Small- Large Conifer and patches of Aspen and willow
13	64.295336	-144.497598	930	Mostly Flat with steep Right Side; Open Spruce and Birch
14	64.343704	-144.447126	918	Steep uphill at front then medium rolling; Open Spruce with Aspen and birch patches
15	64.367790	-144.393026	833	Gentle uphill; Large open conifer with some patchy willow
16	64.410311	-144.317395	956	Medium uphill; Mostly large, medium density spruce
18	64.471180	-144.185484	1155	Flat with steep hill at back corners; Open Tundra with Patches of spruce and Willow
19	64.521904	-144.223663	1282	Undulating steep slopes; Mostly tundra with some patchy spruce and lots of willow
20	64.556967	-144.230356	1289	Flat; Open tundra with some scrub willow
21	64.577881	-144.279712	1240	Gentle downhill slope; Open tundra with willow thickets
22	64.611215	-144.327297	1200	Slight upslope; Open tundra with some scrub willow
23	64.660956	-144.403017	1181	Flat; Open Tundra with very patchy Willow
24	64.697908	-144.424936	1168	Flat; Open Tundra with small spruce and willow patches
25	64.729371	-144.389028	1102	Flat; Open tundra with some scrub willow
26	64.772408	-144.376894	1078	Flat; Open Tundra with very patchy Willow
27	64.810953	-144.372616	1056	Flat; Open Tundra with very patchy Willow
28	64.873757	-144.304282	984	Mildly Rolling ; Open tundra with small willow and spruce patches
29	64.925729	-144.285727	998	Flat; Open Tundra with Spruce Patch
33	65.070166	-144.182173	965	Flat; Open tundra with a few Spruce/willow glades
34	65.070162	-144.269500	1098	Flat with Steep climb in back left corner; Open Tundra with Spruce Patch
36	65.140013	-144.347884	844	Mildly Rolling ; Open Tundra with forest patches
38	65.227020	-144.321169	839	Steep Slope; Tall Spruce, Medium density forest
40	65.311125	-144.233375	690	Medium Rolling; Open Conifer with some willow
41	65.347793	-144.286148	658	Steep slope at front, medium rolling; Sparse spruce with thick patches, willow
43	65.425729	-144.237673	618	Medium Rolling; Open patches interspersed with open low spruce
47	65.552158	-144.222380	593	Medium Rolling; Large to small open spruce
48	65.605317	-144.171845	549	Flat; Very open spruce, likely very wet in summer
49	65.656385	-144.151954	518	Flat; Very open spruce, likely very wet in summer
50	65.694029	-144.116502	544	Flat, with medium steep hill on right side; Lots of old burn sections with open and old growth patches
51	65.739847	-143.944344	623	Medium down slope into valley; Medium Coniferous with bands of willow/alder and some big old spruce
52	65.777987	-143.851151	696	Medium slope downhill from road; Sparse-Thick Medium black spruce
53	65.827788	-143.794683	724	Medium slope downhill from road; Open tundra in front into open spruce forest at back
54	65.864199	-143.712337	755	Gentle slope with river valley; patchy spruce in tundra matrix
55	65.857388	-143.544518	694	Gentle slope into valley; Open tundra in front into open spruce forest at back
56	65.919950	-143.534445	621	Medium down slope into valley; Mixed forest with some very large spruce in patches
57	65.916932	-143.432642	593	Downhill into valley; Large black, White spruce and Birch trees with willow interspersed
58	65.969533	-143.363969	571	Mild Slope downhill from road; Half in recent burn, other half open conifer forest with willow sections

Site	Location		Elevation (m)	Anecdotal Description Terrain; Vegetation
	Latitude	Longitude		
59	66.014398	-143.282014	565	Gently rolling; Mostly in burn with patches of live trees throughout
60	66.064922	-143.294986	597	Gentle slope into valley; Mostly burned with Spruce patches
61	66.111762	-143.241142	599	Slight slope into valley; Open to Medium Conifer
62	66.161216	-143.178720	587	Slight slope into valley; half medium density black spruce, half in burn
63	66.163512	-143.043477	597	Flat; Burned right corner, other wise Open conifer
64	66.192860	-143.016241	591	Gently rolling; Medium spruce forest, with burned sections
65	66.215341	-142.913824	684	Slight slope into valley; Medium to sparse conifers
66	66.271800	-142.792996	572	Gentle down slope; low-medium density Conifer, open sections and willow patches
67	66.291045	-142.709871	598	Flat; Open Conifer with some willow
68	66.357367	-142.749772	629	gentle slope; Medium Conifer with big old patches
69	66.395506	-142.717556	536	Medium slope downhill from road; Small open Spruce
70	66.457778	-142.643130	455	Gentle uphill; Open conifer with some big trees and open tundra
71	66.491129	-142.558541	630	sloping into valley; low-medium density Conifer, open tundra sections and willow patches
72	66.516009	-142.500983	679	Down steeply into valley; half tundra with old growth and open spruce patches
73	66.543474	-142.393383	633	Gentle downhill slope; Tundra grading into increasingly thick spruce and tamarack
74	66.590252	-142.317319	695	Mildly Rolling ; Sparse spruce with willow throughout
75	66.632973	-142.326550	675	Mildly Rolling ; Open Tundra with small spruce patches
76	66.684063	-142.364256	679	Medium Rolling; Patches of spruce and shrub birch in matrix of tundra
77	66.735586	-142.372190	668	Flat with gentle valley; Sparse willow and shrub spruce
78	66.774729	-142.359167	620	Flat; Open tundra with some scrub willow
79	66.827984	-142.363937	617	Medium Rolling; Large sparse spruce and willow patches
80	66.872574	-142.353755	555	Flat; Open tundra with some scrub willow
81	66.932440	-142.275454	579	rolling into small valley; Patchy tundra/ spruce forest/ willow scrubland mix
82	66.962911	-142.211017	710	Flat; Open Tundra
83	66.995416	-142.230981	708	Flat with shallow creek valley; Open Tundra
84	67.045975	-142.224787	824	Steep down slope with gentle sloping basin; Open Tundra
85	67.093467	-142.160618	739	Flat; some willow sprigs- mostly open
86	67.112729	-142.101096	635	Flat; Very open- few sparse spruce and willow
87	67.140743	-142.030345	680	Medium upslope; Very open- few sparse spruce and willow
88	67.155988	-141.974114	658	Over steep hill; Very open- few sparse spruce and willow
89	67.183422	-141.834269	862	Steep upslope; some willow sprigs- mostly open
90	67.197082	-141.697828	503	Flat uphill slope; Open tundra with some scrub willow

Table 2. Raw snow tracking data. The number of tracks detected for each species for each triangle.

Site	Caribou	Ermine	Red Fox	Spruce Grouse	Wolverine	Snowshoe Hare	Lynx	Marten	Moose	Ptarmigan	RedSquirrel	Least Weasel
2	0	7	0	0	0	267	0	2	0	0	16	0
3	0	1	2	0	0	184	4	1	0	0	119	0
4	0	4	0	4	0	68	0	2	1	0	8	7
5	0	1	0	0	0	359	0	8	1	0	18	0
6	0	1	1	2	0	1057	21	0	0	0	60	0
7	0	0	0	0	0	182	3	0	0	0	8	0
8	0	0	0	6	0	529	0	2	4	0	27	0
9	0	0	0	4	0	223	3	19	7	0	87	0
10	0	2	0	0	0	30	0	0	0	0	0	0
11	0	1	0	0	0	0	0	3	0	0	0	0
12	0	0	0	8	2	140	4	12	5	0	52	1
13	0	2	0	0	0	31	0	1	3	5	10	1
14	0	1	0	1	1	48	4	21	0	0	117	0
15	0	0	0	0	0	0	0	2	0	0	13	0
16	0	0	0	0	0	0	0	12	0	0	2	0
18	0	0	1	0	0	32	0	0	0	42	0	0
19	0	0	5	0	0	0	0	1	0	415	0	0
20	0	0	0	0	0	0	0	0	0	9	0	0
21	0	0	7	0	0	13	0	0	0	375	0	0
22	0	0	0	0	2	0	0	0	0	120	0	0
23	0	0	3	0	0	0	0	0	0	26	0	0
24	0	0	1	0	0	0	0	0	0	119	0	0
25	0	0	7	0	0	0	0	0	0	6	0	0
26	0	5	2	0	0	0	0	0	0	0	0	0
27	0	0	8	0	0	0	0	0	0	21	0	0
28	0	0	15	0	0	0	0	0	0	15	0	0
29	0	7	0	0	0	5	0	0	0	2	6	0
33	0	0	8	0	0	0	0	0	0	7	0	0
34	0	0	5	0	0	2	0	0	0	1	19	2
36	0	0	12	0	2	0	0	0	0	6	26	0
38	6	0	0	0	0	0	0	1	0	0	57	5
40	72	0	0	17	0	12	0	4	0	0	4	0
41	0	1	4	0	2	27	2	30	0	52	57	0
43	19	2	0	0	0	0	0	0	0	0	12	4
47	0	4	0	0	1	40	0	16	0	0	25	0
48	0	3	0	0	0	0	0	0	0	0	0	1
49	0	4	0	0	0	51	2	12	0	5	5	0
50	0	2	0	1	1	0	0	25	0	0	23	1
51	290	0	0	2	3	91	0	45	0	0	5	0
52	0	0	0	0	3	128	0	54	0	8	0	0
53	97	5	5	5	0	22	0	8	0	0	0	0
54	45	0	0	0	0	3	0	0	0	2	0	0
55	21	0	2	0	0	28	0	3	0	0	0	0
56	0	1	0	0	0	204	0	23	3	5	32	0
57	61	0	0	0	0	47	0	29	0	0	111	0
58	4	1	0	0	0	69	0	43	0	0	14	0

Site	Caribou	Ermine	Red Fox	Spruce Grouse	Wolverine	Snowshoe Hare	Lynx	Marten	Moose	Ptarmigan	RedSquirrel	Least Weasel
59	0	0	3	0	0	26	0	13	2	7	0	0
60	0	4	0	0	0	0	0	4	0	0	0	0
61	7	0	2	0	1	27	0	15	0	0	0	0
62	18	5	0	0	0	19	0	21	0	0	0	0
63	0	0	0	0	0	12	0	11	0	0	0	0
64	30	0	0	0	0	30	0	24	0	50	0	0
65	12	0	0	0	0	2	0	22	0	0	0	0
66	0	0	0	0	1	0	0	12	0	0	0	0
67	0	0	0	0	0	7	0	12	0	0	0	0
68	0	0	0	0	0	14	0	13	0	0	3	0
69	0	0	0	0	0	37	0	16	0	0	0	0
70	0	0	0	0	0	6	0	5	0	18	3	0
71	0	2	5	0	0	10	0	4	0	0	8	0
72	5	0	7	0	0	0	0	18	0	0	0	0
73	0	6	4	0	0	3	0	3	0	24	0	0
74	0	0	0	0	2	0	0	0	0	33	0	0
75	0	6	0	0	0	0	0	0	0	3	0	0
76	0	0	2	0	0	0	0	0	0	0	0	0
77	0	0	3	0	1	0	0	0	0	11	0	0
78	0	0	0	0	0	0	0	0	0	0	0	0
79	0	2	9	0	4	7	0	6	0	29	4	0
80	0	0	0	0	0	0	0	0	0	8	0	0
81	0	0	0	0	0	11	0	13	0	70	0	0
82	0	0	0	0	0	0	0	0	0	3	0	0
83	0	0	1	0	0	0	0	0	0	20	0	0
84	0	0	9	0	0	0	0	0	0	284	0	0
85	0	0	3	0	0	0	0	0	0	1	0	0
86	0	0	0	0	0	0	0	0	0	11	0	0
87	0	0	5	0	2	0	0	0	0	13	0	0
88	0	0	10	0	1	0	0	0	0	25	0	0
89	0	0	0	0	0	0	0	0	0	113	0	1
90	0	0	13	0	0	0	0	0	0	10	0	0

Table 3. Raw trapping data. The Capture per trap night summarized for each trap site.

Site	Red-backed Vole	Collared lemming	Brown Lemming	Long-tailed Vole	Tundra Vole	Meadow Vole	Taiga Vole	Deer Mouse	Masked Shrew	Northern Bog Lemming
2	19.64	0.00	0.00	0.00	1.79	1.79	0.00	0.00	1.79	0.00
3	7.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	6.92	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	6.32	0.00	0.00	0.00	0.00	0.00	0.00	2.11	0.00	1.05
6	5.83	0.00	0.00	0.00	0.00	0.00	0.00	1.67	0.00	0.00
8	1.30	0.00	0.00	0.00	0.00	0.00	0.00	3.90	0.00	0.00
9	37.40	0.00	0.00	0.00	0.00	0.00	0.81	0.00	0.00	0.00
10	27.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	7.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	24.62	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
13	3.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
14	18.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.33	0.00
15	21.11	0.00	0.00	0.00	1.11	0.00	0.00	0.00	5.56	0.00
16	15.32	0.00	0.00	0.00	1.61	0.00	0.00	0.00	0.81	0.00
18	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
19	1.37	0.00	1.37	0.00	0.00	0.00	0.00	0.00	0.68	0.00
20	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
21	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
22	0.00	0.00	0.00	0.00	0.68	0.00	0.00	0.00	0.00	0.00
23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
26	2.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	0.00	0.00	0.72	0.00	0.00	0.00	0.00	0.00	0.72	0.00
28	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00
29	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
34	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
38	5.33	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00
41	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
47	2.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
48	2.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	4.67	0.00	0.00	0.00	0.00	0.00	1.33	0.00	0.00	0.00
51	16.67	0.00	0.00	0.00	0.00	0.00	2.67	0.00	0.00	0.00
52	6.67	0.00	0.00	0.00	0.00	0.00	1.33	0.00	0.00	0.00
56	14.00	0.00	0.00	0.00	0.00	0.00	1.33	0.00	0.00	0.00
57	12.67	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00
58	2.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00

Site	Red-backed Vole	Collared lemming	Brown Lemming	Long-tailed Vole	Tundra Vole	Meadow Vole	Taiga Vole	Deer Mouse	Masked Shrew	Northern Bog Lemming
59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
61	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
62	9.80	0.00	0.00	0.00	0.00	0.00	1.96	0.00	0.00	0.00
65	12.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
66	18.67	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00
67	18.67	0.00	0.00	0.00	0.00	0.00	7.33	0.00	0.00	0.00
68	13.33	0.00	0.00	0.00	0.00	0.00	4.67	0.00	0.00	0.00
69	6.67	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
70	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
72	8.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
73	17.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00
74	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
75	0.67	0.00	0.00	0.00	0.67	0.67	0.00	0.00	0.00	0.00
76	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
78	0.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
79	11.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
81	10.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
82	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
83	6.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
84	10.67	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00
85	0.00	0.00	0.00	0.00	0.71	0.00	0.00	0.00	0.00	0.00
86	6.67	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
87	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
88	16.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
89	14.67	0.00	0.00	2.00	1.33	0.00	0.00	0.00	0.00	0.00
90	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00