Biodiversity, biogeography and life history of ground-dwelling spiders (Araneae) in the Yukon Territory, Canada

Joseph J Bowden

Department of Natural Resource Sciences
McGill University
Montréal, Québec, Canada

February 2011

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Abstract

Spiders (Arachnida: Araneae) are one of the most diverse and abundant taxa in the Arctic and are affected by fine scale changes in their environment, including temperature, precipitation, and habitat structure. This thesis describes research that occurred across the boreal forest tundra transition zone in the Yukon Territory, Canada. This study system provides an opportunity to test hypotheses about biogeographic patterns and determinants of diversity and life history of spiders in the north. There were four objectives of this research: first, to determine which environmental factors most influence spider assemblage structure (i.e., composition, richness, abundance) at a regional scale in the Arctic; second, to understand patterns of spider assemblages across latitudinal and elevational gradients; third, to understand relationships of life history traits (i.e., body size, body condition, fecundity, reproductive effort) and some of the factors (i.e., density, parasitism, developmental timing) that might influence these traits; and fourth, to determine the effects of elevation on life history traits (i.e., body size, fecundity) in the region. I employed the use of pitfall traps and visual surveys to collect ground-dwelling spiders across latitude and elevation at a regional scale spanning the boreal forest tundra transition zone. My results show that, at a regional extent, spatially structured changes in vegetation best explain the patterns of spider assemblage structure. Elevation has significant effects on spider composition, species richness and overall abundance, but species-specific responses differed along the gradient. For wolf spiders (Lycosidae), female body size best explained variation in fecundity and body condition was the best predictor for relative reproductive effort. I found evidence for egg size-number tradeoffs and very high incidence of parasitism in some populations (e.g., 52% of individual egg sacs) of the species studied. I found that body size (which is correlated with fecundity) varies with elevation, between the sexes and among species. This thesis provides quantitative data about the regional biogeography of arctic spider assemblages, as well as relationships between life history traits for northern wolf spiders. These data can also serve as a foundation upon which to develop and test hypotheses in the contexts of biodiversity, biogeography, life history and climate change in the Arctic.

Résumé

Les araignées (Arachnida: Araneae) font partie des taxons les plus riches et abondants en Arctique et sont affectées par les changements environnementaux à faible échelle. Cette thèse décrit les recherches menées dans le territoire du Yukon, Canada, au niveau de la transition entre la forêt boréale et la toundra. Ce système d'étude nous donne l'opportunité de déterminer les patrons biogéographiques de diversité et d'histoires de vies des araignées. Quatre objectifs ont été poursuivis lors de cette étude. Premièrement, déterminer les facteurs environnementaux influençant le plus la structure des assemblages d'araignées (c.-à-d., composition, richesse spécifique, abondance) à l'échelle régionale en Arctique. Deuxièmement, comprendre les patrons d'assemblages d'araignées le long de gradients d'altitude et de latitude. Troisièmement, comprendre les relations entre les traits d'histoire de vie (c.-à-d., taille, condition, fécondité, effort reproductif) et certains des facteurs pouvant potentiellement influencer ces traits (c.-à-d., densité, parasitisme, chronologie du développment). Enfin, déterminer les effets de l'altitude sur les traits d'histoire de vie (c.-à-d., taille et fécondité) à l'échelle régionale. J'ai utilisé des pièges fosse et des collectes visuelles afin de collecter les araignées du sol sur une région couvrant la zone de transition entre la forêt boréale et la toundra. Mes résultats montrent qu'à l'échelle régionale, ce sont les changements géographiques de végétation qui expliquent le mieux la structure des assemblages d'araignées. L'élévation a également un effet significatif sur la composition, la richesse spécifique et l'abondance des araignées mai les réponses de chaques espèces à ce gradient sont variables. Chez les araignées-loup (Lycosidae), la taille des femelles est le meilleur prédicteur de leur fécondité, mais la condition explique le mieux les variations d'effort reproductif. J'ai également mis en évidence un équilibre entre le nombre et la taille des oeufs ainsi qu'une forte incidence de parasitisme (p. ex., 52 % par sac d'oeufs) chez certaines populations. J'ai enfin montré que la taille, étant corrélée à la fécondité, varie avec l'altitude. Cet effet n'est cependant pas équivalent selon l'espèce ou le sexe des individus considérés. Les recherches présentées dans cette thèse nous ont permis d'obtenir des données quantitatives sur la biogéographie régionale des assemblages d'araignées et d'apporter des informations sur les traits d'histoire de vie des araignées-loup nordiques. Ces données pourront servir de base afin de développer et tester de nouvelles hypothèses sur la manière dont la biodiversité, sa répartition biogéographique et ses traits d'histoire de vie, sont affectés par le changement climatique.

Translation: *Raphael Royaute*

Thesis Format and Contributions of Co-Authors

This thesis is a composition of four manuscripts, three of which are co-authored by me and my supervisor Dr. Christopher M Buddle, as well as a general introduction and conclusions. Chapters two and three have been published in the journals *Écoscience* and *Arctic*, respectively. Chapters four and five will be submitted to peer-reviewed journals for publication. For each of the research chapters within this thesis I planned or helped plan the experimental design with input from my supervisor and committee members: Dr. Murray Humphries and Dr. Terry Wheeler. I was responsible for fieldwork, laboratory work (i.e., identification, measurement and weighing of individuals), obtaining funding, and statistical analyses. I prepared all manuscripts with valuable input from my supervisor. All non-authored contributors (i.e., financial or logistical support) to the manuscripts are acknowledged within each original manuscript.

Contributions to Knowledge

My research makes the following novel and important contributions to knowledge in the areas of spider biodiversity, biogeography and life history in the Arctic:

- Habitat variables (i.e., vegetation structure and composition) serve well to explain regional scale patterns in ground-dwelling spider assemblages in the Arctic (Chapter 2). This confirms a large body of literature from temperate regions, but the generality of the importance of vegetation in explaining biogeography of spiders in the north has never been tested. This is an important contribution because patterns of diversity are not scale invariant and the factors that determine patterns at local spatial scales are less important at large spatial scales.
- My study design provides a unique and well replicated broad scale study of Arctic terrestrial spider assemblages (Chapter 2). Understanding the similarities and idiosyncrasies of elevational and latitudinal diversity patterns is extremely relevant to the impacts of climate change on species ranges. In the context of climate induced range shifts, my data show current quantitative information on many species across a range of latitudes and elevations that can be used to compare with future range data.
- The large scale and intensive quantitative sampling regime provides a benchmark for Arctic arthropod biodiversity knowledge in light of the impacts of climate change on the Arctic fauna (Chapters 2, 3 & 4), but these data can also be used for hypothesis development and testing in the contexts of biodiversity and biogeography.

- I used a spatially nested design (Chapter 3) to study the effects of elevation on spider assemblages and show that multiple mountains can be used as spatial replicates in large scale studies of biodiversity. This allows other researchers some assurance that multiple mountain transects can be used in studies concerned with elevational gradients.
- I discovered many unique species (e.g., *Mughiphantes marusiki* Tanasevitch, *Asiceratinops* sp.) with seemingly very restricted ranges in the northern Yukon Territory, namely from the tundra and higher elevations (Chapters 2 & 3). These species add to biodiversity knowledge in Canada and that the rarity of these species could have implications for conservation biology due to their restricted distributions and rarity.
- I describe novel life history trait relationships in three common wolf spider species in the Arctic (Chapter 4). These results can be used for models of life history evolution and form an important basis upon which to formulate and test hypotheses in the context of climate induced changes to populations:
    - I show important reproductive trait relationships and tradeoffs in Arctic wolf spider species that can be used in future studies to understand other related life history traits and population dynamics
    - I provide evidence that some life history phenomena (e.g., egg sac parasitoids) could play an important role in the life history evolution of wolf spiders in the region studied
- I show that patterns of sexual size dimorphism differ among species and can differ along an elevational gradient. These body size and fecundity results contribute to

the understanding of intraspecific biogeographical patterns in spiders and are of interest in the broader field of biogeography beyond the realm of arachnology (Chapter 5).

Acknowledgements

I would first like to thank my wonderful wife (Karen) for her undying love and support throughout my graduate studies. I would secondly like to thank my supervisor Dr. Chris Buddle, without his knowledge and mentorship I would not have developed into the scientist I am today. He emits and exemplifies a passion for arthropod ecology and science in general.

I would like to thank my committee members Drs. Murray Humphries and Terry Wheeler for their invaluable input through my PhD, with a special thank you to Murray for helping me get to the Yukon and reading to me during the drive. Thank you to my many lab mates over the years. I had great role models like Tara Sackett, Michel Saint-Germain and Maxim Larrivée upon my entrance to the lab. I would like to express a special thank you to my good friend Max. I would also like to acknowledge my other friends and colleagues I have met in my lab and in the department of Natural Resource Sciences for help with logistics, statistics and drafts of manuscripts. A special thanks to Zach Sylvain whom I became good friends with and Alida Mercado with whom I have spent the most time with at McGill, Quinn Fletcher and Guillaume ‘the rock’ for putting up with me bothering them about statistics so frequently, Chris Borkent for bringing a smile to my face nearly every day, Marie-Anne Hudson for many discussions, and many others I am probably forgetting as I write these words.

I would like to thank many agencies for financial and in-kind support over the years: NSERC, Indian and Northern Affairs Canada (NSTP), Yukon Territorial Government, the Yukon First Nations for use of their lands, the Center for Forest

Research-Centre D'Étude de la Forêt, especially Melanie Desrochers, McGill University and Walmart Canada. Thank you to my friends in the Yukon Territory: Karen and Pat Milligan and Kathy Webster. I would also like to thank Charles Dondale for help identifying many difficult spiders.

Last but not least I would like to thank my dear family and friends, especially my son Padraig (thesis baby) for trying to help me write some of my thesis despite the fact that the letters and numbers he pounded out on the keyboard did not form actual words.

Table of Contents

Chapter 1: Introduction and Literature Review

Chapter 2: Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada.

Chapter 3: Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada.

Chapter 4: Life history of three tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada.

Chapter 5: Fecundity and sexual size dimorphism of Arctic wolf spiders (Araneae: Lycosidae) along an elevational gradient.

Chapter 6: Summary, Conclusions and Future Directions

List of Tables

List of Figures

CHAPTER ONE

1.1. Introduction

There has been growing interest in Arctic arthropod ecology (Strathdee and Bale 1998; Høye and Forchhammer 2008; Høye et al. 2009) and concern about the effects of climate change on the unique flora and fauna of northern regions (Hansell et al. 1998, Hodkinson et al. 1998; Callaghan et al. 2004a). Arctic arthropods, as well as plants, are predicted to be acutely affected by changes to the Arctic climate (Strathdee and Bale 1998, Callaghan et al. 2004a). There have been numerous faunistic studies of Arctic terrestrial arthropods (e.g., Danks and Downes 1997) with some focus on Arctic spiders (Arachnida: Araneae) (e.g., Leech 1966; Leech and Ryan 1972). However, there is a growing realization that data on current intra- and inter-specific patterns in Arctic arthropods (e.g., Roininen et al. 2002; Hodkinson et al. 2004) is required in order to quantify future changes to populations and communities due to climate change (Høye et al. 2009). Data on ecological structure (i.e., numbers, abundances and kinds of species) and life history of Arctic arthropods are rare or lacking (but see, Simpson 1993, Høye et al. 2009, Høye and Hammel 2010).

Large scale gradients in space (e.g., elevation and latitude) allow the examination of many environmental factors that determine patterns of species assemblages (Sanders et al. 2003; Jiménez-Valverde and Lobo 2007; Finch et al., 2008; Whitehouse et al. 2009). Biome transitions represent another large scale phenomenon that structure species assemblages. The boreal forest-tundra transition zone is one of the largest biome transition zones globally (Payette et al. 2001) and serves as an important biological filter across which many environmental factors change (Strathdee and Bale 1998).

In this thesis I consider regional scale (200-4000km, Waide et al. 1999) patterns of ecological structure (composition, richness and abundance) and the life history traits of Arctic spider species. The first two manuscripts contained in this thesis are concerned with biogeographic patterns of spider assemblages, their diversity and the factors that underpin this diversity (Chapters 2 and 3). The third and fourth manuscripts are about life history and some population parameters of common spider species in the region, and the relationships among them (Chapter 4), as well as, the effects of elevation on some of these traits (Chapter 5).

1.2. Literature Review

Study Region

The climate of the Yukon Territory, Canada is characterized by short summers of long daily photoperiod and long winters of short daily photoperiod. Daily ambient temperatures in the northern region of the Yukon average 12.0°C ± 0.06 (Mean ± SE) in July and -19.6°C ± 0.1 in January (Environment Canada 2011). The terrain/topography is highly variable and this, as well as its interior location, is reflected in the highly variable climate.

In this region the boreal forest is dominated by black spruce (*Picea mariana* Mill.) and scattered willow (*Salix* sp.), dwarf birch (*Betula glandulosa* Michx.), white spruce (*Picea glauca* Moench) and aspen (*Populus tremuloides* Michx.) and some low lying vegetation composed of *Ledum* sp., *Vaccinium* sp., *Empetrum* sp., lichens and grasses

(Scudder 1997). This habitat transitions northward across a patchy matrix of even sparser and stunted black spruce trees into the tundra with an increasingly open area dominated by peat moss and lichen. The tundra is dominated by peat moss (*Sphagnum sp*.), lichen with sparse dwarf birch (*Betula glandulosa*) and stunted willow (*Salix spp.*), *Ledum* sp., *Vaccinium* sp., *Empetrum* sp. and grasses (Scudder 1997).

Arctic arthropods and climate change

The arctic contains over 4000 described arthropod species (Callaghan et al. 2004b), and just over 2000 species in Arctic North America (Danks 1992); however, many others are yet to be discovered in areas such as northwestern North America (Marusik and Koponen 2002). There has been comprehensive research on adaptations of arthropods in the Arctic (reviewed in, Danks et al. 1994; Danks 2004).There have also been many faunal inventories and these provide a wealth of descriptive knowledge about Arctic arthropods (Leech 1966; Danks 1981; Danks and Downes 1997; Pickavance 2006). Quantitative ecological studies (e.g., Roininen et al. 2002; Coulson et al. 2003; Hodkinson et al. 2004 for assemblages; Simpson 1993; Høye et al. 2009; Høye and Hammel 2010) about insects and spiders in the Arctic are required, however, to allow for hypothesis building and testing, for example regarding the factors that determine patterns of species assemblages and life histories in the Arctic fauna. This is also important in the context of climate change to enable accurate comparisons of current data with future populations and communities.

Strathdee and Bale (1998) reviewed the potential mechanisms driving patterns of diversity and distribution in Arctic arthropods. Northern arthropods are likely influenced by thresholds related to humidity and temperature extremes, or the relative homogeneity of the northern landscape and simplicity of vegetation (Strathdee and Bale 1998). In contrast to tropical regions in which species interactions may be common, biotic factors such as competition are thought to be rare or restricted to small patches for arctic arthropod communities (Hansell al. 1998; Strathdee and Bale 1998). This suggests that spatially distributed changes in vegetation or climate may be more important to the structuring of arthropod assemblages in the Arctic.

One such spatially structured phenomenon in the north is the boreal forest-tundra transition (Payette et al. 2001). This transition zone represents the largest biome transition globally and may function as a contemporary environmental filter for many species in the region (Danks 1992; Strathdee and Bale 1998). Many factors change across this transition zone and it could, therefore, function as a hard barrier to dispersal for many species (Strathdee and Bale 1998). This barrier may manifest due to physiological tolerance of a given species (Case et al. 2005) that has developed over time in adaptation to a particular environment. Allopatric events such as glaciation can have an influence on current patterns of diversity and distribution (Hawkins and Porter 2003; Alsos et al. 2005).

The global climate is changing (Callaghan et al. 2004a; Hansen 2006) and there is growing evidence that these changes will have profound effects on the Arctic (Sturm et al. 2001; Jia et al. 2006; Post and Forchhammer 2008; Høye et al. 2009). Arthropods in the Arctic are abundant and respond rapidly to habitat change (Danks 1981; Danks and Downes 1997); they are, therefore, predicted to be acutely affected by changes in climate. For this reason, they are an exceptional taxon for documenting and understanding effects of a changing climate on Arctic biota (e.g. Høye et al. 2009)).

Biogeography of terrestrial arthropods

Biogeography is the study of patterns of intra- (populations) and interspecific (communities) variation in space and time (Lomolino 2006). It entails investigations of species richness, distributions, origins, ranges, extinctions, movements, morphology, physiology, behaviour and genetics. One of its basic tenets is that biological phenomena (e.g. species diversity and distributions) follow non-random patterns in space and time, and that species encounter gradients and barriers as they distribute themselves across the landscape (Lomolino 2006). Classic broad scale patterns in terrestrial biodiversity include the latitudinal and elevational gradients; these are generally predicted to produce a negative relationship (Willig et al. 2003; Hodkinson 2005). These gradients represent some of the most frequently documented, but least understood patterns in ecology and biogeography (Rohde 1992; Colwell and Lees 2000; Lomolino 2001; Willig et al. 2003). Arthropods are well suited for large scale studies of species diversity (Gotelli and Ellison 2002; Andrew and Hughes 2004; Hodkinson 2005; Almeido-Neto et al. 2006). Terrestrial arthropods have shown numerous intra- and interspecific patterns and include positive (Sanders et al. 2003; Blanckenhorn and Demont 2004; Hodkinson 2005), unimodal (Olson 1994; Sanders 2002; Sanders et al. 2003; Hodkinson 2005) and negative (Olson 1994; Blanckenhorn and Demont 2004; Hodkinson 2005) responses to elevational and latitudinal gradients. These include patterns in body size, polymorphism, diversity, phenology and many other life history and physiological parameters (Schmoller 1970; Chown and Klok 2003; reviewed in Hodkinson 2005). Many large scale terrestrial arthropod studies have displayed patterns that are concordant with the global latitudinal pattern of species diversity (Gotelli and Ellison 2002; Andrew and Hughes 2004; Rodriguero and Gorla 2004) and the similar pattern of decreasing diversity/density towards higher elevation (Otto and Svensson 1982; McCoy 1990; Olson 1994; Sanders

2002; Sanders et al. 2003; Almeida-Neto et al. 2006; Chatzaki et al. 2005). Still, some have found reversed trends in diversity for some groups (Owen and Owen 1974; Kouki 1994).

Spider species diversity

There are over 300 species of spider represented in the Yukon Territory, Canada (Dondale et al. 1997) and many (i.e., 8%) are endemic to Northwestern North America (Marusik and Koponen 2002). Some general patterns have come out of these qualitative studies: the Family Linyphiidae (sheet-web spiders) appears to dominate the species represented; often accounting for at least one third of the species discovered (Davis 1936; Leech 1966; Dondale et al. 1997; Pickavance 2006). It is thought that the proportion of Linyphiidae in local assemblages also increases with increasing latitude (Dondale et al. 1997).

Spiders are a favourable taxon for studying determinants of diversity at broad spatial scales (e.g. regional and continental) and for testing questions related to biogeography and landscape ecology at a regional scale (Jiménez-Valverde and Lobo 2007; Finch et al., 2008; Whitehouse et al. 2009). Spiders are well represented in terms of species richness and abundance at northern latitudes, occur in many habitat types and can be collected easily and in a repeatable fashion (e.g., Buddle et al. 2000; Larrivée and Buddle 2009). Spiders are also important to local food web dynamics (Wise 2004) and ecosystem processes (e.g., nutrient cycling, Lawrence and Wise 2000). Their taxonomy is readily accessible and relatively well known (Ubick et al. 2005).There is also a good body of literature about the factors that determine patterns of spider diversity at various spatial scales (e.g., Rypstra et al. 1999; Beals 2006; Finch et al. 2008; Whitehouse et al. 2009).

Biodiversity is concerned with variation at the genetic, species and ecosystem levels (Gaston and Spicer 2004). Diversity at the species level is considered in this thesis and is equivalent to the number of species (richness) in a given locality, but is not mutually exclusive from abundance (numbers of individuals of a given species) and composition. Although the factors that determine the structure of biological assemblages vary in space and time, their relative importance also varies. At the smallest spatial scale (local), patterns of species diversity are traditionally thought to be determined by biological interactions such as competition and predation (Ricklefs 1987; Menge and Olson 1990; Levin 1992). With increasing spatial scale, larger temporal scale factors (e.g., dispersal, environmental factors) become increasingly important (Ricklefs and Schluter 1993). Climate (e.g., Currie et al. 2004), history and evolution are thought to be most important in explaining the broadest scale patterns (i.e., continental/global) of species assemblages (Ricklefs and Schulter 1993).

Patterns of spider species diversity are subject to changes in spatial and temporal scale. At local spatial scales, spiders are influenced most by micro-environmental conditions including humidity (Turnbull 1973; DeVito et al. 2004), temperature (Turnbull 1973; Devito et al. 2004), vegetation structure (Uetz 1991; Greenstone 1984; Rypstra et al. 1999) and plant species composition (Beals 2006) and appear to respond to acute changes in these parameters (Moring and Stewart 1994; Weeks and Holtzer 2000). For example, Moring and Stewart (1994) found that species of wolf spiders in the genera *Pardosa* and *Alopecosa* partitioned themselves on a scale of meters adjacent to a river in Colorado, USA. They suggested that acute changes in species abundances were due to fine scale changes in habitat. There is, however, some evidence that competition and predation (e.g., intra-guild) could be important to the structuring of spider assemblages at very small spatial scales (Buddle 2002; Rypstra and Samu 2005; Wise 2006).

At continental to global spatial extents, patterns in spider assemblage structure have been correlated with latitude and climate variables, specifically precipitation and temperature (Finch et al. 2008; Whitehouse et al. 2009). At a regional extent, Jiménez-Valverde and Lobo (2007) suggest that vegetation structure best explains spider assemblage structure, while Schaffers et al. (2008) provide support for vegetation composition. A meta-analysis of spider assemblages in Europe points to the importance of climatic variables (Finch et al. 2008). Hence, if any of the aforementioned factors change along spatial or environmental gradients then a change in assemblage structure is likely to track these changes.

Across elevational gradients, ground dwelling spiders have been shown to follow unimodal patterns in richness (Koponen 1987; Chatzaki et al. 2005), with distinct assemblages emerging along the cline (Otto and Svensson 1982; Koponen 1987; Chatzaki et al. 2005). These differences in richness may be attributed to changes in habitat with increases in elevation (Koponen 1987) and although the highest species richness was detected at low and mid elevations, the highest abundance of individuals was detected at high elevations with open habitat (Koponen 1987; Chatzaki et al. 2005).

Life history of spiders

Life history is a schedule of events throughout ontogeny and is concerned with traits that affect the survival and reproduction of individuals. Life history includes traits such as fecundity, parity, and phenology and is shaped by natural selection (Roff 2002). Tradeoffs among and between these traits comprise a central theme to life history theory

(Stearns 1989). Life history traits are also linked to population and community dynamics (Tokeshi 1999; Roff 2002; Bonsall et al. 2004). For example, body size, which is strongly correlated to many life history traits, and phenology of individuals can affect the temporal dynamics of a given population (e.g., Miller-Rushing et al. 2010) and tradeoffs among these traits can affect the coexistence of species in a local community (e.g., Bonsall et al. 2004). There is evidence that life history traits may help form the basis of spatial gradients (Cardillo 2002). Cardillo (2002) suggests that, for birds, there is an important link between life history traits (e.g., clutch size), species richness, and latitude.

Body size is very important to the most important life history traits of individuals and is correlated with many major life history events (Roff 2002). In spiders, like many other groups, body size is related to competitive ability (Samu et al. 1999; Buddle et al. 2003), energetics (Carrel and Heathcote 1976), fecundity (Simpson 1993; Buddle 2000) and overall fitness (Walker et al. 2003). Life history traits vary among individuals, among populations and among species. Such variation in these traits is subject to natural selection which leads to combinations of traits that should optimize lifetime reproductive success. Tradeoffs, a central theme to life history theory, among traits occur due to the limited time and energy available for each component (Roff 2002).

Spiders, often species in the family Lycosidae (wolf spiders), have been used frequently as model organisms with which to examine life history traits and the interrelationships among them (e.g., Schmoller 1970; Simpson 1993; Buddle 2000; Brown et al 2003; Hendrickx and Maelfait 2003; Reed and Nicolas 2008). There exists much literature about spider life history on species from more temperate regions (e.g., Kessler 1971; Brown et al. 2003; Hendrickx and Maelfait 2003; Walker et al. 2003; Reed and Nicolas 2008), less is known about the traits of Arctic species (but see Simpson 1993;

Høye et al. 2009; Høye and Hammel 2010). Many of these studies have investigated the relationships among female size, fecundity and propagule size and show that female size explains much of the variation in fecundity (e.g., approximately 33.42% ± 4.79%, mean ± SE) (Simpson 1993; Buddle 2000; Brown et al. 2003; Hendrickx and Maelfait 2003; Walker et al. 2003; Reed and Nicolas 2008) within wolf spider species. Høye and Hammel (2010), for example, have shown that body size varies significantly in a wolf spider across an elevational gradient in Greenland. These data suggest that abiotic factors impose an important selective force on the life history traits within species.

One commonly investigated trait tradeoff is between egg size and number and has been frequently investigated in terrestrial arthropods, including many spiders (Simpson 1993; Fox and Czesak 2000; Hendrickx and Maelfait 2003; Brown et al. 2003; Walker et al. 2003). Simpson (1993) supported a tradeoff between fecundity and average offspring size in an Arctic wolf spider in one year of a two year study. Such tradeoffs may be mediated by a number of biotic or abiotic factors. In general, tradeoffs appear to be more pronounced in relatively resource poor environments (Messina and Fox 2001; Roff 2002; Hendrickx and Maelfait 2003) with larger eggs being favoured (e.g., Benton and Uetz 1986; Hendrickx and Maelfait 2003). It could be predicted that in populations where resources are scarce due to high densities (e.g., competition) or high incidence of predation or parasitism, for example, tradeoffs would be more prevalent. For example, there is evidence that smaller, faster developing propagules are produced in environments where there is high incidence of parasitism (Messina and Fox 2002).

Strong environmental and spatial gradients represent model systems for studying adaptation and variation in life history traits. Because environmental factors vary greatly in space, such gradients can help determine the extent of life history variation in a given species. Spatial gradients are often considered gradients in resource availability reflecting the harshness of local climate with increasing elevation (Hodkinson 2005). Changes across elevation have yielded significant changes in life history characteristics of terrestrial arthropods (e.g., body size, fecundity, phenology) (Gutiérrez and Menéndez 1998, Karl et al. 2008, and reviewed in Hodkinson 2005). These studies have yielded mixed results with examples of positive and negative responses to such clines (Chown and Klok 2003, reviewed in Hodkinson 2005, Stillwell et al. 2007). Changes in body size associated with these clines are generally associated with developmental timing or local climate (Mousseau and Roff 1989, Chown and Klok 2003, Stillwell et al. 2007). The reproductive investment of female arthropods is linked to body size, male quality (Wedell and Karlsson 2003) and ultimately resource availability (Fox and Czesak 2000). One might expect changes in context, which occurs along a gradient (e.g., environmental, spatial), to manifest in changes of life history characteristics and even population dynamics (Plaistow and Benton 2009). Such geographical variation in life history characteristics, such as body size, has also been found to differ between the sexes (Stillwell et al. 2007, Høye and Hammel 2010), resulting in patterns of sexual size dimorphism (SSD).

Sexual size dimorphism is the difference in mean body size between males and females, with males generally being larger in the endotherms and females being the larger sex in ectotherms (Fairbairn 2007). Closely related phenotypic traits such as the difference in body size between the sexes and developmental timing may have important implications for life history evolution and fitness (Roff 2002). If the sexes within a given species respond differently to geographic variation in abiotic and/or biotic factors (Foellmer and Moya-Laraño 2007, Stillwell et al. 2010), the degree and direction of SSD could vary along spatial or environmental gradients. This can be due to differential responses incurred by genetics or phenotypic plasticity between the sexes (Stillwell and Fox 2007, Stillwell and Fox 2009). Variation in SSD over geographic clines has been shown in some groups (Schäuble 2004, Blanckenhorn et al 2006, Høye and Hammel 2010) and this can be analogous to variation over time related to climate changes (Høye et al. 2009).

Summary

This literature review shows that the boreal forest-tundra transition serves well as a system across which to study biogeographical patterns of diversity and life history in terrestrial arthropods. Because so many environmental and historically influenced factors (e.g., elevation, climate, and habitat) change in the region of study, it functions well as a system in which to formulate and test hypotheses about the determinants of diversity and life history adaptations in the Arctic fauna. Furthermore, within the framework of biogeography, quantitative datasets can be formed to examine the effects of climate change on Arctic arthropods.

Global climate changes are predicted to profoundly affect the Arctic and its flora and fauna (Hansell et al. 1998; Jia et al. 2006; Post et al. 2009). Terrestrial arthropods are expected to respond acutely to these changes (Callaghan et al. 2004a) and significant variation in arthropod life history traits has been shown over a relative recent and short time scale (Høye et al. 2009).

Large scale, quantitative data on Arctic arthropod assemblages will help to further the development of predictive models or future studies on the effects of climate change on arthropod diversity. Variation in the Arctic climate has been linked to long term patterns in terrestrial arthropod body size (Høye et al. 2009) and such life history traits play a critical role in the dynamics of populations (Roff 2002) and communities (Tokeshi 1999).

1.3. Thesis Outline and Objectives

The general objective of this thesis was to determine patterns of spider species diversity and life history in the region of the boreal forest-tundra transition. The first half of this thesis evaluates determinates of diversity for ground dwelling spider assemblages at a regional scale using latitudinal and elevational gradients. The objectives of the first manuscript (Chapter 2) were to determine the patterns of spider species diversity across the boreal forest-tundra transition using a latitudinal transect, and to test hypotheses regarding the factors that determine these patterns. I formulated three complementary hypotheses: first, gradients in ground dwelling spider assemblage structure are due primarily to vegetation composition and/or structure; second, gradients in spider assemblage structure are primarily due to gradients in temperature and precipitation (climate variables); third, Arctic spider assemblages respond most strongly to spatial variables which represent spatially structured factors (e.g. biological factors, historical processes) or unmeasured factors that cannot be fully explained by our data (Borcard et al. 1992). Chapter 3 tests the effects of elevation and latitude on spider assemblage structure (richness, abundance and composition) using mountains as spatial replicates within each latitude. I hypothesized that there would be significant differences among elevation and latitude in species composition, richness and abundance (measured as activity density) and predicted that species richness and abundance would decrease with increasing elevation and latitude. The second half of the thesis is concerned with life history traits of the dominant wolf spider species in the region. I first tested whether body size or body condition better explained variation in fecundity and relative reproductive effort (Chapter 4). I also tested the hypothesis that females who produce larger progeny produce fewer progeny and *vice versa*. I evaluated the natural densities, developmental timing and egg parasitism of these species and relate these to the life history trait data. I predicted that body size would best explain variation in fecundity and that body condition would best explain variation in relative reproductive effort. I predicted that there would be a tradeoff between egg size and number. I predicted that the biological phenomena (density, Parasitism, developmental timing) measured would provide some insight into the life history of the spiders. Following detection of substantial site variation in reproductive traits among the species, I sought to determine the effects of elevation (which can be viewed as a proxy for resource availability) on fecundity and sexual size dimorphism using species with broad elevational distributions (Chapter 5). I tested the hypothesis that fecundity, body size and the difference in body size between the sexes would significantly differ with changes in elevation.

CHAPTER TWO

This chapter constitutes the first large scale quantitative study of ground-dwelling spiders in the Arctic. We used a latitudinal transect spanning the boreal forest-tundra transition zone in the Yukon Territory, Canada to determine patterns of, and factors determining the structure (composition, richness and abundance) of spiders in the region.

This chapter is a copy and is reproduced with permission from the journal Écoscience. This article is cited as Bowden, J. J. and Buddle, C. M. 2010. Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada. Écoscience 17(3): 287-297. Copyright 2010, with permission from Écoscience.

Determinants of ground dwelling spider assemblages at a regional scale in the Yukon Territory, Canada

2.1. Abstract

Arctic fauna is undergoing significant alteration in response to global climate change, yet we know little regarding the factors that determine species assemblages at northern latitudes. We used a latitudinal transect to assess environmental determinants of ground dwelling spider assemblages across the boreal forest –tundra transition at a regional scale. Using multivariate techniques, we tested three complementary hypotheses regarding the factors that best explain patterns of assemblage structure. We predicted that spider assemblages would respond most strongly to vegetation composition and structure, and that climate and spatial variables would explain less of the variation in the data. We sampled ground dwelling spiders using pitfall traps placed at thirty-six sites along the latitudinal transect. We constructed three separate matrices of spatial, climate and vegetation variables with each matrix representing a hypothesis. We used redundancy analysis with variation partitioning to determine which matrix of environmental variables best explained patterns in a matrix of spider abundances. We then used a separate redundancy analysis to determine which environmental variables best explained the variation in measures of species richness and activity density. We collected a total of 2890 individual spiders representing 103 species, 58 genera and 13 families. Our analysis supports the hypothesis that vegetation composition and its related structure best explain patterns in northern spider assemblages at a regional scale.

2.2. Introduction

Determining the factors underlying the structure of species assemblages across broad spatial scales is fundamental to ecology and biogeography (Lomolino 2006). Determining these factors will also aid in understanding large-scale changes in biodiversity related to climate change (Andrew and Hughes 2004). The structure of species assemblages (i.e., species richness, abundance, composition) differs across spatial scales because the factors that determine these patterns also vary with scale (Willis and Whittaker 2002). For example, the examination of broad scale patterns of species diversity has revealed the importance of latitude at regional to continental extents (e.g. Gotelli and Ellison 2002; Finch et al. 2008; Whitehouse et al. 2009). Ecological studies across spatial gradients (e.g., latitudinal and elevational) can help elucidate which factors (e.g., spatially dependent or independent changes in habitat) are most important in structuring species assemblages (Gotelli and Ellison 2002; Hawkins et al. 2003; Sanders 2003; Baselga 2008).

Environmental gradients such as biome transitions represent broad scale phenomena that can profoundly affect community structure (e.g., Pfeiffer et al. 2003). These transitions represent rapid changes in physiognomy relative to the adjacent habitats/biomes and can have variable influences on taxa (Ries et al. 2004). For example, a given taxon may view a transition zone as suitable habitat, amplifying the measured response across the transition (Ries et al. 2004). The division between northern boreal forests and the tundra is one of the largest biome transition zones in the world (Payette et al. 2001), yet there are few data about how communities change across this ecotone. Although plants appear to respond readily to changes in climate (e.g. Payette et al. 2001;

Walker et al. 2006; Lenoir et al. 2008) across habitats and with time, it is less apparent how other taxa respond to these broad scale gradients. It is also important to consider that spatial changes in ecological phenomena may not occur in a linear fashion or at just one scale (Borcard and Legendre 2002), especially across environmental gradients. The importance of particular factors that determine species assemblages varies not only with the spatial scale of analysis, but also with the taxon of interest (Hawkins et al. 2003).

Spiders are a model taxon for studying determinants of diversity at broad spatial scales (e.g. regional and continental) and for testing questions related to biogeography and landscape ecology (Jiménez-Valverde and Lobo 2007; Finch et al., 2008; Whitehouse et al. 2009). Spiders are diverse, abundant, occur in many habitat types and can be collected easily and in a repeatable fashion (e.g., Buddle et al. 2000; Larrivée and Buddle 2009). At local spatial extents, spiders are governed by micro-environmental conditions including humidity (Turnbull 1973; DeVito et al. 2004), temperature (Turnbull 1973; Devito et al. 2004), vegetation structure (Uetz 1991; Rypstra et al. 1999) and plant species composition (Beals 2006), and appear to respond to fine changes in these parameters (Moring and Stewart 1994; Weeks and Holtzer 2000). At continental-global spatial extents, patterns in spider assemblage structure have been correlated with latitude and climate variables, specifically precipitation and temperature (Finch et al. 2008; Whitehouse et al. 2009). At a regional extent Jiménez-Valverde and Lobo (2007) suggest that vegetation structure best explains spider assemblage structure, while Schaffers et al. (2008) provide support for vegetation composition. A meta-analysis of spider assemblages in Europe points to the importance of climatic variables (Finch et al. 2008).

Despite many inventories of spiders in northern regions (e.g. Dondale et al. 1997; Koponen et al. 2001; Marusik et al. 2001) there have been few large-scale quantitative studies of spider assemblages in northern North America and little is known about changes in arthropod assemblages across the boreal forest-tundra biome transition. We collected spiders along a latitudinal gradient of 3.25 degrees latitude, intersecting the boreal forest – tundra transition zone in northwestern North America. Our objective was to establish the relative influence of factors determining patterns in northern spider assemblage structure at a regional scale (i.e. 200-4000 km, Waide et al. 1999) across the boreal forest-tundra transition. We formulated three main hypotheses: 1) Gradients in ground dwelling spider assemblage structure are due primarily to vegetation composition and/or structure; 2) Gradients in spider assemblage structure are primarily due to gradients in temperature and precipitation (climate variables); 3) Arctic spider assemblages respond most strongly to spatial variables which represent spatially structured factors (e.g. biological factors, historical processes) or unmeasured factors that cannot be fully explained by our data (Borcard et al. 1992). We predict that spider assemblages will respond most strongly to changes in habitat structure and plant species composition due to the extensive literature showing this at many spatial extents. We also predict that climate and spatial variables will explain less of the variation in northern spider assemblages.

2.3. Materials and Methods

Study Design, Sampling and Specimen Processing

We sampled the ground-dwelling spider fauna using pitfall traps at 36 (15 boreal, 13 tundra, 8 transition) sites along a latitudinal transect from 63.940 to 67.194 °N, alongside the Dempster Highway in the Yukon Territory, Canada (Figure 2.1). Sites averaged 10.47 ± 7.25 km (mean ± SD) apart, with a maximum distance of 27 km in straight line distance. We opted to use pitfall traps given the precedent in the literature for this sampling approach with large-scale projects (e.g. Gotelli and Ellison 2002; Bonte et al. 2003; Chatzaki et al. 2005; Buddle et al. 2006), and since pitfall traps collect in a consistent and repeatable manner. This technique allowed us to replicate our design over 390 km in linear distance; other sampling methods were not practical at this spatial scale. Each pitfall trap consisted of a plastic circular container ten centimeters in diameter and fifteen centimeters in depth with a rain cover of plastic corrugate (approx. 12 x 12 cm), positioned 5 centimeters above each trap. Ten pitfall traps were placed in each site in a triangular fashion, 9 forming the perimeter and 1 in the center, 10 meters apart from each other. A 1:1 ratio of water to propylene glycol was used as a preservative in each pitfall trap.

Our transect began in the contiguous boreal forest, continued over a section of alpine tundra, across a second forested section (taiga) and into the contiguous northern tundra (Figure 2.1). Although we recognized 3 habitat types across this transect, the transition from boreal forest to tundra is quite gradual in this region. The boreal sites were dominated by black (*Picea mariana*) and white (*Picea glauca*) spruce with sparse aspen (*Populus tremuloides*); the tundra sites were treeless and were dominated by peat moss (*Sphagnum sp*.) and dwarf birch (*Betula glandulosa*) with sparse willow (*Salix spp.*); transition sites were characterized as being an intermediate habitat, largely open tundra with sparse black spruce (*Picea mariana*). Elevation along the sampled transect ranged from 444 to 1297 meters. Sites were chosen in attempt to minimize the heterogeneity within each broader habitat type.

Spiders were collected between 10 June 2005 and 19 July 2005; pitfall traps were active for no less than 26 days and no more than 35 days. This time frame was selected because it represents the active period for adult spiders at these latitudes (Pers. Obs., Niemelä et al. 1994, Koponen 1999). These data represent one season of sampling, however, Buddle et al. (2000) found little and no significant variation from year to year in species richness and composition, respectively, in northern boreal spider assemblages. All traps were emptied twice and arthropods were preserved in 70% ethanol. Due to trap disturbance at many sites, we had to randomly sub-sample five of the ten traps and from these we identified all adult spiders to species. Immature specimens were identified to the lowest taxonomic level possible, but were not used in species-level analyses. Voucher specimens are deposited in the Lyman Entomological Museum (Ste Anne de Bellevue, Québec).

Environmental Variables

Three separate matrices of variables were used to test the aforementioned hypotheses: 'climate', 'spatial' and 'vegetation'. At each site, five 4-meter diameter circular plots were sampled for vegetation. These plots were situated in the four cardinal directions about the perimeter with one in the center of a 22 meter diameter circle about the center of each pitfall trapping triangle. Percent cover of canopy, lichens, mosses and each species of herb and shrub were also estimated providing us with a measure of average percent cover at each site. All trees were counted and identified to the lowest possible taxonomic level within an 11 meter diameter circle plot at the center of each pitfall triangle. The amount of coarse woody debris (CWD) was also calculated at each site using two 50-meter crisscrossing transects over the center of the pitfall triangle. This data collection provided us with a matrix of nineteen species of plants plus five other site variables related to local vegetation structure (percent cover of litter, lichen, moss, percent canopy cover, CWD). We used the Hellinger transformation (Legendre and Gallgher 2001) on the plant species data.

Because processes that determine local species assemblages and species diversity operate at various spatial scales, it is important to incorporate spatial variables into statistical models that capture variation in species data at multiple scales (Borcard and Legendre 2002; Borcard et al. 2004). In order to incorporate such variables into our statistical analysis we used the Vegan package version 1.18-0 (Oksanen 2009) for the R environment version 2.9.1 (R Development Core Team, 2009) to obtain multi-scale spatial variables for PCNM (principal coordinates of neighbour matrices) analysis from our original latitude and longitude values in Cartesian coordinates (Borcard and Legendre 2002). We used a truncation distance of 27 kilometers as this was the largest distance between two sites. This process yielded 24 PCNM variables plus the three original spatial variables (latitude, longitude and elevation).

WorldClim version 1.4 (Hijmans et al. 2005) was used to obtain bioclimatic variables that composed the climate matrix. Climate variables for each site were extracted using Arc GIS® version 9.3 (Environmental Systems Research Institute 2008). The variables used to test the climate hypothesis were: annual mean temperature, temperature seasonality standard deviation *100, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation seasonality (coefficient of variation), precipitation of the wettest quarter and precipitation of the driest quarter. All of the aforementioned environmental variables were standardized by column to a mean of zero and a standard deviation of one to make appropriate comparisons among them.

Response Variables

The response variables that we used to examine spider assemblage structure consisted of a matrix of spider species by sites as well as a separate matrix which consisted of a number of univariate measures of diversity. We chose to express the spider species data without the influence of singleton and doubleton (species represented by one or two individuals) species, in order to maximize the potential of detecting relationships between the species composition data and the measured environmental variables. The matrix analyzed consisted of all 36 sites and 51 species and was transformed to a Hellinger distance matrix. The Hellinger transformation is well supported (Legendre and Legendre 1998; Legendre and Gallagher 2001) and a useful method of transformation because it allows for the use of canonical ordination techniques such as redundancy analysis (RDA, Rao 1964) to explain the variation of a species matrix containing many zeros (Legendre and Gallagher 2001).

Other important components to species assemblage structure are richness, the number of species, and total abundance, the number of individuals (Magurran 2004). We used measures of species richness and abundance to assess the relative importance of the environmental variables to aspects of spider species diversity. The response variables that we used were raw spider species richness (RawRich), the abundance based coverage estimator (ACE), Chao's incidence based estimator (Chao 2) and the second order jackknife (Jack 2) species estimator, obtained using Estimates for Windows version 8.0.0 (Colwell, 2006), and raw and standardized (to 30.8 trap days) abundance (RawAbun, Std

Abun) which was measured as activity density. ACE, Chao 2 and Jack 2 were selected as estimators due to their relative accuracy in predicting 'true' species richness for small numbers of samples (Colwell and Coddington 1994) and their general support over other richness estimators (reviewed in Magurran 2004).

A permutation selection procedure available in the Vegan package (function 'ordistep') was then used to reduce the number of variables representing each the vegetation and spatial matrices for the spider species matrix. We ran both forward and backward selection and retained the variables with a p-value = 0.05 and excluded variables with a p-value > 0.1. The resultant model for vegetation retained the variables: *Alnus*, *Andromeda*, *Empetrum*, *P. glauca*, *P. mariana*, *Potentilla*, *Rosa*, *Shepherdia*, percent canopy cover, litter and coarse woody debris. The resultant model for the spatial matrix retained the PCNM variables 1-5, 8 and 16. This process was repeated for the measures of spider species richness and activity density. We ran the selection procedure with the same criteria for the indices of species richness and activity density to select reduced matrices representing the spatial and vegetation components. The variables representing vegetation that were retained for the model were: *Alnus*, *Betula glandulosa*, *Empetrum*, *P glauca*, *P mariana*, *Potentilla*, *Rubus*, *S. reticulata*, *Shepherdia* and *V uliginosa*. The only spatial variable retained was PCNM 6.

Statistical Analyses

We used the technique of variation partitioning (Borcard et al. 1992) to determine the relative influence of multiple complementary sets of hypotheses (Legendre 2008) on spider community composition (a matrix of spider species). Variation partitioning was initially described by Borcard et al. (1992) to partial out the influence of spatially structured variation in a species matrix. We used the program VARCAN version 1.0 (Peres-Neto, 2006) which runs all canonical and partial canonical analyses (RDA for our data) required to determine the amount of variation explained by each environmental matrix omitting the effects of the other matrices (the marginal effects, Lepš and Šmilauer 2003), each fraction including the effects of other environmental matrices (conditional variation explained, Lepš and Šmilauer 2003) and the total variation explained. A permutation procedure further tests whether a particular fraction explains a significant portion of the total variation in the data (Peres-Neto et al. 2006). We used 9999 permutations to test the contribution of each fraction. The program also corrects for the number of samples and the number of explanatory (environmental) variables used in the analysis (Peres-Neto et al. 2006) by calculating an adjusted R^2.

In order to examine which specific variables, defined by the matrices of environmental data, best explained patterns of variation in the spider species matrix we ran a redundancy analysis using Canoco for Windows version 4.55 (ter Braak and Šmilauer 2002) to interpret the relationships. Redundancy analysis is an ordination technique that is a direct extension from multiple linear regression where each ordination vector is a linear projection of the distribution of the objects in space (in our case using Hellinger distance) (Legendre and Legendre 1998). We also used the program Canoco to run an RDA to examine which determinants best explained the variation in the measures of species richness and activity density. We used the selected variables for each dataset in each model and focused the scaling on inter-species distances and data were centered by species.

2.4. Results

In total, 2890 individual spiders were collected, representing 103 species, 58 genera and 13 families. Activity density averaged 80.54 ± 6.32 individuals/site (mean ± 1 SE) (range: 23 -156). Spider species richness averaged 13.56 ± 0.58 species/site (range: 7 - 22). Four species, all from the family Lycosidae (wolf spiders), comprised 61% of the total catch: *Pardosa lapponica* Thorell (27%), *P. uintana* Gertsch (15%), *P. moesta* Banks (11%) and *P. sodalis* Holm (8%). Other dominant spider families included the Linyphiidae (micro-sheet web spiders), which was also the most species rich, Gnaphosidae (ground spiders) and Thomisidae (crab spiders) (Appendix 2.1).

Spider assemblage structure

Variation partitioning revealed that vegetation composition and its associated structural components were the most important determinants of ground dwelling spider assemblages (Figure 2.2) in the northern Yukon Territory. The marginal effect (independent of the influence of other variables) of vegetation explained a significant portion of the spider species data ($p < 0.05$, Monte Carlo permutation). Even when the conditional (dependent) effects of vegetation were tested it still explained 13.6% of the variation and was the only fraction that contributed a significant portion of the variation explained ($p = 0.031$). The spatial and climate components did not have significant conditional effects on the total variation ($p > 0.05$). A great deal of the conditional variation was explained by spatially structured climate and vegetation. Independently (marginal effects), space and climate each explained a significant ($p < 0.05$) amount of the spider species variation.

The specific variables that best explained patterns of variation in the spider species data were percent canopy cover (intraset correlation for axis one was 0.83) and other vegetation variables specifically *P. mariana*, *Shepherdia* and *Rosa* with correlations of 0.53, 0.55 and 0.54, respectively (Figure 2.3). The most important climate variables that contributed to the structuring of the ordination were maximum temperature of the warmest month and annual mean temperature which had intraset correlations of 0.73 and 0.57 with the first axis of the biplot, respectively (Not Shown). The spatial variables that most contributed to the structuring of the spider assemblages were the second and third PCNM variables which had correlations with axis one of -0.4 and -0.72, respectively (Not Shown), and PCNM 4 which correlated strongly (0.44) to the second axis. These PCNM variables correspond to broader scale variation in the data that is not associated with linear gradients (e.g. latitude). There was a separation of tundra sites on the left side of the ordination diagram and boreal sites represented on the right side with sites that were identified as intermediate transition sites lying close to the center of the biplot (Figure 2.3). Some species displayed high habitat fidelity (Figure 2.4), for example, *P. uintana* was only collected at forested sites, while *P. sodalis* was only collected at tundra sites. Other species (e.g. *P. moesta* and *Alopecosa aculeata*) were impartial to the habitat transitions and were collected along the entirety of the latitudinal transect.

We assessed diversity patterns using raw spider species richness and estimated richness via extrapolation using Chao 2 and the second order Jackknife estimators. All three indices of diversity which fell along the first axis of the RDA biplot were related to the plant species variables: *Alnus* and *Rubus* (correlations with first axis of -0.48 and -0.4, respectively) and inversely related to *S. reticulata* (0.45) (Figure 2.5). These measures of species richness were also partially related to higher temperatures and forest areas. Raw abundance (measured as activity density) and standardized abundance were related most strongly to smaller vegetation more common in tundra sites (e.g., *B. glandulosa*) and lower temperatures (Figure 2.5). Specifically, higher species richness appears to be related to sites with more structural vegetation, and higher activity density to sites with less vegetation structure.

2.5. Discussion

We tested the relative influence of vegetation, climate and spatial variables on patterns of northern spider assemblage structure at a regional scale across the forest-tundra transition zone. Our analysis, using ground dwelling spiders collected in northwestern North America, suggests that vegetation composition and its associated structural components, particularly whether a habitat is open (tundra) or relatively closed (boreal), dictates assemblage structure across this biome transition. We also assessed the relative influence of the aforementioned environmental variables on species diversity using measures of species richness and activity density. We found that variables indicating vegetation contributed most to patterns in northern spider diversity.

We found no linear trends in the data and there was no support for the spatial variables latitude, longitude and elevation in determining these ground dwelling spider assemblages. Specifically, one might expect latitude or elevation to have had significant effects on these arthropods given the range of these variables at the regional scale of study. Latitude and elevation have been shown in many studies to affect spider assemblages over broad spatial gradients (Andrew and Hughes 2005; Chatzaki et al. 2005; Finch, Blick and Schuldt 2008; Whitehouse et al. 2009) and in other arthropods at a regional scale (Gotelli and Ellison 2002). We did, however find large overlap of the multi-scale spatial variables with other variables of interest (large fraction revealed via variation partitioning), highlighting the importance of broad scale spatially structured habitat along the transect. We found relatively little support for the sole effects of the PCNM variables; however the variables that were selected for the final statistical model did represent broader scale spatial variation (PCNM 2, 3 and 4).

Our finding that vegetation composition and structure best explained patterns in spider species composition and diversity patterns has been supported by others at local to regional spatial scales (Uetz 1991; Balfour and Rypstra 1998; Jiménez-Valverde and Lobo 2007; Drapela et al. 2008). For example, in a study assessing the relative importance of vegetation structure, climate and spatial variables to the structuring of foliage dwelling spider species richness in Spain, Jiménez-Valverde and Lobo (2007) concluded that vegetation structure was the most important determinant. Drapela et al. (2008) found that all of their measures of epigeic spider assemblage structure (richness, activity density and composition) were most strongly related to structural variables (i.e. proportion of woodland areas and non-crop area) in a study of factors affecting spider assemblages in an agricultural setting at local and landscape scales. Muff et al. (2009) also found, at a local scale, that the amount of light availability (openness) best explained patterns of ground dwelling spider assemblages across an alpine-timberline ecotone. We also found that species richness tended to be higher in more vegetated sites which supports the idea that composition and structure increases spider species richness (Uetz 1991; Rypstra et al. 1999); however, we also tended to find higher activity density in tundra sites. While more species requiring structure for web attachment were collected in forested habitats, our pitfall trapping technique yielded more individuals (namely wolf spiders) from open tundra habitats which is a common occurrence in studies of ground dwelling spiders (e.g., Koponen 1987; Hurd and Fagan 1992; Buddle et al. 2000).

There is a long history in the literature regarding the importance of habitat, specifically habitat structure, in determining the structure of spider assemblages; particularly with studies across successional gradients (e.g., Lowrie 1948; Bultman et al. 1982; Hurd and Fagan 1992; Kaufmann 2001). As vegetation composition and structure are intrinsically linked, we also suggest that composition is an important component to the structuring of spider assemblages. The effects of vegetation composition on spider assemblages have been displayed by others at local and regional spatial scales (Beals 2006; Schaffers et al. 2008). The support for the importance of vegetation and its associated structure is made clearer in our study by the species specific responses displayed in the RDA biplot. We have established that the first axis of the ordination is generally an axis of habitat from the boreal to the tundra and that most of the dominant spider species collected along our transect are best fit to this axis. Specifically, the wolf spiders which are favoured by the pitfall collecting technique (e.g., Buddle et al. 2000) responded strongly to the changes in vegetation along the transect. *P. uintana* was collected in high abundance in the southern and northern forested sites and not at all in the tundra. Conversely, *P. sodalis* which is endemic to northwestern North America and northeastern Siberia (Dondale et al. 1997) was only collected at the southern and northern tundra sites, whereas *P. moesta* and *A. aculeata* which are found throughout the forested and non-forested boreal latitudes of North America were collected across the entire sampling transect. Species such as the dictynid *Hackmania prominula* which require structure to construct webs were also only collected in forested sites.

We found that climate variables explained the least conditional amount of variation in spider assemblages from the northern Yukon Territory. The importance of climate variables to the structuring of spider assemblages has been supported at a regional scale by others (e.g., Finch et al. 2008) and the effects of temperature and precipitation on spiders have been well documented (Turnbull 1973, DeVito et al. 2004). Finch et al. (2008) found that local variation in mean annual temperature, along with plant species richness and elevation range was positively correlated with spider species richness at a regional scale in Europe. However, despite the general attention that climate has received as a determinant of species diversity patterns (Hawkins et al. 2003; Currie et al. 2004) and its importance displayed in some systems, we found relatively little support for climate in our study. Similarly, Jiménez-Valverde and Lobo (2007) found that climate played a relatively minor role in determining patterns of spider species richness in Spain, being overshadowed by the effects of vegetation structure. In their study maximum temperature was the only climate variable that was significantly related to their species richness data. Similarly, we found that few elements of climate, specifically maximum and minimum temperatures and the annual range in precipitation ('PrecipSe'), were important determinants of spider diversity patterns and composition, respectively. Spiders are likely governed more by microclimatic conditions provided by the local habitat in which they live, while broader scale climate changes in space may be less detectible with respect to these arthropods.

There were naturally differences in broad vegetation composition along the sampled transect; however, our purpose was to determine how ground dwelling spider assemblages changed across the forest-tundra transition. Despite the fact that sites were not entirely selected without bias (forest cover changed over the gradient), these differences did not necessarily have to reflect changes in spider assemblages. While finding some support for broad scale spatial variables across our transect, had we conducted sampling evenly across a relatively homogeneous habitat it is possible that we would have detected more support for smaller scale spatial autocorrelation related to mechanisms such as dispersal (Bonte *et al*., 2004). Other biological factors such as food availability (Halaj et al. 2000) and interactions such as competition and predation (Turnbull 1973, Wise 2006) may also affect species assemblages at various spatial scales, although it has been argued that competition with ground-dwelling spiders may be relatively rare (Wise 1993; Buddle 2002). The glacial history of this region (Schweger 1997), may also play an important role in determining species composition of this region across the boreal-tundra transition zone. Further consideration of these potential mechanisms and others should aid in explaining more of the variation in patterns of spider assemblage patterns in the north at various spatial scales.

2.6. Acknowledgements

The authors would like to thank Troy Pretzlaw and Elise Bolduc, Dr. Charles Dondale (Canadian National Collection) and Dr. Murray Humphries (McGill University) for logistical support and Melanie Desrochers (Centre d'Étude de la Forêt) for help with constructing one of the figures. We would also like to thank the Tetlit Gwitch'n, Nacho Nyak Dun, Vuntut Gwitch'n, Tr'ondëk Hwëch'in Han Nation and the Yukon Territorial Government. Financial support was provided by the Northern Scientific Training Program, the National Science and Engineering Research Council of Canada, and McGill University.

2.7. Literature Cited

Andrew, N. R. and Hughes, L. 2004. Species diversity and structure of phytophagous beetle assemblages along a latitudinal gradient: predicting the potential impacts of climate change. Ecological Entomology 29: 527-542.

Andrew, N. R. and Hughes, L. 2005. Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. Austral Ecology 30: 281-297.

Balfour, R. A. and Rypstra, A. L. 1998. The influence of habitat structure on spider density in a no-till soybean agroecosystem. Journal of Arachnology 26: 221-226.

Baselga, A. 2008. Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography 31: 263-271.

Beals, M. L. 2006. Understanding community structure: a data-driven multivariate approach. Oecologia 150: 484-495.

Bonte, D., Criel, P., Van Thournout, I. and Maelfait, J. P. 2003. Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. Journal of Biogeography 30: 901-911.

Bonte, D., Baert, L., Lens, L. and Maelfait, J. P. 2004. Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. Ecography 27: 343-349.

Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principle coordinates of neighbour matrices. Ecological Modelling 153: 51-68.

Borcard, D., Legendre, P., Avois-Jacquet, C. and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826-1832.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Buddle, C. M. 2002. Interactions among young stages of the wolf spiders *Pardosa moesta* and *P. mackenziana* (Araneae : Lycosidae). Oikos 96: 130-136.

Buddle, C. M., Spence, J. R. and Langor, D. W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424-436.

Buddle, C. M., Langor, D. W., Pohl, G. R. and Spence, J. R. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biological Conservation 128: 346-357.

Bultman, T. L., Uetz, G. W. and Brady, A. R. 1982. A comparison of cursorial spider communities along a successional gradient. Journal of Arachnology 10: 23-33.

Chatzaki, M., Lymberakis, P., Markakis, G. and Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. Journal of Biogeography 32: 813-831.

Colwell, R. K. and Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 345: 101-118.

Colwell, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples, version 8. [Online] URL: http://viceroy.eeb.uconn.edu/EstimateS.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E. and Turner, J. R. G. 2004.

Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7: 1121-1134.

DeVito, J., Meik, J. M., Gerson, M. M. and Formanowicz, D. R. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae : Lycosidae) correspond with microhabitat distributions. Canadian Journal of Zoology 82: 1119-1125.

Dondale, C., Redner, J. and Marusik, Y. M. 1997. Spiders (Araneae) of the Yukon. Pages 73-113 *in* H. Danks and J. Downes (eds), Insects of the Yukon. Canadian Museum of Nature, Ottawa, Ontario.

Drapela, T., Moser, D., Zaller, J. G. and Frank, T. 2008. Spider assemblages in winter oilseed rape affected by landscape and site factors. Ecography 31: 254-262.

ESRI 2008, ArcGIS version 9.3: Environment systems, Research Institute Inc. Redlands, CA.

Finch, O. D., Blick, T. and Schuldt, A. 2008. Macroecological patterns of spider species richness across Europe. Biodiversity and Conservation 17: 2849-2868.

Gotelli, N. J. and Ellison, A. M. 2002. Biogeography at a regional scale: Determinants of ant species density in New England bogs and forests. Ecology, 83: 1604-1609.

Halaj, J., Ross, D. W. and Moldenke, A. R. 2000. Importance of habitat structure to the arthropod food-web in Douglas -fir canopies. Oikos 90: 139-152.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J. F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E. and Turner, J. R. G. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84: 3105-3117.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Hurd, L. E. and Fagan, W. F. 1992. Cursorial spiders and succession: Age or habitat structure? Oecologia 92: 215-221.

Jimenez-Valverde, A. and Lobo, J. M. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecological Entomology 32: 113-122.

Kaufmann, R. 2001. Invertebrate succession on an alpine glacier foreland. Ecology 82: 2261-2278.

Koponen, S. 1987. Communities of ground-living spiders in six habitats on a mountain in Québec, Canada. Holarctic Ecology 10: 278-285.

Koponen, S. 1999. Common ground-living spiders in old taiga forests of Finland. The Journal of Arachnology 27: 201-204.

Koponen, S., Vygandes, R. and Dapkus, D. 2001. Changes in structure of ground-living spider (Araneae) communities on peatbogs along a transect from Lithuania to Lapland. Norweigian Journal of Entomology 48: 167-174.

Larrivée, M. and Buddle, C. M. 2009. Diversity of canopy and understorey spiders in north-temperate hardwood forests. Agricultural and Forest Entomology 11: 225-237.

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Elsevier, Amsterdam.

Legendre, P. and Gallagher, E. D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271-280.

Legendre, P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. Journal of Plant Ecology 1: 3-8.

Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P. and Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768-1771.

Lepš, J. and Šmilauer, P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

Lomolino, M. 2006. Biogeography. Sinauer Associates, Sunderland.

Lowrie, D. C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351.

Magurran, A. 2004. Measuring biological diversity. Wiley-Blackwell, Malden.

Marusik, Y., Koponen, S., Vinokurov, N. and Nogovitsyna, S. 2001. Spiders (Araneae) from northernmost forest-tundra of northesatern Yakutia (70^{O}35'N, 134^{O}34'E) with description of three new species Arthropoda Selecta 10: 351-370.

Moring, J. B. and Stewart, K. W. 1994. Habitat partitioning by the wolf spider (Araneae, Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River, Colorado. Journal of Arachnology 22: 205-217.

Muff, P., Kropf, C., Frick, H., Nentwig, W. and Schmidt-Entling, M. H. 2009. Co-existence of divergent communities at natural boundaries: spider (Arachnida: Araneae) diversity across an alpine timberline. Insect Conservation and Diversity 2: 36-44.

Niemelä, J., Pajunen, T., Haila, Y., Punttila, P. and Halme, E. 1994. Seasonal activity of boreal forest-floor spiders (Araneae). Journal of Arachnology 22: 23-31.

Oksanen, J. 2009. Vegan: R functions for vegetation ecologists. http://cc.oulu.fi/~jarioksa/softhelp/vegan.html

Payette, S., Fortin, M. J. and Gamache, I. 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. Bioscience 51: 709-718.

Peres-Neto, P. R. 2006. VarCan: Variation estimation and partitioning in canonical analysis. [Online] URL: http://esapubs.org/archive/ecol/E087/158/Guide.pdf

Peres-Neto, P. R., Legendre, P., Dray, S. and Borcard, D. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87: 2614-2625.

Pfeiffer, M., Chimedregzen, L. and Ulykpan, K. 2003. Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. Journal of Biogeography 30: 1921-1935.

Platnick, N. 2009. The World Spider Catalog Online, version 10.0. American Museum of Natural History, New York, New York.

R Development Core Team. 2009. R: a language and environment for statistical computing, version 2.9.0. R Foundation for Statistical Computing. Vienna, Austria.

Rao, C. 1964. The use and interpretation of principal component analysis in applied research Sankhyā 26: 329-358.

Ries, L., Fletcher, R. J., Battin, J. and Sisk, T. D. 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology Evolution and Systematics 35: 491-522.

Rypstra, A. L., Carter, P. E., Balfour, R. A. and Marshall, S. D. 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. Journal of Arachnology 27: 371-377.

Sanders, N. J., Moss, J. and Wagner, D. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12: 93-102.

Schaffers, A. P., Raemakers, I. P., Sykora, K. V. and Ter Braak, C. J. F. 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89: 782-794.

Schweger, C. 1997. Late Quaternary Paleoecology of the Yukon: A Review. Pages 59-72 *in* H. Danks and J. Downes (eds), Insects of the Yukon. Biological Survey of Canada, Ottawa, Ontario.

ter Braak, C. J. F. and Šmilauer, P. 2002. Canoco for Windows, version 4.5. Biometris – Plant Research International. Wageningen, The Netherlands.

Turnbull, A. L. 1973. Ecology of true spiders (Araneomorphae). Annual Review of Entomology 18: 305-348.

Uetz, G. 1991. Habitat structure and spider foraging. Pages 325-348 *in* S. S. Bell, E. D. McCoy, H. R. Mushinsky. (eds), Habitat structure: The physical arrangement of objects in space. Chapman and Hall, London.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P. and Parmenter, R. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H.

E., Jonsdottir, I. S., Klein, J. A., Magnusson, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen, A., Totland, O., Turner, P. L., Tweedie, C. E., Webber, P. J. and Wookey, P. A. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103: 1342-1346.

Weeks, R. D. and Holtzer, T. O. 2000. Habitat and season in structuring ground-dwelling spider (Araneae) communities in a shortgrass steppe ecosystem. Environmental Entomology 29: 1164-1172.

Whitehouse, M. E. A., Hardwick, S., Scholz, B. C. G., Annells, A. J., Ward, A., Grundy, P. R. and Harden, S. 2009. Evidence of a latitudinal gradient in spider diversity in Australian cotton. Austral Ecology 34: 10-23.

Willis, K. J. and Whittaker, R. J. 2002. Species diversity: Scale matters. Science 295: 1245-1248.

Wise, D. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge.

Wise, D. H. 2006. Cannibalism, food limitation, intraspecific competition and the regulation of spider populations. Annual Review of Entomology 51: 441-465.

2.8 Figure captions

Figure 2.1 – Thirty-six sites were established to collect ground dwelling spiders along a 390 km transect in the Yukon Territory. The transect began in the boreal forest to the south, crossed the Mackenzie mountain range (indicated as non forest), into a northern region of forest and into the northern contiguous tundra (indicated as non forest).

Figure 2.2 – Partitioning of ground dwelling spider species variation into spatial, climate and vegetation components. Values in the fractions represent adjusted R^2 (as percent) coefficients of conditional effects of the four matrices of environmental variables. Marginal effects of the explanatory components are shown in parentheses.

Figure 2.3 – Redundancy analysis biplot showing all 36 sites sampled and the environmental variables that most strongly influenced (t-values of regression coefficients $-1.4 < 1.4$ and intraset correlations $-0.3 < 0.3$) the spider data matrix. The measured environmental variables explained 41% (R^2_{Adj}, $p < 0.05$) of the variation in the species data. Open circles represent forested sites, black circles represent tundra sites and grey circles represent intermediate or transition sites. (%CanCov = percent canopy cover, PrecipSE = precipitation seasonality).

Figure 2.4 – Biplot showing the spider species represented by more than fifteen individuals and that best fit (between 25% and 100%) the first two axes of the RDA. The species with the best fit were also among the most abundant species collected and belonged to the family Lycosidae: *Pardosa lapponica* and *Pardosa sodalis*, *Pardosa*

moesta, Pardosa uintana Pardosa glacialis and *Alopecosa aculeata*. The other two best fit species were *Hackmania prominula* family Dictynidae and *Xysticus britcheri* family Thomisidae.

Figure 2.5 – Biplot diagram showing the first two axes of a redundancy analysis of indices regressed on measured environmental variables. The environmental variables explained 44.2% ($R^2_{Adj,}$ $p < 0.05$) of the variation in the indices. Only the variables that most strongly influenced (t-values of regression coefficients $-1.7 < 1.7$ and intraset correlations $-0.18 < 0.18$) the indices are shown. (MaxTemp = maximum temperature, MinTemp = minimum temperature, TSeasStD = temperature seasonality standard deviation).

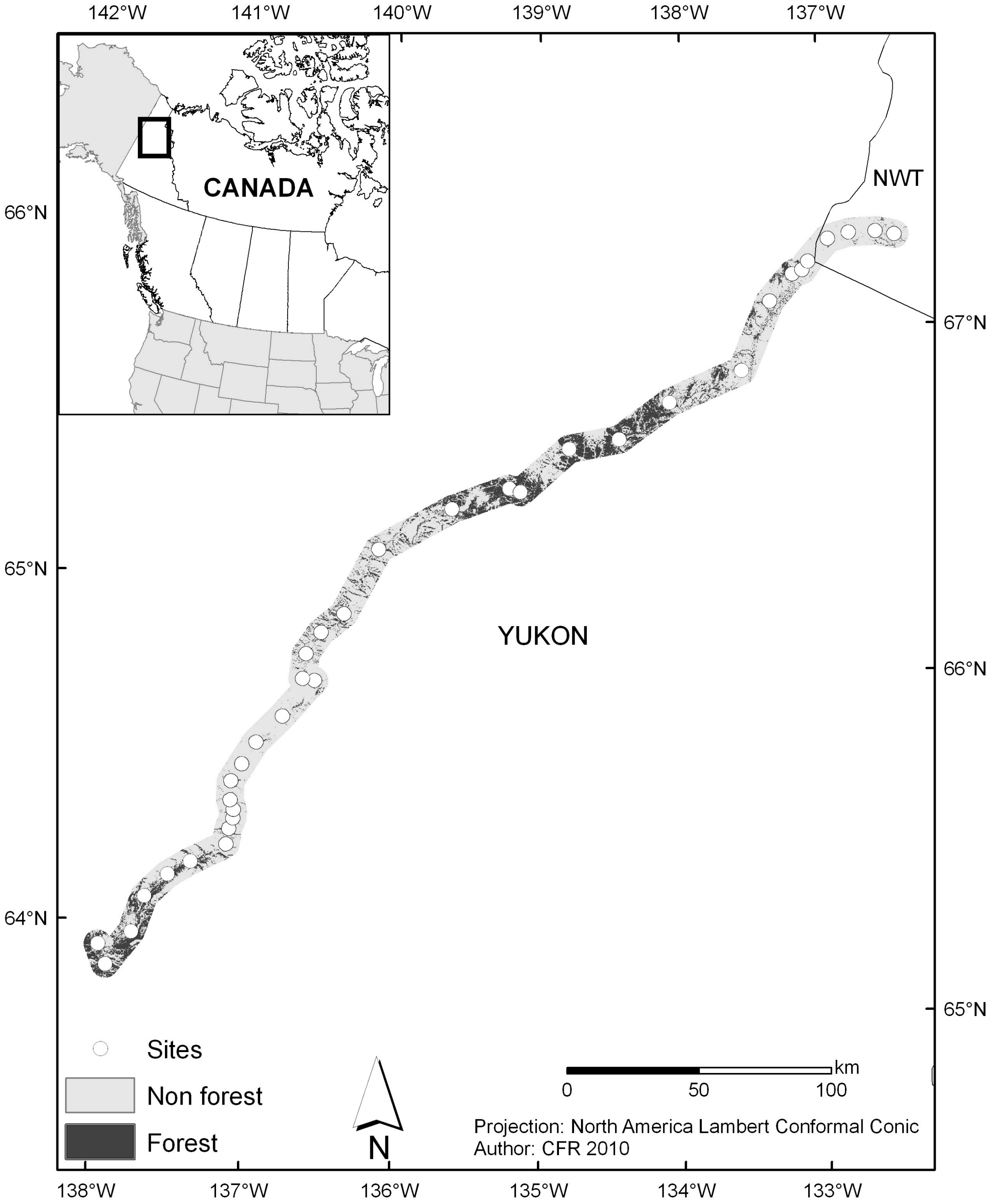
142°W
141°W
140°W
139°W
138°W
137°W
CANADA
NWT
YUKON
66°N
65°N
64°N
67°N
66°N
65°N
Sites
Non forest
Forest
N
km
0
50
100
Projection: North America Lambert Conformal Conic
Author: CFR 2010
138°W
137°W
136°W
135°W
134°W
133°W

Figure 2.1

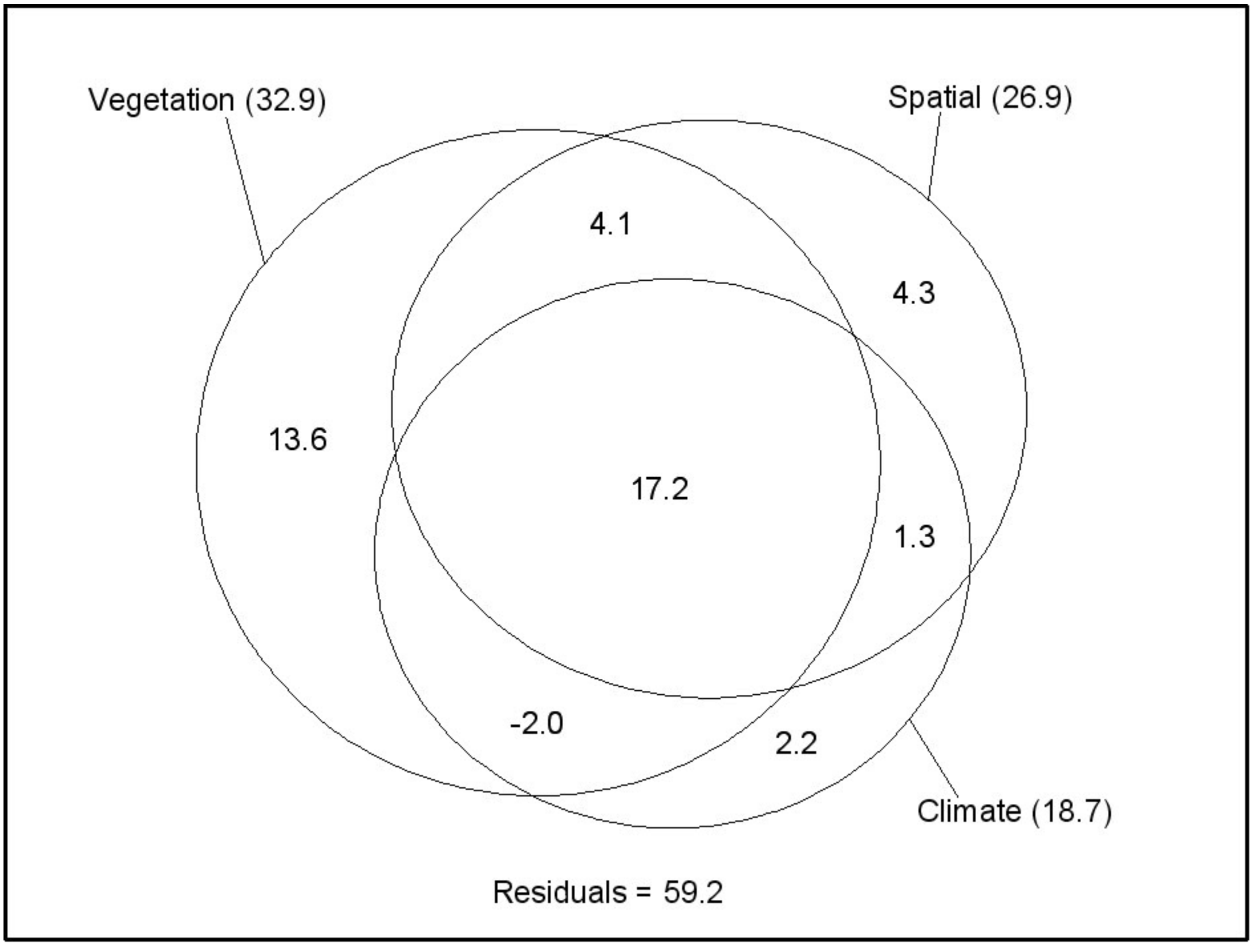
Vegetation (32.9)
Spatial (26.9)
4.1
4.3
13.6
17.2
1.3
-2.0
2.2
Climate (18.7)
Residuals = 59.2

Figure 2.2

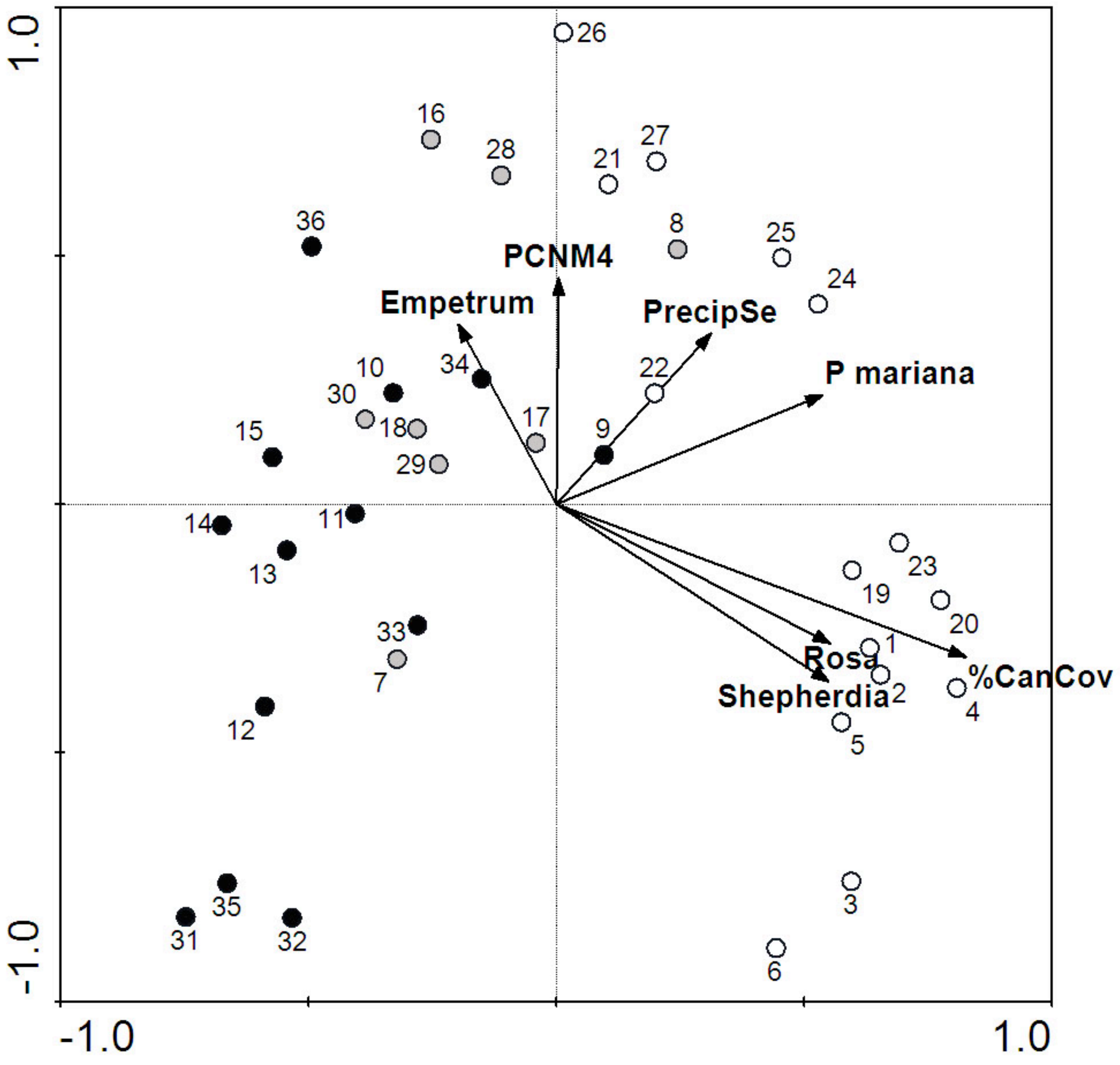
1.0
-1.0
-1.0
1.0
PCNM4
Empetrum
PrecipSe
P mariana
Rosa
Shepherdia
%CanCov
26
16
28
27
21
36
8
25
24
22
10
34
30
18
17
9
15
29
14
11
13
23
19
20
33
7
1
2
4
12
5
3
35
31
32
6

Figure 2.3

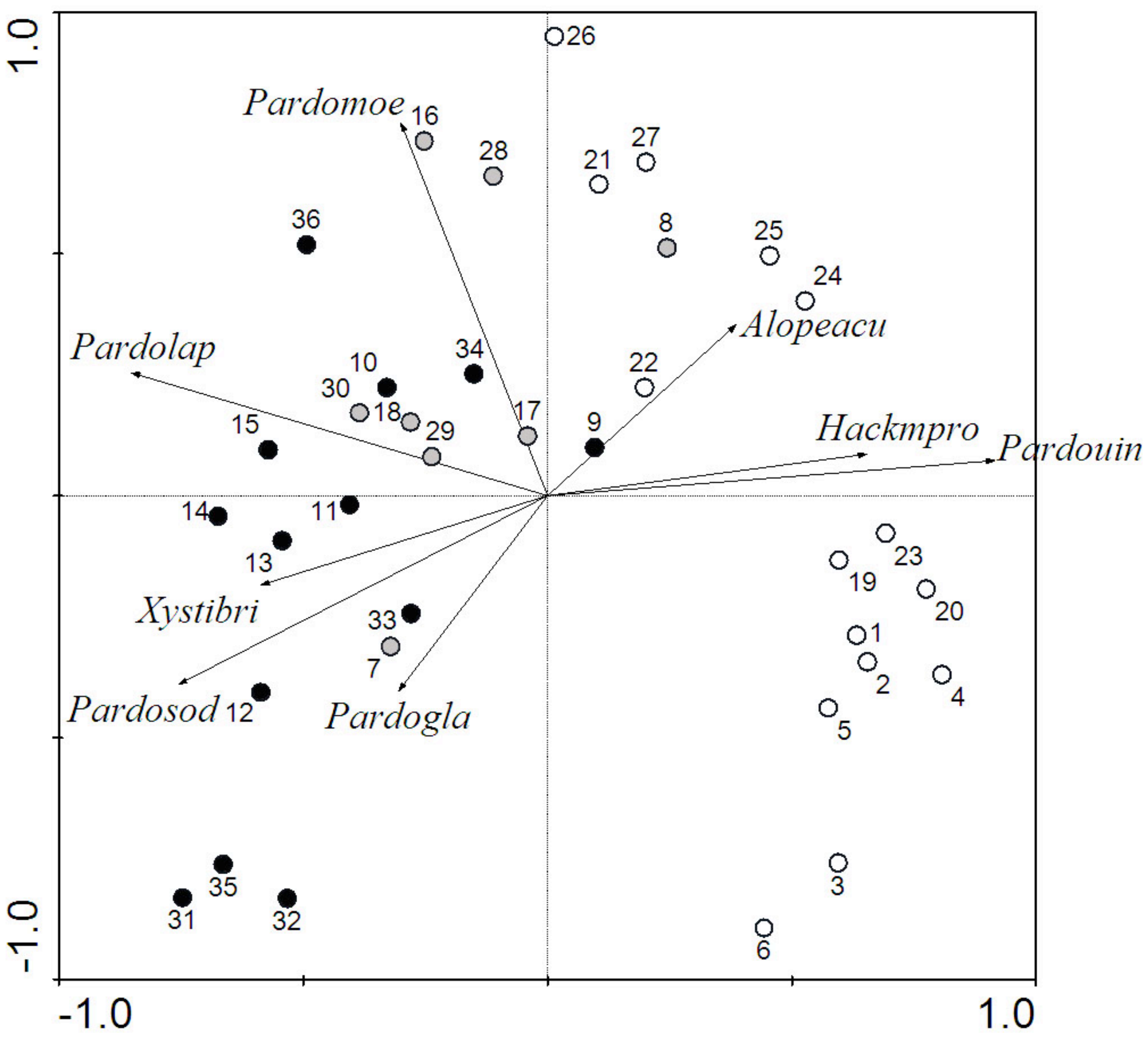
1.0
-1.0
-1.0
1.0
Pardomoe
Pardolap
Alopeacu
Hackmpro
Pardouin
Xystibri
Pardosod
Pardogla
26
16
28
21
27
36
8
25
24
34
10
30
18
29
17
9
22
15
14
11
13
33
7
12
23
19
20
1
2
4
5
35
31
32
3
6

Figure 2.4

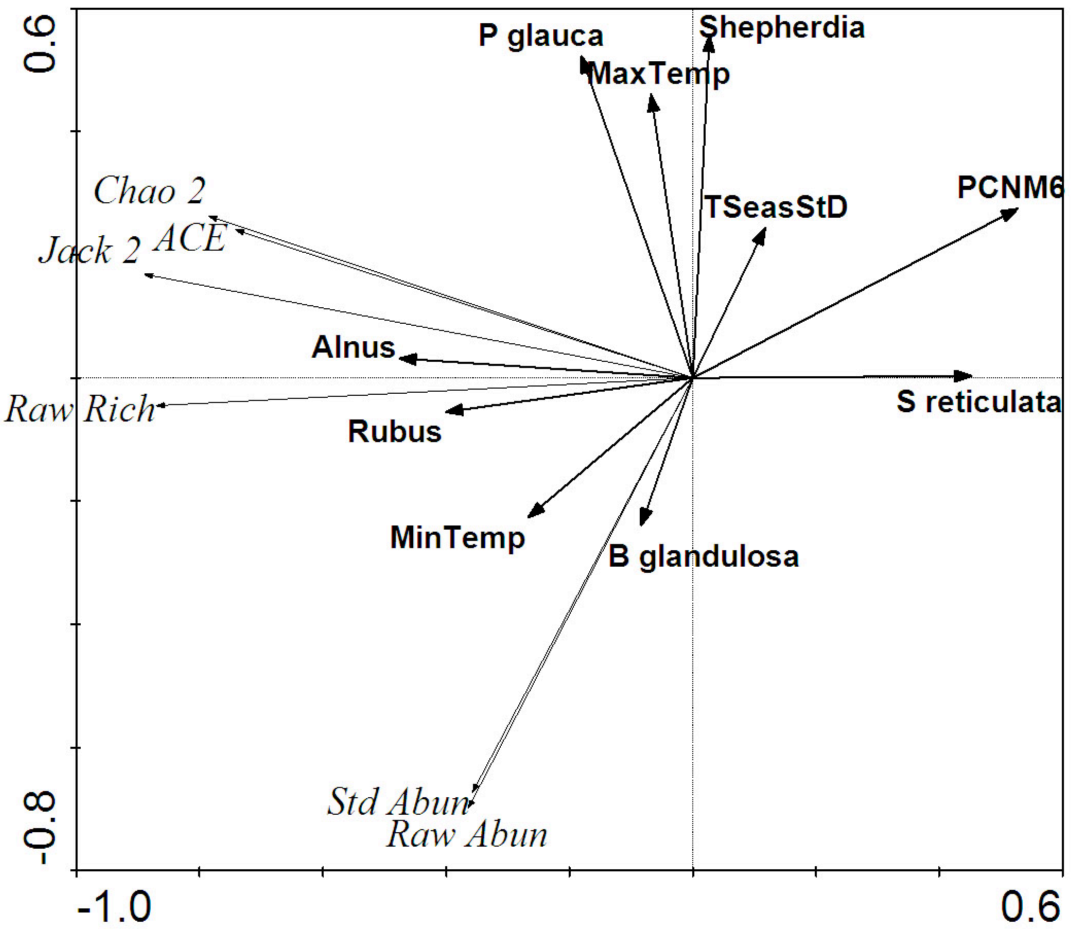
0.6
-0.8
-1.0
0.6
P glauca
Shepherdia
MaxTemp
Chao 2
ACE
Jack 2
TSeasStD
PCNM6
Alnus
Raw Rich
Rubus
S reticulata
MinTemp
B glandulosa
Std Abun
Raw Abun

Figure 2.5

2.9. Appendix

Appendix 2.1. – Complete list of ground dwelling spider species collected from the latitudinal transect along the Dempster Highway, Yukon Territory, Canada and record status.

Species	Family	Total Collected	New Record Yukon	New Record North America
Agelenopsis utahana (Chamberlin and Ivie)	Agelenidae	5		
Arctobius agelenoides (Emerton)	Amaurobiidae	4		
Hypsosinga groenlandica Simon	Araneidae	2		
Clubiona praematura Emerton	Clubionidae	1		
Dictyna major Menge	Dictynidae	1		
Hackmania prominula (Tullgren)	Dictynidae	48		
Gnaphosa borea Kulczynski	Gnaphosidae	16		
Gnaphosa brumalis Thorell	Gnaphosidae	2		
Gnaphosa microps Holm	Gnaphosidae	56		
Gnaphosa orites Chamberlin	Gnaphosidae	6		
Haplodrassus hiemalis (Emerton)	Gnaphosidae	47		
Haplodrassus signifer (C.L. Koch)	Gnaphosidae	3		
Micaria alpina L. Koch	Gnaphosidae	10		

Micaria nr *constricta*	Gnaphosidae	2	
Micaria pulicaria (Sundevall)	Gnaphosidae	6	
Micaria tripunctata Holm	Gnaphosidae	10	
Hahnia cinerea Emerton	Hahniidae	11	
Hahnia glacialis Sorensen	Hahniidae	34	
Agyneta jacksoni (Braendegaard)	Linyphiidae	2	*
Agyneta nigripes (Simon)	Linyphiidae	2	*
Agyneta nr *amerosaxatilis*	Linyphiidae	1	
Agyneta olivacea (Emerton)	Linyphiidae	20	
Agyneta simplex (Emerton)	Linyphiidae	8	*
Asiceratinops sp 1	Linyphiidae	6	*
Bathyphantes simillimus (L. Koch)	Linyphiidae	35	
Ceraticelus sp	Linyphiidae	3	
Ceratinopsis labradorensis Emerton	Linyphiidae	1	
Ceratinopsis stativa (Simon)	Linyphiidae	2	
Cnephalocotes obscurus (Blackwall)	Linyphiidae	2	
Diplocentria bidentata (Emerton)	Linyphiidae	12	
Dismodicus alticeps Chamberlin and Ivie	Linyphiidae	1	
Erigone nr *psychrophila*	Linyphiidae	1	

Eskovia exarmata (Eskov)	Linyphiidae	1		
Gonatium crassipalpum Bryant	Linyphiidae	18		
Hilaira herniosa (Thorell)	Linyphiidae	16		
Horcotes sp.	Linyphiidae	1		
Hybauchenidium aquilonare (L. Koch)	Linyphiidae	3		
Improphantes complicatus (Emerton)	Linyphiidae	6		
Incestophantes duplicatus (Emerton)	Linyphiidae	2		
Lepthyphantes alpinus (Emerton)	Linyphiidae	33		
Linyphiidae sp 1	Linyphiidae	18		
Linyphiidae sp 2	Linyphiidae	13		
Linyphiidae sp 4	Linyphiidae	1		
Linyphiidae sp 5	Linyphiidae	1		
Macrargus multesimus (O.Pickard-Cambridge)	Linyphiidae	1		
Mecynargus monticola (Holm)	Linyphiidae	1		
Mecynargus sphagnicola Holm	Linyphiidae	1		
Mughiphantes marusiki (Tanasevitch)	Linyphiidae	1	*	*
Nr *Acartauchenius pilifrons*	Linyphiidae	2		
Nr *Dicephalus cristatus*	Linyphiidae	1		
Nr *Maso sundevalli*	Linyphiidae	1		

Nr *Typhocrestus pygmaeus*	Linyphiidae	3	
Pelecopsis mengei (Simon)	Linyphiidae	24	
Perro polaris Eskov	Linyphiidae	1	
Pitiohyphantes phrygianus (L. Koch)	Linyphiidae	2	
Poeciloneta sp	Linyphiidae	1	
Procerocymbium sibiricum Eskov	Linyphiidae	4	
Scotinotylus nr *protervus*	Linyphiidae	1	
Semljicola obtusus (Emerton)	Linyphiidae	1	*
Sisis rotundus (Emerton)	Linyphiidae	7	
Tapinocyba bicarinata (Emerton)	Linyphiidae	3	*
Tapinocyba matanuskae Chamberlin and Ivie	Linyphiidae	1	
Tapinocyba nr *matanuskae*	Linyphiidae	2	
Tibioplus diversus (L. Koch)	Linyphiidae	1	
Tiso aestivus (L. Koch)	Linyphiidae	3	
Walckenaeria atrotibialis O.P.-Cambridge	Linyphiidae	1	*
Walckenaeria castanea (Emerton)	Linyphiidae	1	
Walckenaeria communis (Emerton)	Linyphiidae	1	
Walckenaeria karpinskii (O.Pickard-Cambridge)	Linyphiidae	3	*
Zornella cultrigera (L. Koch)	Linyphiidae	5	

Alopecosa aculeata (Clerck)	Lycosidae	131
Alopecosa hirtipes (Kulczński)	Lycosidae	1
Alopecosa pictilis (Emerton)	Lycosidae	2
Arctosa alpigena (Doleschall)	Lycosidae	19
Pardosa furcifera (Thorell)	Lycosidae	141
Pardosa fuscula (Thorell)	Lycosidae	13
Pardosa glacialis (Thorell)	Lycosidae	17
Pardosa hyperborea (Thorell)	Lycosidae	4
Pardosa lapponica (Thorell)	Lycosidae	796
Pardosa mackenziana (Keyserling)	Lycosidae	3
Pardosa moesta Banks	Lycosidae	315
Pardosa podhorskii (Kulczynski)	Lycosidae	1
Pardosa sodalis Holm	Lycosidae	231
Pardosa tesquorum (Odenwall)	Lycosidae	2
Pardosa uintana Gertsch	Lycosidae	446
Pardosa xerampelina (Keyserling)	Lycosidae	1
Pirata zelotes Wallace and Exline	Lycosidae	2
Philodromidae sp 1	Philodromidae	1
Thanatus arcticus Thorell	Philodromidae	9

Chalcoscirtus alpicola Emerton	Salticidae	1	
Dendryphantes nigromaculatus (Keyserling)	Salticidae	1	
Robertus fuscus (Emerton)	Theridiidae	1	
Robertus sp	Theridiidae	1	
Bassaniana utahensis (Gertsch)	Thomisidae	2	*
Ozyptila arctica Kulczyński	Thomisidae	22	
Ozyptila sincera canadensis Kulczyński	Thomisidae	4	
Xysticus britcheri Gertsch	Thomisidae	157	
Xysticus emertoni Keyserling	Thomisidae	8	
Xysticus luctuosus (Blackwall)	Thomisidae	4	*
Xysticus nr *durus*	Thomisidae	1	
Xysticus nr *ellipticus*	Thomisidae	2	
Xysticus nr *obscurus*	Thomisidae	4	
Xysticus triangulosus Emerton	Thomisidae	5	

CHAPTER THREE

In chapter two I tested three complimentary hypotheses regarding the environmental factors that best explain patterns of spider species assemblages in the Yukon Territory using a latitudinal transect across the boreal forest-tundra transition zone. The results show that spatially structured changes in vegetation along the gradient were most important, however, the effects of elevation on spider species assemblages were not explicitly tested. In the following chapter I follow this up by investigating further the effects of spatial gradients using a a nested analysis of elevation and latitude and their effects on spider assemblage structure.

This chapter is a copy and is reproduced with permission from the journal Arctic. This article is cited as Bowden, J. J. and Buddle C. M. 2010. Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. Arctic 63: 261-272. Copyright 2010, with permission from the Arctic Institute of North America (AINA).

Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada

3.1. Abstract

Arthropod assemblages in the Arctic are set for substantial changes in response to climate change, yet we know little about the ecological structure of many groups in the north. We tested the effects of elevation and latitude on northern spider assemblages by sampling along nine mountains across three latitudes in the Yukon Territory, Canada. Spiders were collected in 216 pitfall traps placed at four elevations along each of the nine mountains, representing 36 sites sampled across three latitudes (i.e., distinct mountain ranges). We collected 1954 individuals representing 89 species, 57 genera and 12 families of spiders. Using nested ANOVAs, we found significant main effects of latitude, elevation, and an interaction of the two factors on species richness and abundance. Using MRPP and NMS ordination, we also found significant effects of latitude and mountain on species composition, but within each of the three latitudes, only elevation produced significant effects. Our study suggests that changes along spatial gradients associated with changes in habitat can have significant effects on the structure of spider assemblages, but responses vary among mountain ranges. We show that within a given mountain range individual mountains may be used as spatial replicates for studies about northern arthropod assemblages.

3.2. Introduction

The effects of spatial gradients (e.g., elevational and latitudinal) on species assemblages remain a central theme to biogeography (Willig et al. 2003; Hodkinson

2005; Willig and Bloch 2006). The patterns resulting from the effects of latitude and elevation have been well studied for many organisms at many spatial scales (reviewed in Willig et al. 2003 and Hodkinson 2005). There are fundamental ecological reasons for understanding these patterns of change across spatial gradients; specifically, understanding the effects that these gradients have on patterns of biodiversity and global distributions of species. However, spatial gradients may also serve a more applied mandate; for example, using latitudinal or elevational transects to test climate change predictions (e.g., Andrew and Hughes 2004; Parmesan 2006). Such studies suggest that high latitude and high elevation species are at greatest risk for range contraction and potential extinction in future climate change scenarios (Parmesan 2006). Despite the abundance of biogeographical studies focused on tropical and temperate zones (e.g., Gotelli and Ellison 2002, Willig et al. 2003, Andrew and Hughes 2004, Ruggiero and Hawkins 2008), there are relatively few studies that explore spatial patterns of species assemblages occurring in northern systems (but see Otto and Svensson 1982, and meta-analyses by Cardillo 2002; Currie et al. 2004; Kotwicki et al. 2005; Qian et al. 2009).

The patterns arising from biogeographical studies include positive, negative, hump-shaped and neutral responses of species to changes in elevation and latitude. Latitude tends to be negatively correlated with species richness (e.g., Cushman et al. 1993; Lyons and Willig 2002; Finch et al. 2008), with some exceptions (e.g., Dixon et al. 1987; Kouki et al. 1994). Studies of elevation, which mimic environmental changes associated with latitude at a more abrupt spatiotemporal scale (Hodkinson 2005), tend to show decreases in diversity with increasing elevation, but these responses are not often linear (Rahbek 1995). Studies examining patterns of abundance across spatial gradients are less common. However, terrestrial arthropod community abundance has shown either a decrease or no effect with increases in elevation or latitude. For example, Otto and Svensson (1982) and McCoy (1990) show decreases in spider abundance with increases in elevation, while Chatzaki et al. (2005) found no significant effect of elevation on spider abundance (measured as activity) along an elevational gradient in Crete. Andrew and Hughes (2005) found, in an analysis of the effects of latitude on various terrestrial arthropod feeding guilds, that predators showed the only significant latitudinal trend.

At regional and continental scales, spider species richness has been correlated with latitude and mean annual temperature (Finch et al. 2008, Whitehouse et al. 2009). Spiders (Arachnida: Araneae) are a model taxon for investigating the effects of spatial gradients on species assemblages at regional scales (i.e., 200-4000 km, Waide et al. 1999). Spiders readily respond to acute changes in habitat heterogeneity (Downie et al. 1995), temperature and humidity (DeVito et al. 2004). The fine spatial scale at which spiders partition these abiotic changes (Moring and Stewart 1994) makes them suitable to assess species assemblage patterns across spatial gradients at regional extents. Over a broad elevational gradient, ground dwelling spider richness has shown a hump-shaped response to changes in elevation (Chatzaki et al. 2005). Jimenez-Valverde and Lobo (2007), however, found that spider richness was more strongly correlated with habitat complexity and maximum temperature than with elevation at a regional scale of investigation.

There are other ecological reasons why spiders represent a model taxon for biogeographic research: spiders are eurytopic and thus can be collected in varying habitats encountered along spatial transects (e.g., Chatzaki et al. 2005). Spiders are important to local food web dynamics (Wise 2004) and ecosystem processes (i.e., nutrient cycling, Lawrence and Wise 2000), and their taxonomy is readily accessible and relatively well known (Ubick et al. 2005). Spiders are also well represented in terms of species richness and abundance at northern latitudes (Buddle et al. 2000) and many faunal inventories illustrate this (Dondale et al. 1997; Marusik and Koponen 2002; Marusik et al. 2004; Pickavance 2006). These studies, however, have not led to quantitative regional studies of factors determining patterns of spider assemblage structure in the far north.

Our objective was to determine the effects of elevation and latitude on spider assemblage structure. Specifically, we sought to determine the changes that occurred in species richness, activity density and composition across elevation and latitude in the Yukon Territory, Canada. We predicted that spider species richness and activity density would be affected by both latitude (across all mountain ranges) and elevation, and that they would generally decrease with increasing elevation and/or latitude. Because spiders are adapted to a rather narrow set of abiotic parameters (e.g., temperature, humidity and habitat), we also predicted that composition would significantly differ among latitudes and elevations.

3.3. Materials and Methods

Experimental Design and Sampling

Sampling was conducted in three mountain ranges in the northern Yukon Territory, Canada (Figure 3.1): the Tombstone Range (64.309N, 138.141W), the Ogilvie Range (65.158N, 138.148W), and the Richardson Range (66.725N, 136.114W). This region of the Yukon transitions northward from boreal forest to Arctic tundra (Payette et al. 2001). At the most southern latitude, the valley of the Tombstone Range is a patchy matrix of black and white spruce (*Picea mariana* Mill., and *P. glauca* Moench, respectively) with non forested areas of sphagnum, *Ledum* sp., *Vaccinium* sp., *Empetrum* sp., lichens, grasses and patches of willow (*Salix* spp.) and dwarf birch (*Betula glandulosa* Michx.) up to 1.5 meters high. This habitat transitions into alpine tundra characterized by a thin sphagnum layer and stunted vegetation with patches of barren ground and rock with increasing elevation. The third mountain of the Tombstone Range differs slightly and is dominated by thick willow stands approximately one meter high. The Ogilvie Range contains thin boreal forest in the valley that is dominated by black spruce and large willows. With increasing elevation the forest thinned to sparse black spruce and willow along the mountain side. The Ogilvie Range was the only mountain range in which trap disturbance occurred during the study period. Two pitfall traps were consistently disrupted at one of the lowest elevation sites in this range hence the potential influence of this disturbance on the data is discussed along with biological explanations. Open tundra is characterized by a thick sphagnum layer, *Ledum* sp., *Vaccinium* sp., *Empetrum* sp., *Eriophorum* sp., lichens and stunted *Salix* spp. and *Betula glandulosa* Michx. and dominates the valley of the Richardson Mountains. This transitions through a thinning sphagnum layer to rock in the mountains.

Ground dwelling spiders were collected using pitfall traps at each of the three mountain ranges. Pitfall trapping is useful for studying arthropod biodiversity at large spatial scales (e.g., Gotelli and Ellison 2002; Chatzaki et al. 2005; Whitehouse et al. 2009) and allows for consistent and repeatable sampling. Each pitfall trap consisted of a transparent plastic container (6 cm diameter, 7 cm depth) half filled with 1:1 water and propylene glycol and covered with a square of plastic corrugate (14 x 14 cm, about 2 cm above each trap) held into the ground by wire. We placed each trap into the ground so the rim was flush with the substrate surface. We established three transects within each mountain range (latitude). This design allowed for spatial replication, maintaining the same elevation within each range. Many altitudinal studies have chosen to maximize altitudinal variation along a single transect (e.g., Olson 1994; Chatzaki et al. 2005; Cardelus et al. 2006). We opted to maximize spatial replication to detect and develop generalizations about landscape and regional scale patterns in arthropod diversity (e.g., Sanders et al. 2003; Almeida-Neto et al. 2006).

We sampled sites at four different elevations along each of the three mountains within each of the three ranges. The four sites on each mountain were established every 100 meters in elevation for a total of 36 sites in the region. Each site consisted of six pitfall traps placed ten meters apart. The mountain transects were initiated in valleys and ran up the three mountains selected in each range. Elevation in the Tombstone Range began at 1060 meters in the valley and ended at 1360 meters. The Ogilvie’s ranged from 660 meters in the valley and ended at 960 meters at the top of the mountains. In the Richardson Range, pitfall trapping began at 760 meters of elevation in the valley and ended at 1060 meters on the mountain tops. Although actual elevation varied among latitudes, there was no difference within each range and (other than noted above) we maintained habitat among mountains within each range at a given elevation. The overall design of our study was four elevations (sites) within each mountain, three mountains within each latitude (mountain range) and three latitudes within the region.

We collected spiders with pitfall traps between 14 June and 22 July 2006; traps were open for an average of 27.5 days ± 0.294 (mean ± SE). There was no effect of sampling effort on trap captures so we did not standardize the data for sampling effort. We chose this time frame because it includes the highest activity period for spiders in the north (Pers. Obs., Buddle and Draney 2004). Although these data only represent one year of collection, past studies from northern Alberta, Canada, suggest that arthropod community data do not change significantly from year to year (e.g., Buddle et al. 2000). All traps were emptied twice and all arthropods were preserved in ethanol. The spiders collected were pooled by elevation per mountain, so the six pitfall traps were treated as a site. All specimens were identified to species level following nomenclature by Platnick (2009). Immature specimens were omitted from analyses and voucher specimens deposited at the Lyman Entomological Museum (Ste Anne de Bellevue, Québec).

Statistical Analyses

We focused on three main response variables: species richness, abundance (as measured by activity density), and composition. All species data were transformed ($x' = \log(x+1)$) to improve monotonicity and maximize the amount of variation explained by the ordination. Species richness and activity density data were transformed to a logarithmic scale (base 10) to achieve normality for parametric tests.

Two separate nested analyses of variance (ANOVA) were calculated using the transformed data for species richness and activity density. ANOVA models were calculated using latitude and elevation as random main effects and mountain as a random factor nested in latitude. We tested for the main effects of latitude and elevation, the nested effect of mountain and for the interaction between latitude and elevation. We used package ‘lme4’ (Bates and Maechler 2009) for the R statistical software version 2.8.0 (R Development Core Team, 2008). To explore variability in species richness and activity density among elevations due to the significant interaction, we ran six one-way ANOVA’s within each mountain range using SPSS version 15 (SPSS Inc., Chicago IL).

To examine the effects of elevation and latitude on patterns of community composition, we ran a non-metric multidimensional scaling (NMS) ordination (Kruskal 1964) with the software program PC-ORD version 4.17 (McCune and Mefford 1999). A detrended correspondence analysis (DCA) was first completed and used as a starting configuration for the NMS ordination. To achieve the optimum NMS solution, we used step-down in dimensionality beginning at six axes. The best solution is that which minimizes stress (the relationship between the original species data and the data represented in ordination space) while maintaining the interpretability of the data by obtaining the fewest dimensions. The ordinations were run using Sørensen (Bray-Curtis) distance with 400 iterations, 20 runs with real data, 50 runs with randomized data, and an instability criterion of 0.00005. A Monte Carlo simulation using randomized data ($n = 50$) was run to determine the probability that a similar final stress could have been achieved by chance (McCune and Grace 2002).

We used rank-transformed multi-response permutation procedures (MRPP) (Mielke and Berry, 2001) to test for differences in species composition among latitudes, elevations and mountains. We also tested for differences among elevations within latitudes in case of variation. This non-parametric statistical procedure tests whether there are significant compositional differences (i.e., average within-group ranked distances) between two or more sample groups defined *a priori*. MRPP is a good complement to, and helps improve the interpretability of NMS ordinations, by providing a measure of effect size given by the chance-corrected within-group agreement statistic ‘A’ (McCune and Grace 2002).

To examine how individual species responded to the elevational gradient in each of the mountain ranges, we plotted the transformed activity density of the most dominant species. We also used indicator species analysis (Dufrêne and Legendre 1997), using PC-ORD, to determine if a given species was abundant at a particular elevation or group of elevations (i.e. low or high) and the fidelity to that group. We chose to run two sets of indicator species analysis using species that were both represented by more than ten individuals and present in at least eight sites to determine whether each species was a significant indicator of a particular elevation or elevation group.

Because different spider families use different ecological strategies (e.g., for hunting) and likely have different environmental requirements, we also examined family-level patterns in our data. We were especially interested in determining whether there were ordered changes in proportions of individuals represented by the families in our data. To examine how different families of spiders respond to changes in elevation, we plotted a bar chart showing the proportional differences in relative abundance of the dominant spider families.

3.4. Results

We collected and identified a total of 1954 individual spiders representing 89 species, 57 genera and 12 families (Appendix 3.1). Activity density averaged 54.27 ± 6.82 (mean ± SE) individuals per site (elevation/mountain), while species richness averaged 11.36 ± 0.71 species per site (range: 4-23). The four most abundant species all belonged to the family Lycosidae: *Pardosa lapponica* (Thorell) (626 individuals), *P. uintana* Gertsch (209 individuals), *Alopecosa aculeata* (Clerck) (161 individuals), and *P. glacialis* (Thorell) (100 individuals), and represented 56 percent of the total number captured. The Linyphiidae was the family with the most species and accounted for 43 species collected in the region.

Richness

There were significant main effects of latitude and elevation on species richness, however there was also a significant latitude-elevation interaction according to nested ANOVA (Table 3.1). Average richness was highest in the Tombstone Range at 13.67 ± 1.42 species per site and lowest in the Ogilvie Mountains (9.50 ± 0.58 species per site). Species richness averaged 10.92 ± 1.29 species per site in the most northern part of the study (Richardson Mountains). The significant interaction term indicated differential responses in species richness to elevation among the mountain ranges (Figure 3.2, Table 3.1).

The Richardson Range displayed a decrease in species richness with increasing elevation. The Ogilvie Range did not yield any clear changes in richness with elevation; species richness did not differ between the top of the mountains and the lowest elevation. Species richness in the Tombstone Range decreased along two of the three elevational transects, however one of the mountain transects displayed highest species richness at the highest elevation with little change among the lower elevations (Figure 3.2).

After examining a significant interaction between latitude and elevation with our species richness data, we further explored the variability within each mountain range (i.e., with a one-way ANOVA). The Richardson Range was the only one to display a significant ($F_{3,8} = 10.1$, $p = 0.004$) effect of elevation on species richness (Figure 3.2). There was a non-significant effect of elevation on species richness in the Ogilvie Range

($F_{3,8}$ = 0.464, p = 0.715) and a non-significant effect in the Tombstone Range ($F_{3,8}$ = 3.041, p = 0.093) (Figure 3.2).

Activity Density

Latitude and elevation had significant effects on activity density, however, similar to the species richness data, there was also a significant latitude-elevation interaction (Table 3.1). The largest number of individuals collected per site (86.08 ± 9.37) was in the Tombstone range. The Ogilvie Range and Richardson Range yielded an average of 26.50 ± 2.49 and 50.25 ± 13.66 individuals per site, respectively. The mean activity densities from low to high elevation were 79.44 ± 16.10, 62.22 ± 16.29, 32.22 ± 5.66 and 41.22 ± 9.96 individuals per site, respectively.

Activity density displayed a similar pattern to species richness in yielding range-specific responses to elevation among mountain ranges (Figure 3.2). Again, the Richardson Range showed the only significant change in activity density with increasing elevation ($F_{3,8}$ = 17.62, p = 0.001; Figure 3.2). There were no significant changes in activity density across elevations within the Ogilvie Range ($F_{3,8}$ = 1.383, p = 0.316). In fact, the highest elevation in this range yielded the highest number of individuals (Figure 3.2). The Tombstone Range revealed statistically significant differences in activity density across elevations in that range ($F_{3,8}$ = 5.73, p = 0.022), however there was no consistent pattern in response. Activity density was lowest at the third highest elevation and peaked at the lowest and highest elevations (Figure 3.2).

Analysis at species level revealed that activity density for many single species followed a pattern similar to that of all species in the regional dataset (Figure 3.3). Specifically, some species in the Tombstone Range gradually decreased in abundance with increasing elevation (e.g. *P. uintana*) while others seemed to respond positively to the increase in elevation (e.g. *Alopecosa aculeata*). Indicator species analysis supported these trends as the Lycosidae: *P. lapponica, P. moesta* and *P. uintana* were all significant ($p < 0.05$) indicators of the two lower elevations in the Tombstone Range, while *A. aculeata* was a significant indicator of the two higher elevations in this range. In the Ogilvie Range some species appeared to increase in abundance (e.g. *P. lapponica*) with increasing elevation while others remained unchanged. In fact, *Micaria alpina* L. Koch (Gnaphosidae) was the only significant indicator in the Ogilvie Range and was an indicator of the two lower elevations. Most species in the Richardson Range responded negatively to the increase in elevation, however, a few species (e.g. *P. albomaculata* Emerton) responded positively to the gradient. *Pardosa albomaculata* and *Gnaphosa orites* Chamberlin (Gnaphosidae) were significant indicators of the two higher elevations in this mountain range. *Agyneta jacksoni* Braendegaard (Linyphiidae) and *Xysticus britcheri* Gertsch (Thomisidae) significantly indicated the lowest elevation in this range. *Pardosa sodalis* Holm was also abundantly collected at the lowest elevations in the Richardson Range but was not included in the analysis due to its relatively low incidence.

Composition

Multi-response permutation procedures revealed significant effects of latitude and mountain, as well as an effect of elevation within each of the mountain ranges; there was no significant main effect of elevation (Table 3.2). These results are well supported by the final two dimensional NMS ordination (Figure 3.4). The axes of the NMS ordination explained 84.9% (Axis 1: 20.4 Axis 2: 64.5%) of the variation in the species composition data. The ordination shows a clear separation of sites by latitude and separation of the low and high elevations in the Richardson Range (Figure 3.4). There was no overall clustering of high or low elevation sites across latitudes which illustrates the lack of a significant main effect of elevation displayed by MRPP.

We detected very few changes in the proportion of individuals represented by each family at each of the elevations in each mountain range (Figure 3.5). Although there was no observable linear pattern in the Tombstone Range, we did note a difference between the two low and high level sites. The two lower elevation sites yielded both a higher number of individuals and a higher number of families than the two higher elevation sites. Other than the decrease in the proportion of Thomisidae and the lack of some other families represented at higher elevations, there were no proportional differences by family in the Tombstone Range. The relative proportion of Linyphiidae decrease with increasing elevation in the Ogilvie Range, however there were no other obvious differences in the relative abundance of families represented. The Richardson Range displayed the largest change in activity density (also shown in Figure 3.2), but only showed a decrease in Thomisidae with increasing elevation. The Lycosidae were the most dominant family and typically accounted for ≥ 50% of individuals collected at each elevation, but did not change proportionally among elevations in each range.

3.5. Discussion

It is important to obtain data on species diversity patterns in the north due to the disproportionate effect that climate change is projected to have on the Arctic environment and Arctic biota (Callaghan et al. 2004a). We used a spatially replicated regional scale design to assess the effects of elevation and latitude on spider species richness, abundance and composition in northwestern Canada. We found significant differences in richness and abundance (activity density) among elevations and latitudes, and we detected significant interactions between latitude and elevation for both richness and abundance. Our ordination results showed that mountain range had a larger effect on assemblage structure than elevation or transect (i.e., within a mountain range) although there was evidence of elevational effects within latitude on species composition (i.e., Richardson Range, Figure 3.4). The fact that spider species are typically adapted to a narrow set of abiotic factors (e.g., Moring and Stewart 1994; DeVito et al. 2004), helps explain the changes in species composition among latitudes and elevations within each latitude. : Local climate changes substantially with increasing elevation through adiabatic cooling and changes across spatial gradients beget changes in habitat (Tilman and Pacala 1993). These changes occur more abruptly across elevation than latitude (Hodkinson 2005). However, we found that latitude had a stronger main effect on composition than did elevation. This finding probably reflects the differences in both current habitat and historical events (e.g., glaciations) among the three mountain ranges.

The Richardson Range, the northern-most mountains in this study, displayed the most substantial change in spider composition from low to high elevation, supported by the separation of lower and higher elevation sites on the NMS ordination. The significant differences observed in this mountain range may be due to changes in habitat associated with changes in elevation. For example, at a local spatial scale, Muff et al. (2009) showed significant differences in spider assemblages across an alpine pasture-forest transition. Specifically, more species preferred an open area habitat than a forested one, but the intermediate timberline areas yielded a positive ecotone effect. The authors pointed to the relative importance of habitat (i.e. density and structure of vegetation) than spatial variables in determining patterns of spider assemblages. Our mountain transects in the Richardson Range transitioned from tundra to talus slopes. The compositional differences in this range probably mirror changes in habitat associated with changes in elevation. Species richness and abundance also displayed the largest changes in the Richardson Range (the highest in latitude) across elevations. This suggests a compound effect of latitude and elevation that may correspond to more extreme changes in habitat.

Spider composition in the Ogilvie Range did not exhibit strong changes with increasing elevation (Figure 3.4). One explanation for the lack of change with elevation in this range is, unlike the other ranges, habitat was relatively uniform (i.e., forested) from low to high elevation sites and we can therefore use the Ogilvies as a control for a strict test of elevation independent of habitat effects. We suggest that since no significant effects were detected in the Ogilvie Range, habitat is a more important determinant of spider community composition than elevation across this landscape. During a landscape scale study on a mountain in Québec, Canada, Koponen (1987) found the highest number of species at forest edge, supporting the positive influence of habitat transitions on spider assemblages across elevation. Trap captures were also the highest in open (mountain top) habitats and lowest at lower altitudes in forested sites (Koponen 1987). Another explanation for the lack of change with elevation in the Ogilvie Range may be trap disturbance. The trap disturbance at one of lower sites in this range would have reduced the number of individuals and species caught and may help explain the pattern of no net change with elevation in this range. Species richness, activity density and composition at our most southern site, Tombstone, yielded mixed results. The third highest elevation had the lowest species richness and activity densities (Figure 3.2) and composition did not change across elevation. We attribute these results to habitat effects: two of the three transects were similar in vegetation composition, but the third was on a steeper incline and transitioned from sparse boreal forest to talus slope with increasing elevation.

. At smaller (i.e., local and landscape) spatial scales, spiders have been shown to respond strongly to habitat (Koponen 1987; Rypstra et al. 1999; Muff et al. 2009), whereas at broad spatial scales spiders seem to follow spatial predictors (e.g., latitude) quite well (Finch et al. 2008; Whitehouse et al. 2009). However, habitat complexity has been shown to be more important than spatial predictors (e.g., elevation) in determining spider assemblages at a regional scale in at least one study (Jimenez-Valverde and Lobo 2007). In our Arctic system we show effects of elevation on spider assemblages at the landscape (within a range) scale, and elevation and latitude at a regional (all ranges) spatial scale. However, effects were weaker when habitat differences were weak (i.e., Ogilvie); similarly, when strong habitat differences occurred (i.e., Richardson), differences in spider assemblages across elevation were more pronounced. The results of our study may reflect spatially-structured changes in habitat leading to changes in the spider assemblages.

Studies examining successional gradients have yielded much support for habitat complexity as being a key component to the development of local spider assemblages (Lowrie 1948; Bultman et al. 1982; Buddle et al. 2000; Kaufmann 2001). There exists a parallel between habitat successional gradient studies and our elevational study, as habitats change over spatial gradients in a manner analogous to succession. For example, chronosequences of glacial retreat along an alpine transect have been used to indicate the importance of successional changes in vegetation for spider assemblages (Kaufmann 2001; Gobbi et al. 2006). Kaufmann (2001) pointed to the importance of successional changes in soil and vegetation affecting patterns in spider fauna in an alpine glacial foreland. However, the role of biotic factors cannot be dismissed, as food availability (e.g., Halaj et al. 2000) and processes such as dispersal (e.g., Bonte et al. 2004) may also influence the dynamics and structuring of spider assemblages. For species such as *Pardosa albomaculata*, for example, that are adapted to high elevation the intervening lowlands likely serve as inhospitable habitat, like island habitats in an oceanic matrix. The patch-like distribution of mountains and unevenness of the ground potentially serve as effective barriers for passively dispersing arthropods to suitable mountain habitat (Mani 1968). In the face of climate change these species could be greatly affected by upward elevational range expansions of lowland species otherwise restricted by current climate conditions (Parmesan 2006).

Aside from a decrease in representation with increasing elevation by the Thomisidae in two of the three mountain ranges, we detected no consistent changes in spider families along our mountain transects. Koponen (1987) found substantial differences in ground dwelling spider composition among habitats across an altitudinal gradient in the boreal region of Québec, Canada. Specifically, the relative proportions of Lycosidae were larger in open habitats while the Linyphiidae were proportionately more common in forested habitats. Given this study and others investigating successional gradients (e.g. Bultman et al. 1982), the lack of change in proportions of families represented in our data is surprising. However, we did find that some species within the same family (Lycosidae) displayed very different responses to the elevational gradients which contribute to the understanding of the differences in species composition and activity density detected when using the complete species data. For example, in the Tombstone Range a roughly equal number of species responded positively to the increase in elevation as did the ones that responded negatively.

Although others have found support for the effect of elevation on ground-dwelling spider assemblages (Otto and Svensson 1982; Rushton and Eyre 1992; Chatzaki et al. 2005), our results did not show a consistent effect of elevation on species richness, activity density and/or composition among mountain ranges (latitudes). It is possible that the elevational range sampled was not large enough to detect a consistent and significant pattern, or that patterns are range-dependent. Our design did allow us to effectively sample many types of habitat and assess the effects of spatial factors at a regional scale with good replication. These data also support previous suggestions that data collected from a single mountain transect may not be suitable to make generalizations to larger spatial scales (Sanders et al. 2003).

Climate change is projected to strongly affect arthropod assemblages in the Arctic (Strathdee and Bale 1998; Callaghan et al. 2004a). Because these changes are predicted to occur rapidly, it will be increasingly important to understand patterns of species diversity in the north and obtain baseline data from which to compare future changes as a result of spatial shifts in climate and habitat. Our study quantifies arthropod assemblages in the Arctic and shows that spiders finely partition space and probably habitat along elevational gradients. The low numbers of individuals especially adapted to life at high latitude and high elevation (e.g. *P. albomaculata*) should be of particular concern for future studies of the effects of climate change on arthropod assemblages.

3.6. Acknowledgements

The authors would like to offer sincere thanks to Dr. Charles Dondale (Canadian National Collection), Melanie Desrochers (Centre d'Étude de la Forêt), the Tetlit Gwitch'n, Nacho Nyak Dun, Vuntut Gwitch'n, the Tr'ondëk Hwëch'in Han Nation and the Yukon Territorial Government. Support was provided by the Northern Scientific Training Program (NSTP), the National Science and Engineering Research Council of Canada (NSERC), Walmart Canada and McGill University.

3.7. Literature Cited

Almeida-Neto, M., Machado, G., Pinto-Da-Rocha, R., and Giaretta, A.A. 2006. Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport's rule? Journal of Biogeography 33: 361-375.

Andrew, N.R., and Hughes, L. 2004. Species diversity and structure of phytophagous beetle assemblages along a latitudinal gradient: predicting the potential impacts of climate change. Ecological Entomology 29: 527-542.

Andrew, N.R., and Hughes, L. 2005. Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. Austral Ecology 30: 281-297.

Bates, D., and Maechler, M. 2009. lme4: Linear mixed-effects models using S4 classes. http://r-forge.r-project.org/projects/lme4/

Bonte, D., Baert, L., Lens, L., and Maelfait, J.P. 2004. Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. Ecography 27: 343-349.

Buddle, C.M., and Draney, M.L. 2004. Phenology of linyphiids in an old-growth deciduous forest in central Alberta, Canada. Journal of Arachnology 32: 221-230.

Buddle, C.M., Spence, J.R., and Langor, D.W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424-436.

Bultman, T. L., Uetz, G. W., and Brady, A. R. 1982. A comparison of cursorial spider communities along a successional gradient. Journal of Arachnology 10: 23-33.

Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., et al. 2004a. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. Ambio 33: 436-447.

Cardelus, C.L., Colwell, R.K., and Watkins, J.E. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. Journal of Ecology 94: 144-156.

Cardillo, M. 2002. Body size and latitudinal gradients in regional diversity of New World birds. Global Ecology and Biogeography 11: 59-65.

Chatzaki, M., Lymberakis, P., Markakis, G., and Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. Journal of Biogeography 32: 813-831.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.F., Hawkins, B.A., Kaufman, D.M., et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7: 1121-1134.

Cushman, J. H., Lawton, J. H., and Manly, B. F. J. 1993. Latitudinal patterns in European ant assemblages: Variation in species richness and body size. Oecologia 95: 30-37.

DeVito, J., Meik, J.M., Gweson, M.M., and Formanowicz, D.R. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae: Lycosidae) correspond with microhabitat distributions. Canadian Journal of Zoology-Revue Canadienne De Zoologie 82: 1119-1125.

Dixon, A.F.G., Kindlmann, P., Leps, J., and Holman, J. 1987. Why there are so few species of aphids, especially in the Tropics. American Naturalist 129: 580-592.

Dondale, C., Redner, J., and Marusik, Y.M. 1997. Spiders (Araneae) of the Yukon. In: Danks, H. and Downes, J. (eds.) Insects of the Yukon. Canadian Museum of Nature, Ottawa, pp. 73-113.

Downie, I. S., Butterfield, J. E. L. and Coulson, J. C., 1995. Habitat preferences of sub-montane spiders in northern England. Ecography 18: 51-61.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Finch, O.D., Blick, T., and Schuldt, A. 2008. Macroecological patterns of spider species richness across Europe. Biodiversity and Conservation 17: 2849-2868.

Gobbi, M., Fontaneto, D., and De Bernardi, F. 2006. Influence of climate changes on animal communities in space and time: the case of spider assemblages along an alpine glacier foreland. Global Change Biology 12: 1985-1992.

Gotelli, N.J., and Ellison, A.M. 2002. Biogeography at a regional scale: Determinants of ant species density in New England bogs and forests. Ecology 83: 1604-1609.

Halaj, J., Ross, D.W., and Moldenke, A.R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90: 139-152.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80: 489-513.

Jimenez-Valverde, A., and Lobo, J.M. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecological Entomology 32: 113-122.

Kaufmann, R. 2001. Invertebrate succession on an alpine glacier foreland. Ecology 82: 2261-2278.

Koponen, S. 1987. Communities of ground-living spiders in six habitats on a mountain in Québec, Canada. Holarctic Ecology 10: 278-285.

Kotwicki, L., Szymelfenig, M., De Troch, M., Urban-Malinga., and Węsławski, J.M. 2005. Latitudinal biodiversity patterns of meiofauna from sandy littoral beeches. Biodiversity and Conservation 14: 461-474.

Kouki, J., Niemelä, P., and Viitasaari, M. 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). Annales Zoologici Fennici 31: 83-88.

Kruskal, J. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115-129.

Lawrence, K.L., and Wise, D.H., 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44: 33-39.

Lowrie, D.C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351.

Lyons, S.K., and Willig, M. R. 2002. Species richness, latitude, and scale-sensitivity. Ecology 83: 47-58.

Mani, M. S. 1968. Ecology and biogeography of high altitude insects. The Hague: Dr. W. Junk Publishers.

Marusik, Y.M., and Koponen, S. 2002. Diversity of spiders in boreal and arctic zones. Journal of Arachnology 30: 205-210.

Marusik, Y.M., Koponen, S., and Potapova, N.K. 2004. Spiders (Aranei) from Oymyakon, the cold pole of the northern hemisphere (Yakutia, Siberia). Arthropoda Selecta 13: 69-75.

McCoy, E.D. 1990. The distribution of insects along elevational gradients. Oikos 58: 313-322.

McCune, B., and Grace, J. 2002. Analysis of ecological communities*,* Glenedan Beach, OR, MjM Software Design.

McCune, B., and Mefford, M. 1999. PC-ORD 4: Multivariate analysis of ecological data. MjM Software, Glenedan Beach, OR.

Mielke, P., and Berry, K. 2001. Permutation Methods: A distance function approach*,* New York, Springer-Verlag.

Moring, J.B., and Stewart, K.W. 1994. Habitat partitioning by the wolf spider (Araneae: Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River, Colorado. Journal of Arachnology 22: 205-217.

Muff, P., Kropf, C., Frick, H., Nentwig, W., and Schmidt-Entling, M.H. 2009. Co-existence of divergent communities at natural boundaries: spider (Arachnida: Araneae) diversity across an alpine timberline. Insect Conservation and Diversity 2: 36-44.

Olson, D. M. 1994. The distribution of leaf-litter invertebrates along a Neotropical altitudinal gradient. Journal of Tropical Ecology 10: 129-150.

Otto, C., and Svensson, B.S. 1982. Structure of communities of ground-living spiders along altitudinal gradients. Holarctic Ecology 5(1): 35-47.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37: 637-669.

Payette, S., Fortin, M.J., and Gamache, I. 2001. The subarctic forest-tundra: The structure of a biome in a changing climate. Bioscience 51: 709-718.

Pickavance, J.R. 2006. The spiders of East Bay, Southampton Island, Nunavut, Canada. Arctic 59: 276-282.

Platnick, N. 2009. *The World Spider Catalog Online, Version 8.5*. American Museum of Natural History.

Qian, H., Badgley, C., and Fox, D.L. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. Global Ecology and Biogeography 18: 111-122.

R Core Development Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahbek, C. 1995. The elevational gradient of species richness: A uniform pattern? Ecography 18: 200-205.

Ruggiero, A., and Hawkins, B.A. 2008. Why do mountains support so many species of birds? Ecography 31: 306-315.

Rushton, S.P., and Eyre, M.D. 1992. Grassland spider habitats in north-east England. Journal of Biogeography 19: 99-108.

Rypstra, A. L., Carter, P. E., Balfour, R. A., and Marshall, S. D. 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. Journal of Arachnology 27: 371-377.

Sanders, N. J., Moss, J., and Wagner, D. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12: 93-102.

SPSS for Windows, Evaluation Version 15.0. 2006. SPSS Inc., Chicago IL.

Strathdee, A.T., and Bale, J.S. 1998. Life on the edge: Insect ecology in arctic environments. Annual Review of Entomology 43: 85-106.

Tilman, D., and Pacala, S. 1993. The maintenance of species richness in plant communities. In: Ricklefs, R. and Schluter, D. (eds.) Species diversity in ecological communities. The University of Chicago Press, Chicago, pp. 24-25.

Ubick, D., Paquin, P., Cushing, P., and Roth, V. 2005. Spiders of North America: An Identification Manual, American Arachnological Society.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., and Parmenter, R. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300.

Whitehouse, M. E. A., Hardwick, S., Scholz, B. C. G., Annells, A. J., Ward, A., Grundy, P. R., and Harden, S. 2009. Evidence of a latitudinal gradient in spider diversity in Australian cotton. Austral Ecology 34: 10-23.

Willig, M. R., and Bloch, C. P. 2006. Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. Oikos 112: 163-173.

Willig, M. R., Kaufman, D. M., and Stevens, R. D. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology Evolution and Systematics 34: 273-309.

Wise, D. H. 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48: 181-188.

3.8. Tables and captions

Table 3.1 – Results of nested multifactor analysis of variance for spider species richness and activity density across three mountain ranges in the Yukon Territory, Canada.

Richness				
Factor	*df*	*MS*	*F*	*p-value*
Latitude	2	0.06677	6.8197	0.00624
Mountain	6	0.01863	1.9026	0.13558
Elevation	3	0.0662	6.7618	0.003
Latitude-Elevation	6	0.04215	4.3048	0.00729
Activity Density				
Factor	*df*	*MS*	*F*	*p-value*
Latitude	2	0.83114	58.2162	1.38E-08
Mountain	6	0.03526	2.4696	0.06396
Elevation	3	0.19722	13.8139	6.43E-05
Latitude-Elevation	6	0.21689	15.1914	3.60E-06

Table 3.2 – Results of multi-response permutation procedures displaying main effects of latitude, elevation and mountain and effects of elevation within each mountain range on ground dwelling spider assemblages in the Yukon Territory, Canada.

Factor	*A-Statistic*	*p-value*
Latitude	0.36842145	0
Elevation	0.04694278	0.08902883
Mountain	0.39016795	0.00000043
Tombstone Elevation	0.36965812	0.00041355
Ogilvie Elevation	0.29059828	0.00555148
Richardson Elevation	0.3034188	0.02530073

3.9. Figure captions

Figure 3.1 – Map of sampling region in Yukon Territory, Canada, showing the Tombstone, Ogilvie, and Richardson mountain ranges. Three mountains were selected in each range, and four elevational sites within each mountain transect (one transect and sites shown in inset).

Figure 3.2 – Range-specific effects of elevation and its interactions with species richness and abundance (activity density) of ground-dwelling spider species in the Tombstone, Ogilvie and Richardson ranges. Symbols indicate log-transformed means, and lines show standard error range.

Figure 3.3 – Activity density of each of the most dominant species in response to elevation from the three mountain ranges studied in the northern Yukon Territory, Canada. All species belong to the family Lycosidae.

Figure 3.4 – Non-metric multidimensional scaling ordination of species data. Symbols indicate mountain range (latitude) sampled, ■ – Tombstone, ▲ – Ogilvie, ● – Richardson. Each point represents a site sampled. Shading indicates each of the four elevations where increasing darkness indicates increasing elevation. The error bars represent 95% confidence limits for each of the three ranges sampled. We determined via Monte Carlo simulation ($n = 50$ runs) that the reduction in stress was significantly ($p = 0.0196$) higher than expected by chance.

Figure 3.5 – Proportions of spider families collected from all mountain ranges in the northern Yukon Territory, Canada. Letter indicates the range (i.e., T = Tombstone, O = Ogilvie, R = Richardson) and number (1-4) indicates elevation from low to high. The vertical axis represents the number of individuals represented in each family. The grouping 'other' includes the rare spider families collected which include Araneidae, Clubionidae, Philodromidae, Salticidae, Tetragnathidae and Titanoecidae.

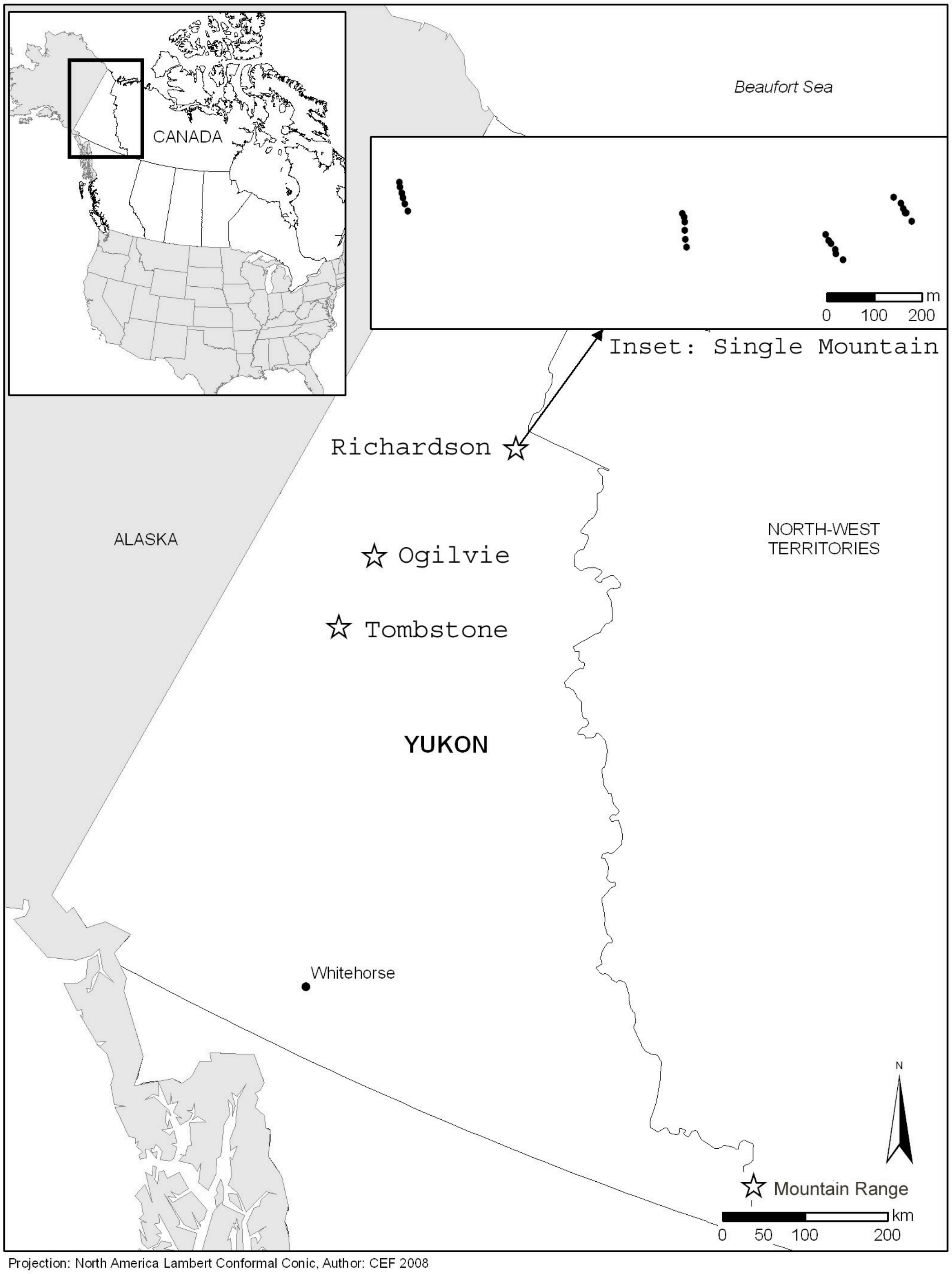
Beaufort Sea
CANADA
0 100 200 m
Inset: Single Mountain
Richardson
ALASKA
Ogilvie
Tombstone
NORTH-WEST TERRITORIES
YUKON
Whitehorse
N
Mountain Range
0 50 100 200 km
Projection: North America Lambert Conformal Conic, Author: CEF 2008

Figure 3.1

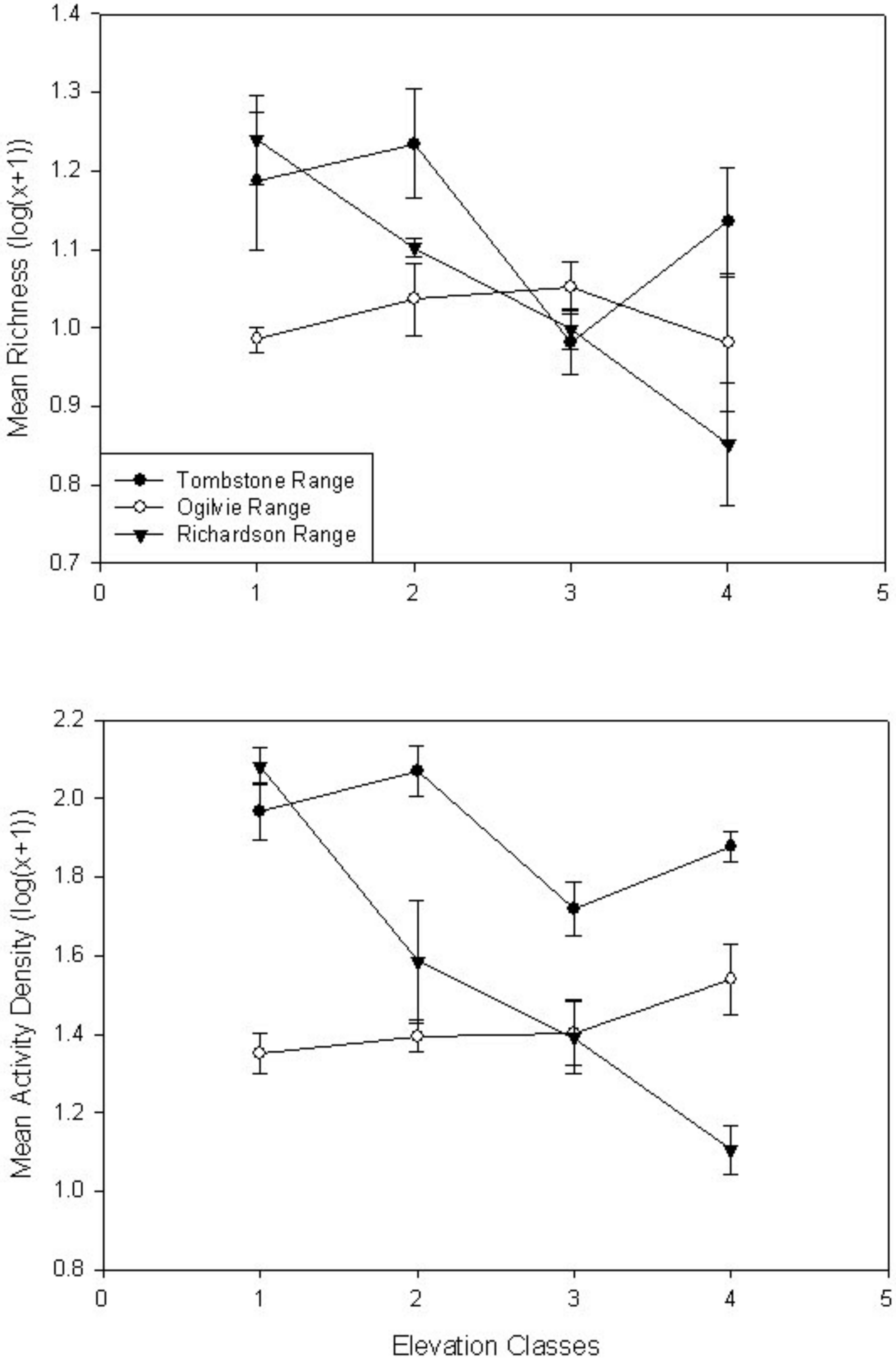
Mean Richness (log(x+1))
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0
1
2
3
4
5
Tombstone Range
Ogilvie Range
Richardson Range
Mean Activity Density (log(x+1))
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0
1
2
3
4
5
Elevation Classes

Figure 3.2

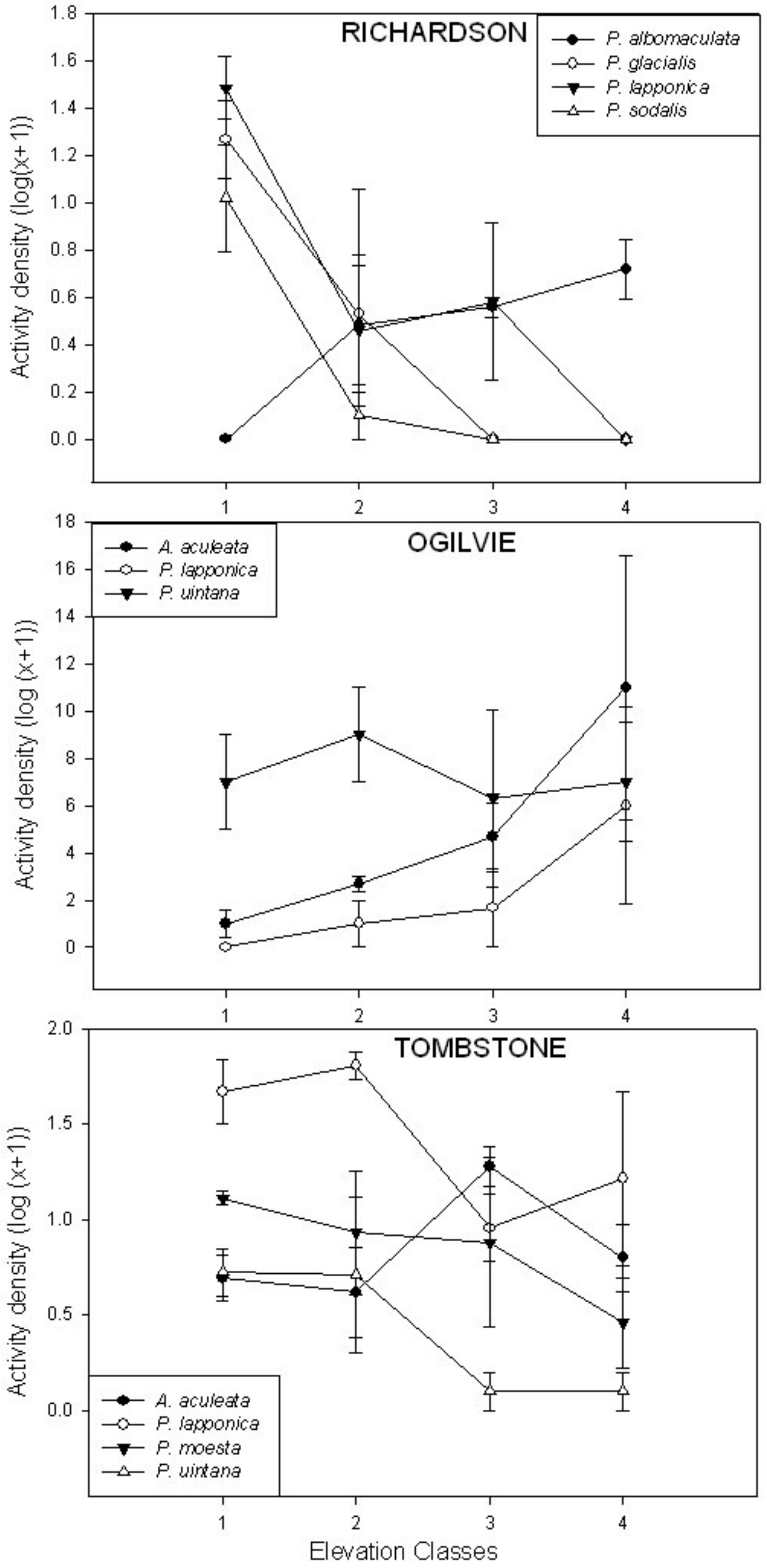
RICHARDSON
P. albomaculata
P. glacialis
P. lapponica
P. sodalis
Activity density (log(x+1))
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
OGILVIE
A. aculeata
P. lapponica
P. uintana
Activity density (log (x+1))
18
16
14
12
10
8
6
4
2
0
1
2
3
4
TOMBSTONE
A. aculeata
P. lapponica
P. moesta
P. uintana
Activity density (log (x+1))
2.0
1.5
1.0
0.5
0.0
1
2
3
4
Elevation Classes

Figure 3.3

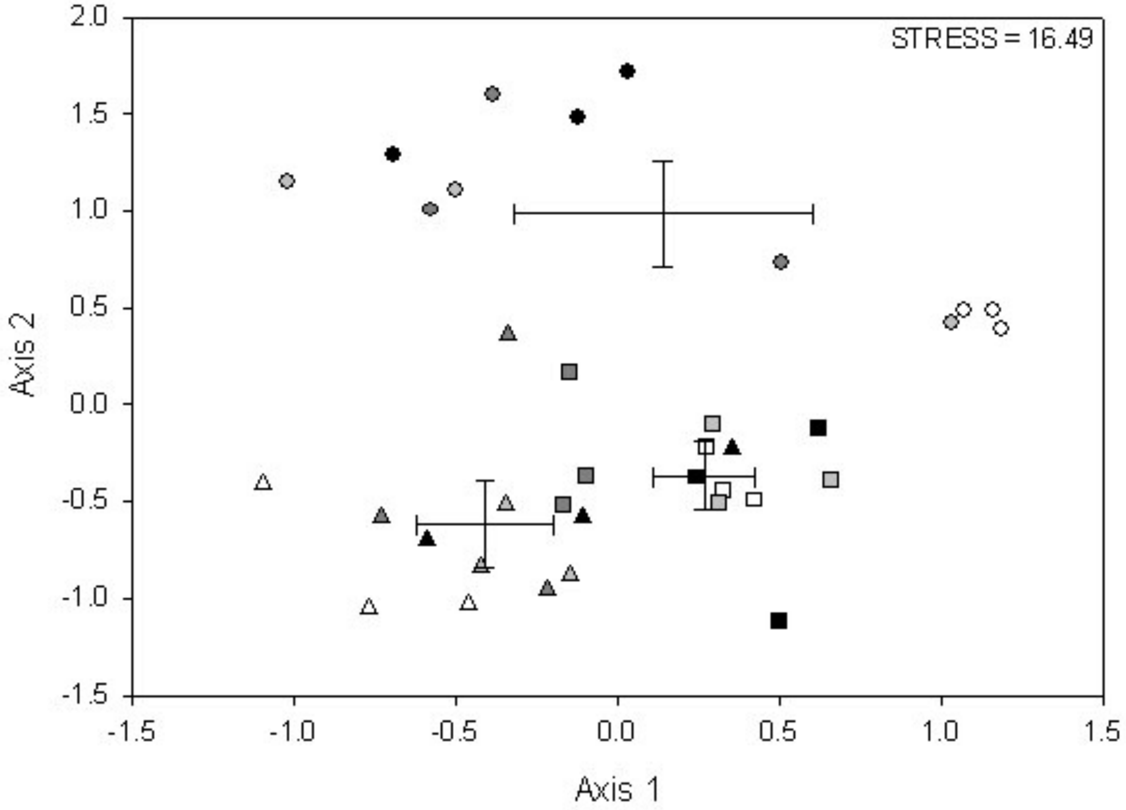
STRESS = 16.49
Axis 2
Axis 1
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5

Figure 3.4

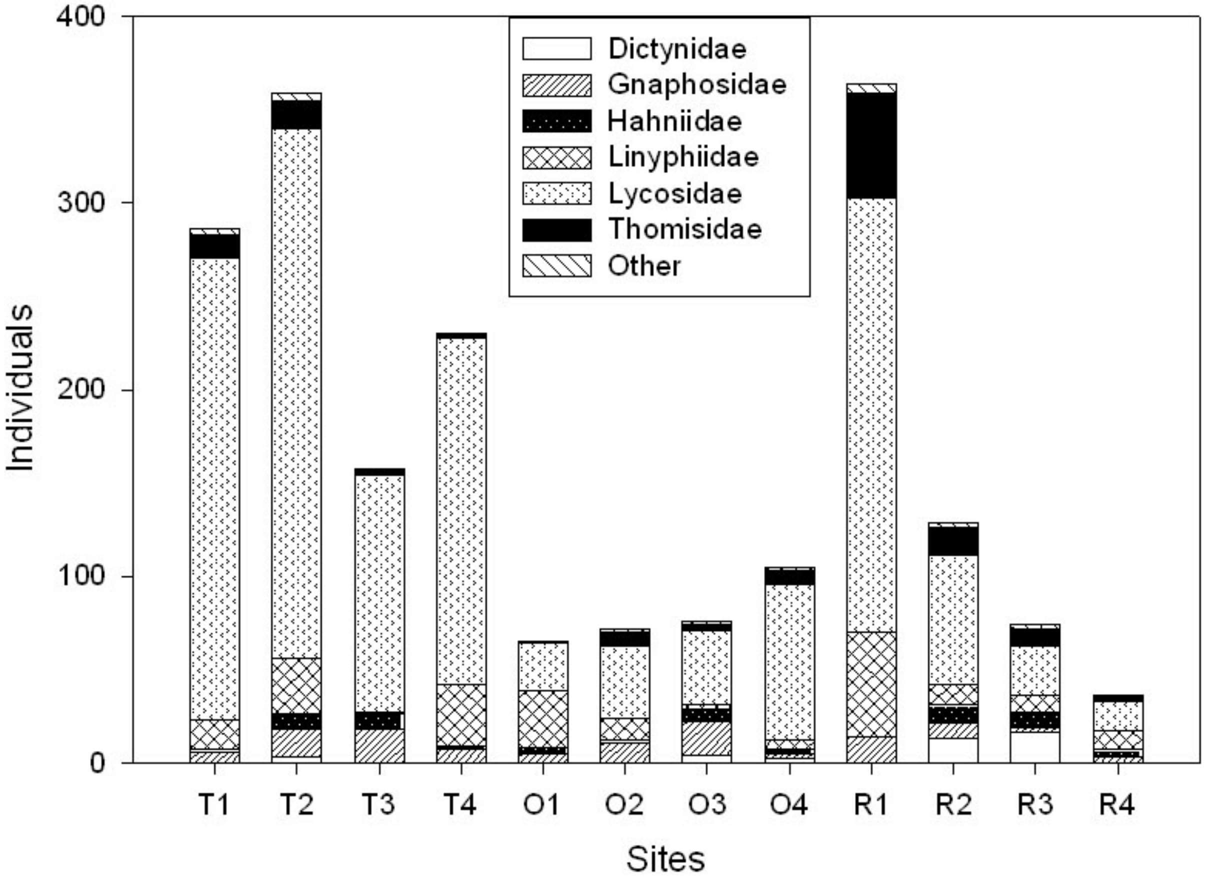
400
300
200
100
0
Individuals
Dictynidae
Gnaphosidae
Hahniidae
Linyphiidae
Lycosidae
Thomisidae
Other
T1
T2
T3
T4
O1
O2
O3
O4
R1
R2
R3
R4
Sites

Figure 3.5

3.10. Appendix

Appendix 3.1 – Spiders collected at four elevations in each of three mountain ranges in the northern region of the Yukon Territory, Canada. The mountain ranges were the Tombstone Range (64.309°N, 138.141°W), Ogilvie Range (65.158°N, 138.148°W) and the Richardson Range (66.725°N, 136.114°W). An asterisk (*) indicates presence of a species.

	Tombstone				Ogilvie				Richardson			
Species	1060m	1160m	1260m	1360m	660m	760m	860m	960m	760m	860m	960m	1060m
Hypsosinga nr *groenlandica*								*				
Clubiona praematura Emerton		*							*			
Hackmania prominula (Tullgren)		*					*	*				
Lathys alberta Gertsch							*			*	*	
Gnaphosa borea Kulczynski	*	*	*	*					*	*	*	
Gnaphosa microps Holm		*		*			*					
Gnaphosa muscorum (L. Koch)			*			*				*		
Gnaphosa orites Chamberlin				*					*	*	*	*
Haplodrassus hiemalis (Emerton)									*	*		
Haplodrassus signifer (C. L. Koch)	*	*	*									

Micaria aenea Thorell							*					
Micaria alpina L. Koch	*	*	*	*	*	*	*					
Micaria constricta Emerton			*			*	*					
Micaria tripunctata Holm	*		*			*	*	*				
Zelotes sula Lowrie & Gertsch							*	*				
Hahnia cinerea Emerton		*		*			*					
Hahnia glacialis Sorensen	*	*	*		*	*	*	*		*	*	*
Agyneta jacksoni (Braendegaard)				*					*	*	*	*
Agyneta olivacea (Emerton)	*			*								
Agyneta simplex (Emerton)			*							*	*	*
Agyneta sp 2	*											
Bathyphantes simillimus (L. Koch)	*	*			*				*	*		
Ceraticelus sp					*	*	*		*			
Ceratinella nr *alaskae*	*											
Ceratinopsis labradorensis Emerton		*			*	*						
Cnephalocotes obscurus (Blackwall)				*								
Diplocentria bidentata (Emerton)	*			*				*				
Erigoninae sp 1									*			
Gonatium crassipalpum Bryant	*	*		*	*	*			*			

Hilaira vexatrix (O.P.-Cambridge)							*			
Hilaria herniosa (Thorell)		*	*							
Hybauchenidium aquilonare (L. Koch)							*	*		*
Hybauchenidium gibbosum (Sorensen)		*		*						
Hypselistes semiflavus (L. Koch)	*	*	*				*			
Improphantes complicatus (Emerton)	*							*		
Incestophantes washingtoni (Zorsch)			*		*					
Islandiana cristatus Eskov				*						
Islandiana sp	*									
Lepthyphantes alpinus (Emerton)				*	*			*		
Linyphiinae sp 1	*	*		*	*		*			*
Linyphiinae sp 2							*			
Linyphiinae sp 4										*
Macrargus multesimus (O.P.-Cambridge)			*			*			*	
Mecynargus monticola (Holm)			*							
Mecynargus sphagnicola (Holm)			*							
Metopobactrus prominulus(O.P.-Cambridge)	*									
Pelecopsis mengei (Simon)			*	*						
Procerocymbium sibiricum Eskov							*			

Satilatlas gertschi Millidge									*	*	*	*
Scotinotylus alpinus (Banks)										*	*	
Silometopoides pampia (Chamberlin)		*		*								
Sisicottus montanus (Emerton)				*								
Sisis rotundus (Emerton)				*				*				
Sitticus ranieri (Peckham & Peckham)								*				
Tapinocyba bicarinata (Emerton)		*			*							
Tarsiphantes latithorax Strand												*
Tunagyna debilis (Banks)						*						
Walckenaeria castanea (Emerton)											*	
Walckenaeria karpinskii (O.P.-Cambridge)	*			*	*							
Zornella cultrigera (L. Koch)	*	*			*							
Alopecosa aculeata (Clerck)	*	*	*	*	*	*	*	*				
Alopecosa pictilis (Emerton)									*		*	
Arctosa alpigena (Doleschall)	*	*		*	*	*		*				
Pardosa albomaculata Emerton							*			*	*	*
Pardosa beringiana Dondale & Redner										*	*	
Pardosa furcifera (Thorell)	*			*				*				
Pardosa fuscula (Thorell)									*			

Pardosa glacialis (Thorell)									*	*		
Pardosa hyperborea (Thorell)	*	*		*				*		*	*	
Pardosa lapponica (Thorell)	*	*	*	*		*	*	*	*	*	*	
Pardosa moesta Banks	*	*	*	*			*	*	*	*		*
Pardosa podhorskii (Kulczynski)									*	*		
Pardosa sodalis Holm									*	*		
Pardosa uintana Gertsch	*	*	*	*	*	*	*	*				
Pardosa xerampelina (Keyserling)										*		
Pirata bryantae Kurata		*										
Thanatus arcticus Thorell	*	*		*					*	*	*	
Chalcoscirtus alpicola Emerton					*	*	*			*		
Chalcoscirtus carbonarius Emerton										*		
Tetragnatha extensa (Linnaeus)												*
Ozyptila arctica Kulczynsk			*			*	*	*			*	
Xysticus britcheri Gertsch	*	*		*		*	*	*	*	*	*	
Xysticus emertoni Keyserling									*			
Xysticus labradorensis Keyserling										*	*	*
Xysticus luctuosus (Blackwall)	*	*						*				
Xysticus nr *alboniger*												*

Xysticus nr *durus*	*	*	*				*	*
Xysticus obscurus Collett	*							
Titanoeca nivalis Simon							*	

CHAPTER FOUR

In the previous two chapters I show that changes in habitat can explain patterns in spider species assemblages along the spatial gradients of latitude and elevation. The differences in presence or absence of a given species are likely due to species-specific responses in their physiology or life history that enable them to colonize and persist in multiple or single habitats. Furthermore, the life history of a species is intimately linked to its local population dynamics which feedback to local community dynamics. In the following chapter I investigate the life history of the dominant ground-dwelling spiders in the region.

Life history of three tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada

4.1. Abstract

We studied populations of three tundra-dwelling wolf spider (Lycosidae) species to determine reproductive trait relationships, natural densities, developmental timing and egg sac parasitism. We collected 451 *Pardosa lapponica* (Thorell 1872), 176 *Pardosa sodalis* Holm 1970 and 117 *Pardosa moesta* Banks 1892 in the summer of 2008. We used log likelihood ratio tests and multiple linear regressions to determine the best predictors of fecundity and relative reproductive effort for these species. Female body size best explained the variation in fecundity and body condition was the best predictor for relative reproductive effort. We tested for a tradeoff between the allocation of resources to individual eggs and the number of eggs produced (fecundity) within each species using simple linear regression. Here, there was variation in detectable egg size-number tradeoffs among sites and these may be related to local variation in resource allocation linked to density-related biotic or abiotic factors. We found mean densities of *P. lapponica* as high as 0.45 and 0.46 individuals per meter squared at two of the sites. We found that while egg sac parasitism (i.e*.*, *Gelis* sp.) was not higher in larger individuals within spider species, it was highest in the largest species (*P. sodalis*). Parasitism loads ranged from one to fourteen individuals per egg sac and incidence reached about 50% in two of the populations of *P. sodalis*. Parasitism may have significant impacts on the life history of wolf spiders in the region.

4.2. Introduction

Life history is an important link between ecology and evolution and underlies population (Roff 2002) and community (Tokeshi 1999; Bonsall et al. 2004) dynamics. Life history characteristics may determine the extinction of local populations (Reynolds 2002) and in the context of communities, coexistence of similar species may be mediated by life history characteristics and the tradeoffs among them (Enders 1976; Tokeshi 1999). Life history traits may vary among species, among populations of the same species and within the same population of a given species (e.g., Brown et al. 2003, Reed et al. 2008). Such variation is subject to natural selection which leads to combinations of traits that should optimize lifetime reproductive success; tradeoffs among life history traits occur due to the limited time and energy available for each component (Roff 2002).

Tradeoffs are fundamental to life history theory (Stearns 1989) and one important tradeoff is between offspring size and number (reviewed in Fox and Czesak 2000; Messina and Fox 2002). This assumes that at pre-maturation, an individual's resources are allocated to growth and maintenance of somatic tissues; once maturation is achieved, resource allocation is shifted to reproductive output (Fox and Czesak 2000). These available resources dedicated to reproduction must balance investment in individual offspring and the number of offspring produced (fecundity); offspring fitness naturally increases with investment per individual (Smith and Fretwell 1974). The particular environment in which an individual lives may influence the detection of a tradeoff. Under resource-rich environments, for example, a tradeoff may not manifest because a female is not resource limited. Hence, selection for larger and fewer offspring may only occur in resource poor environments (Roff 2002).

Among arthropods, larger females generally produce more, and often larger, offspring (Marshall and Gittleman 1994; Fox and Czesak 2000); given this, it is important to control for female size in order to detect tradeoffs between offspring size and number (Fox and Czesak 2000). In some cases, however, it may be advantageous for female arthropods to produce relatively smaller offspring. In environments where parasitism is frequent it may be best to decrease development time by producing smaller propagules that develop faster and are exposed to egg parasites for a shorter period of time (Messina and Fox 2002).

Wolf spiders (Lycosidae) have been used frequently as model organisms with which to examine life history traits and the interrelationships among them (Schmoller 1970; Simpson 1993; Buddle 2000; Brown et al 2003; Hendrickx and Maelfait 2003; Reed and Nicolas 2008). While there has been much work on species from temperate latitudes (e.g. Kessler 1971; Brown et al. 2003; Hendrickx and Maelfait 2003; Walker et al. 2003; Reed and Nicolas 2008), wolf spiders from higher latitudes are seldom the focus of study (but see Simpson 1993). Past research has investigated the relationships among female size, fecundity and propagule size and show that female size explains well variation in fecundity (Simpson 1993; Buddle 2000; Brown et al. 2003; Hendrickx and Maelfait 2003; Walker et al. 2003; Reed and Nicolas 2008) within and among wolf spider species. Tradeoffs between offspring size and number in wolf spiders have been investigated both intra- and interspecifically with mixed results (Simpson 1993; Marshall and Gittleman 1994; Simpson 1995; Hendrickx and Maelfait 2003; Brown et al. 2003; Walker et al. 2003). Simpson (1993) supported a tradeoff between fecundity and average offspring size in an Arctic wolf spider in one year of a two year study and Hendrickx and Maelfait (2003) showed a tradeoff between these reproductive characters in *Pirata* *piraticus* (Clerck) from Belgium. Walker et al. (2003) detected little support for a tradeoff between offspring number and size in *Hogna helluo* (Walckenaer) in the mid-west United States.

Understanding the relationships between and among life history traits in the Arctic is important as this environment offers a unique suite of selection pressures (i.e., biotic and abiotic factors) for arthropods (Simpson 1993; Høye et al. 2009) and it is an environment susceptible to climate change (Hansen et al. 2006). The overall objective of this study was to determine life history characteristics in the dominant wolf spider species of the region. Specifically, we wanted to determine the development of three tundra-dwelling sympatric wolf spiders, the relationships between female reproductive characteristics (i.e., female body size, body condition, relative reproductive output and fecundity) and to test if a tradeoff exists between the investment in offspring size and number. Since reproductive patterns can vary with resource availability in a density dependent fashion we also wanted to determine natural densities of these species at each site. We predicted that female body size would be the best predictor of fecundity (Simpson 1993; Buddle 2000; Brown et al. 2003; Hendrickx and Mailfait 2003; Reed and Nicolas 2008), and that female body condition would best predict the relative reproductive effort (RRE) of each female because condition is likely a better indicator of available resources females could allocate to individual eggs. We also predicted a tradeoff between resource allocation to egg size and number for these Arctic species.

Knowing that some wasp species (*Gelis* sp., Ichneumonidae and *Baeus* sp., Scelionidae) parasitize the egg sacs of female wolf spiders (Pers. Obs.; Cobb and Cobb 2004), we wanted to determine the incidence of these parasitoids in each of the wolf spider species as they may be important to the life histories of the three Arctic species.

We also wanted to know if incidence of parasitoids, specifically *Gelis* sp., was higher in larger individuals within species or if it was higher in one species over the others. Lastly, we wanted to know if larger female spiders supported higher parasitoid loads.

4.3. Materials and methods

Study Region and Species

Sampling was conducted from late June to early August 2008 at three tundra sites in the northern Yukon Territory, Canada. The most southern site was in the Tombstone Mountain Range (64.36261N, 138.19411W, Elev. 1200m), the second site was in the Ogilvie Mountain Range (65.47404N, 137.46.206, Elev. 862m) and the most northern site was in the Richardson Mountain Range (66.55.546, 136.19.874, Elev. 534m). There were three sampling periods (Late June-Early July; Mid-July; Late July-Early August) at each the Tombstone site and the Richardson site (Figure 4.1a) and two sampling periods (Mid-July; Late July-Early August) at the Ogilvie site. Each sampling period consisted of three to four days of collecting in an area of approximately one square kilometer. We selected these three sites because we could obtain collections of spiders from similar habitats while maximizing the spatial extent of our study and the collection of our focal species. All three sites were similar in vegetation composition with representatives of *Ledum* sp*, Vaccinium* sp*, Rubus chamaemorus, Cladonia rangiferina* (and other lichens)*, Empetrum* sp*, Betula gladulosa,* and *Salix* sp.

Live female spiders were collected by hand and live pitfall trapping at each of the three sites. Pitfall traps were constructed of 750ml plastic containers which were dug into the ground with the rim of the container flush with the substrate. Pitfall traps were typically left out for the extent of sampling at each site and were emptied every five to six hours. Our focal species were *Pardosa lapponica* (Thorell 1872) (Figure 4.1b)*, Pardosa sodalis* Holm 1970 (Figure 4.1c) and *Pardosa moesta* Banks 1892 as these were the most abundant species represented on the tundra in this region, respectively (Bowden and Buddle 2010b).

Pardosa lapponica is a Holarctic species (Dondale et al. 1997) found in high abundance on tundra and less frequently in sparse boreal forest (Bowden and Buddle 2010a, 2010b). *Pardosa sodalis* is a 'Beringian' species with records from northwestern North America and northeastern Siberia (Dondale et al. 1997) and is likely restricted to moist tundra (Dondale and Redner 1990). *Pardosa moesta* is found in many habitats (e.g. urban areas, clearcuts, forests, meadows, marshes) throughout much of North America (Dondale and Redner 1990; Buddle et al. 2000; Buddle 2000) and is the smallest wolf spider collected in this region (Bowden and Buddle 2010a, 2010b). Other wolf spider species in the genus *Pardosa* that are less commonly encountered in this study region are *P. furcifera* (Thorell), *P. fuscula* (Thorell), *P. glacialis* (Thorell), *P. podhorskii* (Kulczyński) and *P. xerampelina* (Keyserling) (Bowden and Buddle 2010a, 2010b). Voucher specimens are deposited at the Lyman Entomological Museum, Ste Anne de Bellevue, Québec.

In Egg Sac Developmental Timing

In order to determine the rate at which species were developing we categorized the individuals into four development stages: egg, pre-larva, larva, and nymph (first instar) (Foelix 1996). Using all non-parasitized egg sacs for each species, we calculated the proportion of females with progeny at each of the four developmental stages.

Density Estimates

Densities of the three focal species were estimated using a ring of hard plastic measuring 1.13 meters in diameter (1 m^2 area) and about twelve centimeters high. The ring was haphazardly and firmly placed on the tundra surface in each site and all wolf spiders collected inside the ring were identified and counted. This protocol was adapted from Buddle (2000). This procedure was conducted twice at the Ogilvie site and three times at the Tombstone and Richardson sites. A total of 170, 165 and 115 one meter squared plots were sampled from each the Tombstone, Ogilvie and Richardson sites, respectively. From these data we calculated average density of each species at each site.

Reproductive Relationships

Female spiders were collected and housed in small plastic containers with a small piece of wet cotton. All individuals and their egg sacs were weighed the same day of collection using a Denver Instruments® APX-200 scale and subsequently preserved in 70% ethanol. All specimens were returned to the laboratory where carapace width of each female was measured to determine body size and the respective egg sac dissected, and contents counted to obtain fecundity. Measurements were conducted using a Nikon® SMZ1000 stereomicroscope fitted with an ocular micrometer. All data were ($\log_{10}$ x +1) transformed to ensure assumptions of normality and to improve monotonicity. We calculated body condition of individuals using the residual index (Jakob et al. 1996). We regressed mass on body size (carapace width) to obtain the index which is a measure of mass independent of body size. We tested whether body size (carapace width) or body condition better predicted the reproductive responses: fecundity and relative reproductive effort (egg sac mass:female mass). We used generalized linear mixed models, with maximum likelihood to test the significance of the random factor ‘site’ using log-likelihood ratio tests with package ‘lme4’ (Bates and Maechler 2009) for the R environment (R Development Core Team 2009). These tests indicate whether a larger model (i.e., including the ‘site’ factor) significantly improves the fit of the data over a smaller model. Using these tests, we detected that site had a significant effect on the reproductive responses in two of the species; therefore we decided to separate and analyze the data by site for all three species. We used multiple linear regressions to determine the significance of the terms ‘condition’ and ‘body size’ for each of the reproductive responses for each species at each site based on the F-statistics. To test whether a tradeoff existed for each of these species we obtained the residuals of each, fecundity and average offspring size, regressed on body size. Average offspring size was obtained by dividing the entire egg sac mass by the number of propagules inside. This is a commonly used measure of individual offspring size (e.g., Simpson 1993, Brown et al. 2003) and Hendrickx and Maelfait (2003) determined that the mass of the cocoon itself contributed negligibly to the total egg sac mass. We tested whether there were significant egg size-number tradeoffs within species within each site using linear models of the residuals of fecundity and the residuals of average individual egg mass.

To determine if incidence of *Gelis* (Figure 4.1 d, e) increased with spider size within species we used a logistic regression with presence/absence of *Gelis* as a response and female body size as a predictor. We examined the proportion of spiders parasitized to determine whether *Gelis* preferred one species to others. To determine whether larger spiders host more parasitoids we used linear regressions with spider size as a predictor and the number of parasitoids (using only individuals parasitized) in the respective egg sac as the response. Due to low presence (i.e, 8 individuals parasitized in *P. moesta* and 4 *P. lapponica*) we did not pursue statistical analyses with *Baeus* sp. All multiple linear and simple linear regressions, logisitic regressions and ANOVA's were conducted using the package 'stats' in R version 2.10.1 (R Development Core Team 2009).

4.4. Results

Fecundity and Reproductive Effort

We collected and used a total of 451 *Pardosa lapponica*, 176 *P. sodalis* and 117 *P. moesta* for analysis of reproductive trait relationships. We found that *P. sodalis* reaches the first instar of development earlier than the other two species even though it attains a larger adult size (Table 4.1). The statistical analyses revealed substantial differences in the morphometrics among and within species (Table 4.2). Average body size, mass and egg sac mass were lowest at the Tombstone site for *P. lapponica* and *P. sodalis* but did not differ for each species between the Ogilvie and Richardson sites. Fecundity was lowest for *P. lapponica* at the Tombstone site. There were no notable differences in reproductive characteristics between the Ogilvie and Richardson sites for *P. moesta*. We found that RRE was larger in the Tombstone site than the Ogilvie or Richardson sites for *P. sodalis*, but there were no notable differences in the other two species. We found that female body size was the best fit model for fecundity and was not surpassed by body condition for any species at any site (all p-values for body condition > 0.05). With the exception of *P. sodalis* from the Ogilvie site, final regression models for fecundity were highly significant and well explained the variation in the data. All of the regressions yielded positive relationships between fecundity and body size (Figure 4.2). As predicted, body size did not outperform the fit of body condition to relative reproductive effort for any species at any site (all p-values for body size > 0.05). Body condition better explained the variation in RRE; however, the final regression models for these relationships were not all significant (Figure 4.3). The slopes for all regressions of RRE on body condition were negative.

Egg size – number tradeoff

We detected some significant tradeoffs between egg size and number for all species as revealed by the negative relationships between egg size and number, however there were large differences among sites (Figure 4.4). We found the strongest negative relationships between egg size and number for *P. lapponica* and *P. sodalis* at the Tombstone site and for *P. moesta* at the Ogilvie site. Significant tradeoffs were also detected at the Ogilvie and Richardson sites for *P. lapponica* and *P. sodalis*, respectively. No significant relationship was detected for *P. lapponica* or *P. moesta* at the Richardson site or for *P. sodalis* at the Ogilvie site (Figure 4.4).

Population Densities

Densities for *P. moesta* were higher at the Ogilvie site than the Richardson site (Table 4.3). *P. lapponica* populations differed among sites and were most dense at the Tombstone and Ogilvie sites, which did not differ from one another. The Tombstone and Ogilvie sites were denser than the Richardson site. The highest density populations of *P. sodalis* were found at the Tombstone and Richardson sites which did not differ much from one another. We calculated lower densities of *P. sodalis* at the Ogilvie site than at the Tombstone or Richardson sites and this is reflected in the number of individuals that we were able to hand collect for analysis at this site.

Parasitism

We found that within spider species, incidence of *Gelis* was not higher in larger individuals (no significant differences between presence/absence of parasitoid using logistic regression), but was higher in the largest species (*P. sodalis*). An average of 30% of *P. sodalis* were parasitized; with 52% and 49% of the Tombstone and Richardson populations being parasitized, respectively. Seven percent of the individuals at the Ogilvie site were parasitized. *P. lapponica* had an overall incidence of 21% parasitism. We observed 14%, 44% and 9% parasitism in *P. lapponica* at the Tombstone, Ogilvie and Richardson sites, respectively. Incidence of *Gelis* was lowest in *P. moesta;* we observed that overall 2.5% of the individuals examined were parasitized, 5% at the Ogilvie and 1.2% at the Richardson site. We found no significant effect (all p-values > 0.05) of spider size on parasitoid load for any of the wolf spider species examined.

4.5. Discussion

In our study of life history of Arctic wolf spiders, we have shown that that female body size best explained fecundity and that body condition best explained relative reproductive effort. We found significant tradeoffs between egg size and number independent of body size. There was much variation in the densities of spiders from site to site. We detected very high incidence of egg sac parasitoids collected from most of the populations of females collected and these could play an important role in the life history of these species. We also found that *P. sodalis*, which is the largest species as an adult, is the first to emerge from the egg sac.

Our finding that body size well explained the variation in fecundity for wolf spider species is well supported by the literature (Marshall and Gittleman 1994; Buddle 2000; reviewed in, Fox and Czesak 2000, Brown et al. 2003; Hendrickx and Maelfait 2003). The coefficients of determination calculated in our study (0.233 ± 0.035, mean ± SE) are similar to those in other studies (0.274 ± 0.043) of wolf spider reproduction (Simpson 1993; Buddle 2000; Brown et al. 2003; Hendrickx and Maelfait 2003; Reed and Nicolas 2008). Buddle (2000) calculated an r-squared value of 25.7 for *P. moesta* collected in northern Alberta, Canada and we found similar values for *P. moesta* in our study (31.4 ± 6.5). Average female body size and fecundity in our study were smaller than those reported by Buddle (2000) with averages of 1.911 ± 0.0009 mm and 26.675 ± 0.674 eggs, compared to 2.07 ± 0.02 and 33.06 ± 1.29 eggs, respectively. Average body sizes for *P. lapponica* and *P. sodalis* in our study were 2.256 ± 0.006 mm and 2.605 ± 0.011 mm, respectively. These metrics are very similar to those reported by Dondale and Redner (1990) who measured carapace widths of 2.25 ± 0.18 mm and 2.56 ± 0.29 mm for *P. lapponica* and *P. sodalis*, respectively.

Female body size did not improve significantly the fit of female body condition to relative reproductive effort for any scenario. Although the relative fit of condition has not been previously investigated for wolf spiders, other studies have also shown no significant relationship between female body size and relative reproductive effort (Simpson 1993; Hendrickx and Maelfait 2003). We also show that this relationship is negative, so females with a lower condition likely allocate relatively more to offspring production than did females in better condition and this pattern appears to hold true for many other animal groups (Blueweiss et al. 1978).

Simpson (1993) found no difference in egg number production between two years in two Arctic wolf spiders despite differences in egg sac mass and suggested that females reduced their investment per offspring and not the number of offspring produced, thus they allocate fecundity based on body size and investment per offspring based on condition. Furthermore, experimental (Kessler 1971; Wise 1979; Spence et al. 1996) and field (Hendrickx et al. 2003; Reed and Nicolas 2008) studies have suggested that food resource acquisition can have effects on egg production in spiders. For example, Reed and Nicolas (2008) determined that the highest relative reproductive effort in populations of *Rabidosa rabida* (Walckenaer) and *R. punctulata* (Hentz) were in areas with high population densities. This suggests that reproductive effort may operate in a density dependent manner and may influence the availability of resources to individuals in the same manner. We not only deduced that individuals with lower body condition seemed to invest more in RRE, but in a comparison among species it seems that the largest species (*P. sodalis*) had the highest RRE and the smallest species (*P. moesta*) had the lowest RRE. This finding is similar to Simpson (1993) who also concluded that the larger species in his study had a larger reproductive effort.

Spatial and temporal variation in resource availability can affect reproduction and this may help explain the variable results in egg size and number tradeoffs. We detected instances of significant negative relationships between egg size and number in our focal species, indicating a tradeoff. The egg size-number tradeoff, first formally described by Smith and Fretwell (1974) has been explored both theoretically (Messina and Fox 2001, Roff 2002) and empirically (Simpson 1993; Marshall and Gittleman 1994; Brown et al.

2003; Hendrickx and Maelfait 2003). Many of these studies report a tradeoff between egg size and number, however, the detection of significant negative relationships has been inconsistent (e.g., Simpson 1993, 1995; Marshall and Gittleman 1994; Brown et al. 2003). For example, in tests of a size-number tradeoff of two Arctic wolf spiders over a two year period, Simpson (1993) found that only one species in one year exhibited a significant tradeoff. In three tests of a tradeoff in *Pirata sedentarius* Montgomery in New York, USA, Brown et al. (2003) only detected one instance of a significant negative relationship between egg size and number. In a meta-analysis, Marshall and Gittleman (1994) found little evidence for a tradeoff between egg size and number interspecifically in spiders and argue that relationships between egg size and number for spiders potentially reflects more the need to maximize fecundity under "constraints on minimum egg mass and maximum clutch mass", rather than a tradeoff *per se*. In theory, the detection of a tradeoff between egg size and number is subject to local resource availability. Specifically, females will only be forced to allocate more resources to each individual propagule, thus producing fewer larger progeny under situations of limited resources (Roff 2002). Empirically, alterations to reproductive strategies under restricted resource availability have been exemplified in spiders (Kessler 1971; Benton and Uetz 1984; Hendrickx et al. 2003; Reed and Nicolas 2008). For example, Hendrickx et al. (2003) found that there were significant changes to reproduction tactics by female *Pirata piraticus* in response to various levels of contamination. Females with higher heavy metal burdens, being forced to use available resources for detoxification, produced fewer-larger eggs had a lower reproductive output then females with lower heavy metal concentrations.

Our results varied by site and species. Interestingly, Reed and Nicolas (2008) found that RRE can vary with density of the local population. We note that the significant tradeoff results yielded in our study corresponded to significant differences found in density among and between sites. We detected the strongest and most significant negative relationships between egg size and number at the sites where we found the highest densities of each species. Although we have not conducted an explicit test of the effects of resource limitation in response to density dependence on reproductive relationships, we suggest this is one possible explanation for our results. The fact that we detected significant body size variation among site suggests that there is variation in resource availability among sites. This may be attributed to some unmeasured biotic or abiotic factors (e.g., temperature, humidity, food availability).

We found high incidence of parasitism by *Gelis* on tundra wolf spider egg sacs in the Yukon Territory. To our knowledge, the proportions of parasitized egg sacs reported here is the highest on record in populations of wolf spiders (Eason et al. 1967; Edgar 1971; Cobb and Cobb 2004). For example, Edgar (1971) found egg sac parasitism, by *Gelis* and *Hidryta* to range from 2.9% to 34.8% of individuals in *Pardosa lugubris* (Walckenaer) in Scotland. *Pardosa sodalis,* which is the largest species investigated was also the most frequently parasitized and, on average, developed in the egg sac a few weeks before *P. lapponica* and *P. moesta*. Because we collected spiders throughout most of the active season we discovered that it takes most of the season to mature in the egg sac between June and August. We suggest that, like high elevation species (Schmoller 1970), these species probably take multiple years to reach maturity due to multiple life stages that we collected in pit-fall traps at the same time. Similarly we suspect that these species likely produce just one egg sac per life time. We suggest that spiderlings hatch and over-winter the first season as early instars. Our findings suggest that these parasitoids have important consequences for the reproductive fitness of these northern spider species since *Gelis* destroy the contents of the egg sac. The incidence of parasitism may be in part responsible for the low sample sizes of *P. sodalis* detected at the Ogilvie site.

There have been few studies of spider life history characteristics in the Arctic (but see, Simpson 1993; Høye et al. 2009). Høye et al. (2009) found marked inter-annual variation in body size of *Pardosa glacialis* over a ten year period in Greenland. They pointed to timing of snow melt each year as being an important determinant of this important life history trait. High latitude species, like high elevation species, possess unique life histories and their reproductive traits associated with extreme living differ substantially from their more temperate counterparts (Schmoller 1970; Simpson 1993). Global climate changes, which are predicted to dramatically affect Arctic environments (Sturm et al. 2001, Hansen et al. 2006), may have significant impacts on life history characteristics (Høye and Forchhammer 2008, Høye et al. 2009).

4.6. Acknowledgements

The authors would like to thank Jean-Francois Aublet and William Buddle for help with collection of specimens in the field. The authors would also like to thank the Tetlit Gwitch'n, Nacho Nyak Dun, Vuntut Gwitch'n, Tr'ondëk Hwëch'in Han Nation and the Yukon Territorial Government. Financial support was provided by the Northern Scientific Training Program, the National Science and Engineering Research Council of Canada, and McGill University.

4.7. Literature Cited

Bates, D., and Maechler, M. 2009. lme4: Linear mixed-effects models using S4 classes.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., and Sams, S. 1978. Relationships between Body Size and Some Life History Parameters. Oecologia 2: 257-272.

Bonsall, M. B., V. A. A. Jansen, and Hassell, M. P. 2004. Life history trade-offs assemble ecological guilds. Science 306: 111-114.

Bowden, J. J. and Buddle, C. M. 2010a. Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. Arctic. 63: 261-272.

Bowden, J. J. and Buddle, C. M. 2010b. Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada. Écoscience. 17: 287-297.

Brown, C. A., B. M. Sanford, and Swerdon, R. R. 2003. Clutch size and offspring size in the wolf spider *Pirata sedentarius* (Araneae, Lycosidae). Journal of Arachnology 31: 285-296.

Buddle, C. M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28: 319-328.

Buddle, C. M., J. R. Spence, and Langor, D. W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424-436.

Cobb, L. M., and Cobb, V. A. 2004. Occurence of parasitoid wasps, *Baeus* sp. and *Gelis* sp., in the egg sacs of the wolf spiders *Pardosa moesta* and *Pardosa sternalis* (Araneae, Lycosidae) in southeastern Idaho. The Canadian Field Naturalist 118: 122-123.

Dondale, C., and Redner, J. 1990. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska. Canadian Government Publishing Centre, Ottawa.

Dondale, C. J. Redner, and Marusik, Y. M. 1997. Spiders (Araneae) of the Yukon. Pages 73-113 in Insects of the Yukon (H. Danks, and J. Downes, eds.). Canadian Museum of Nature, Ottawa.

Eason, R. R., W. B. Peck, and Whitcomb, W. H. 1967. Notes on spider parasites including a reference list. Journal of Kansas Entomological Society 40: 422-434.

Edgar, W. D. 1971. Aspects of ecology and energetics of egg sac parasites of the wolf spider *Pardosa lugubris* (Walckenaer). Oecologia 7: 155-163.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69: 991-998.

Foelix, R. F. 1996. Biology of spiders, 2nd ed. Oxford University Press, New York.

Fox, C. W., and Czesak, M. E. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45: 341-369.

Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and Medina-Elizade, M. 2006. Global temperature change. Proceedings of the National Academy of Sciences of the United States of America 103: 14288-14293.

Hendrickx, F., and Maelfait, J. P. 2003. Life cycle, reproductive patterns and their year-to-year variation in a field population of the wolf spider *Pirata piraticus* (Araneae, Lycosidae). Journal of Arachnology 31: 331-339.

Hendrickx, F., Maelfait, J. P., Speelmans, M. and Van Straalen, N. M. 2003. Adaptive reproductive variation along a pollution gradient in a wolf spider. Oecologia 134: 189-194.

Høye, T. T., and Forchhammer, M. C. 2008. Phenology of high-arctic arthropods: effects of climate on spatial, seasonal and inter-annual variation. Advances in Ecological Research 40: 299-324.

Høye, T. T., J. U. Hammel, T. Fuchs, and Toft, S. 2009. Climate change and sexual size dimorphism in an Arctic spider. Biology Letters 5: 542-544.

Jakob, E. M., S. D. Marshall, and Uetz, G. W. 1996. Estimating fitness: A comparison of body condition indices. Oikos 77: 61-67.

Kessler, A. 1971. Relation between egg production and food consumption in species of the genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8: 93-109.

Marshall, S. D., and Gittleman, J. L. 1994. Clutch size in spiders: Is more better? Functional Ecology 8: 118-124.

Messina, F. J., and Fox, C. W. 2001. Offspring size and number. Page 452 in Evolutionary Ecology: Concepts and case studies (C. W. Fox, D. A. Roff, and D. J. Fairbairn, Eds.). Oxford University Press, New York.

R Core Development Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed, D. H., and Nicholas, A. C. 2008. Spatial and temporal variation in a suite of life-history traits in two species of wolf spider. Ecological Entomology 33: 488-496.

Reynolds, J. D. 2003. Life histories and extinction risk. Page 464 in Macroecology: Concepts and Consequences (T. M. Blackburn, and K. J. Gaston, eds.). British Ecological Society, Malden.

Roff, D. A. 2002. Life History Evolution. Sinauer Associates, Inc., Sunderland.

Schmoller, R. 1970. Life histories of alpine tundra arachnids in Colorado. American Midland Naturalist 83: 119-133.

Simpson, M. R. 1993. Reproduction in two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. Canadian Journal of Zoology 71: 451-457.

Simpson, M. R. 1995. Covariation of spider egg and clutch size: The influence of foraging and parental care. Ecology 76: 795-800.

Smith, C. C., and Fretwell, S. D. 1974. Optimal balance between size and number of offspring. American Naturalist 108: 499-506.

Spence, J. R., M. Zimmermann, and Wojcicki, J. P. 1996. Effects of food limitation and sexual cannibalism on reproductive output of the nursery web spider *Dolomedes triton* (Araneae: Pisauridae). Oikos 75: 373-382.

Stearns, S. C. 1989. Trade-offs in life-history evolution. Functional Ecology 3: 259-268.

Sturm, M., C. Racine, and Tape, K. 2001. Climate change - Increasing shrub abundance in the Arctic. Nature 411: 546-547.

Tokeshi, M. 1999. Species Coexistence: Ecological and evolutionary perspectives. Blackwell Science Ltd., Malden.

Walker, S. E., A. L. Rypstra, and Marshall, S. D. 2003. The relationship between offspring size and performance in the wolf spider *Hogna helluo* (Araneae : Lycosidae). Evolutionary Ecology Research 5: 19-28.

Wise, D. H. 1979. Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species (Araneae, Araneidae). Oecologia 41: 289-300.

4.8. Tables and captions

Table 4.1 – In egg sac developmental timing of three tundra wolf spider species shown as number of individuals in each of four developmental stages over each of the three sampling periods.

Sampling Period	Stage	*P. moesta*	*P. lapponica*	*P. sodalis*
Late June-Early July	Egg	2	120	16
	Pre-Larva	2	36	16
	Larva	7	13	24
	Nymph	0	0	2
Mid-July	Egg	14	49	4
	Pre-Larva	5	20	3
	Larva	15	98	20
	Nymph	6	0	53
Late July	Egg	2	12	3
	Pre-Larva	3	7	4
	Larva	7	37	2
	Nymph	55	94	41

Table 4.2 – Life history trait data (means and standard errors) of three wolf spider species collected from three sites in Yukon Territory, Canada. Letters indicate significant ($p < 0.05$) differences among/between means within species using Tukey's HSD for *P. lapponica* and *P. sodalis* and one-way ANOVA for *Pardosa moesta*. No data are available for *P. moesta* at Tombstone.

Species	Site	n	Prosoma	SE	Mass	SE	Fecundity	SE	Sac Mass	SE	RRE	SE
P lapponica	Tombstone	184	2.174a	0.0075	0.022a	0.0002	36.72a	0.66840	0.014a	0.0003	1.7802a	0.1595
P lapponica	Ogilvie	89	2.327b	0.0125	0.027b	0.0004	47.03b	1.32822	0.019b	0.0005	1.5510a	0.0482
P lapponica	Richardson	178	2.304b	0.0088	0.027b	0.0003	44.48b	0.86222	0.017c	0.0004	1.7653b	0.0518
P sodalis	Tombstone	51	2.531a	0.0151	0.033a	0.0006	42.65a	1.80127	0.018a	0.0007	2.0118a	0.1406
P sodalis	Ogilvie	16	2.624b	0.0282	0.035ab	0.0011	48.06ab	3.16948	0.021ab	0.0014	1.8342a	0.1738
P sodalis	Richardson	109	2.637b	0.0140	0.037b	0.0006	48.50b	1.37916	0.021b	0.0006	1.9582a	0.0695
P moesta	Ogilvie	78	1.914a	0.0131	0.014a	0.0003	28.51a	0.85387	0.011a	0.0003	0.6663a	0.0121
P moesta	Richardson	39	1.912a	0.0171	0.014a	0.0005	24.49a	1.11660	0.009a	0.0005	0.6048b	0.0197

Table 4.3 – Mean densities of three wolf spider species collected from the Yukon Territory, Canada. Data represent mean density per meter squared ± standard error.

Species	Tombstone	Ogilvie	Richardson
P. moesta	NA	0.122 ± 0.06	0.016 ± 0.022
P. lapponica	0.447 ± 0.095	0.461 ± 0.122	0.28 ± 0.101
P. sodalis	0.1 ± 0.048	0.017 ± 0.024	0.112 ± 0.067

4.9. Figure captions

Figure 4.1– a) The valley of the Richardson Mountain Range: illustrating the tundra landscape where the spiders were collected, this transitioned to rock at higher elevations (shown in background) b) female *Pardosa lapponica* with egg sac c) female *Pardosa sodalis* with egg sac (Photo credit: WO Buddle) d) *Gelis* sp. e) *Gelis* sp.

Figure 4.2 – Results of fecundity regressed on body size for all three species collected at each of the three sites. ns – not significant, *** - p-value < 0.001

Figure 4.3 – Results of relative reproductive effort regressed on female body condition for each spider species from each site sampled. ns – not significant, * - p-value < 0.05, ** - p-value < 0.01, *** - p-value < 0.001

Figure 4.4 – Regression results for detection of a tradeoff between the residuals of egg size and residuals of egg number. ns – not significant, ** - p-value < 0.01, *** - p-value < 0.001

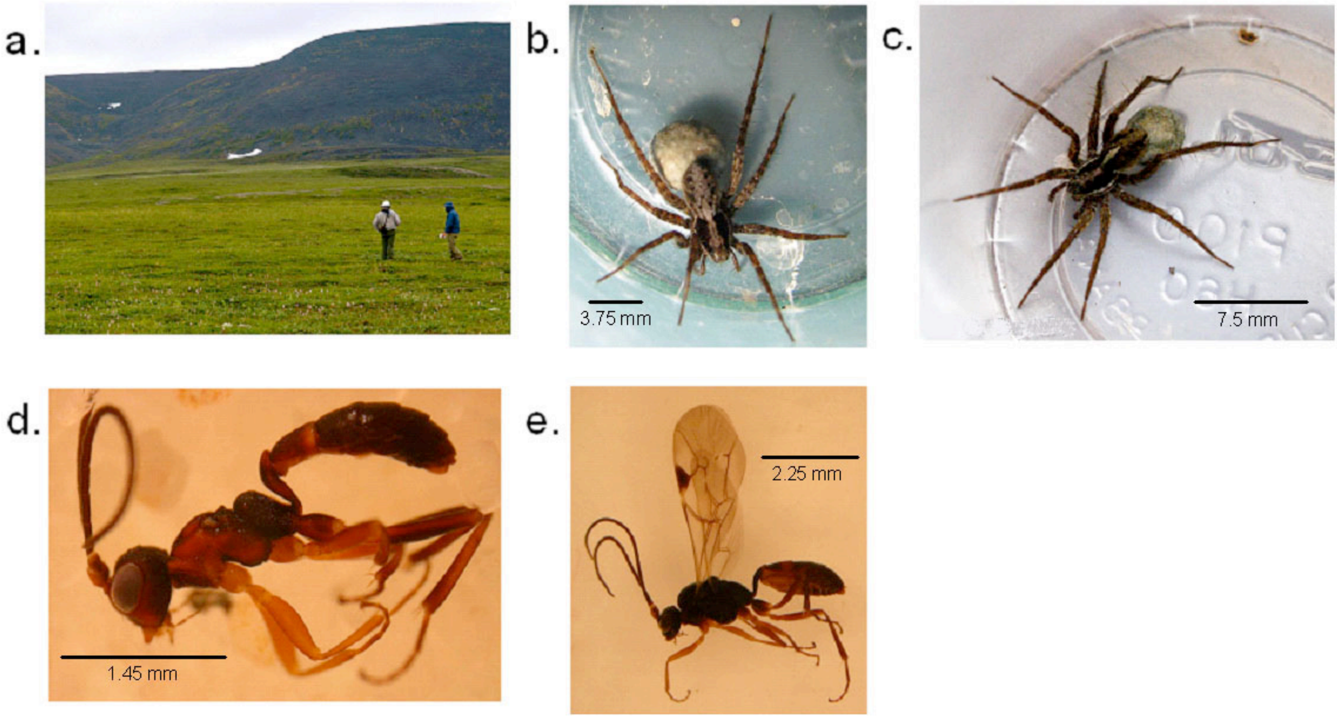

Figure 4.1

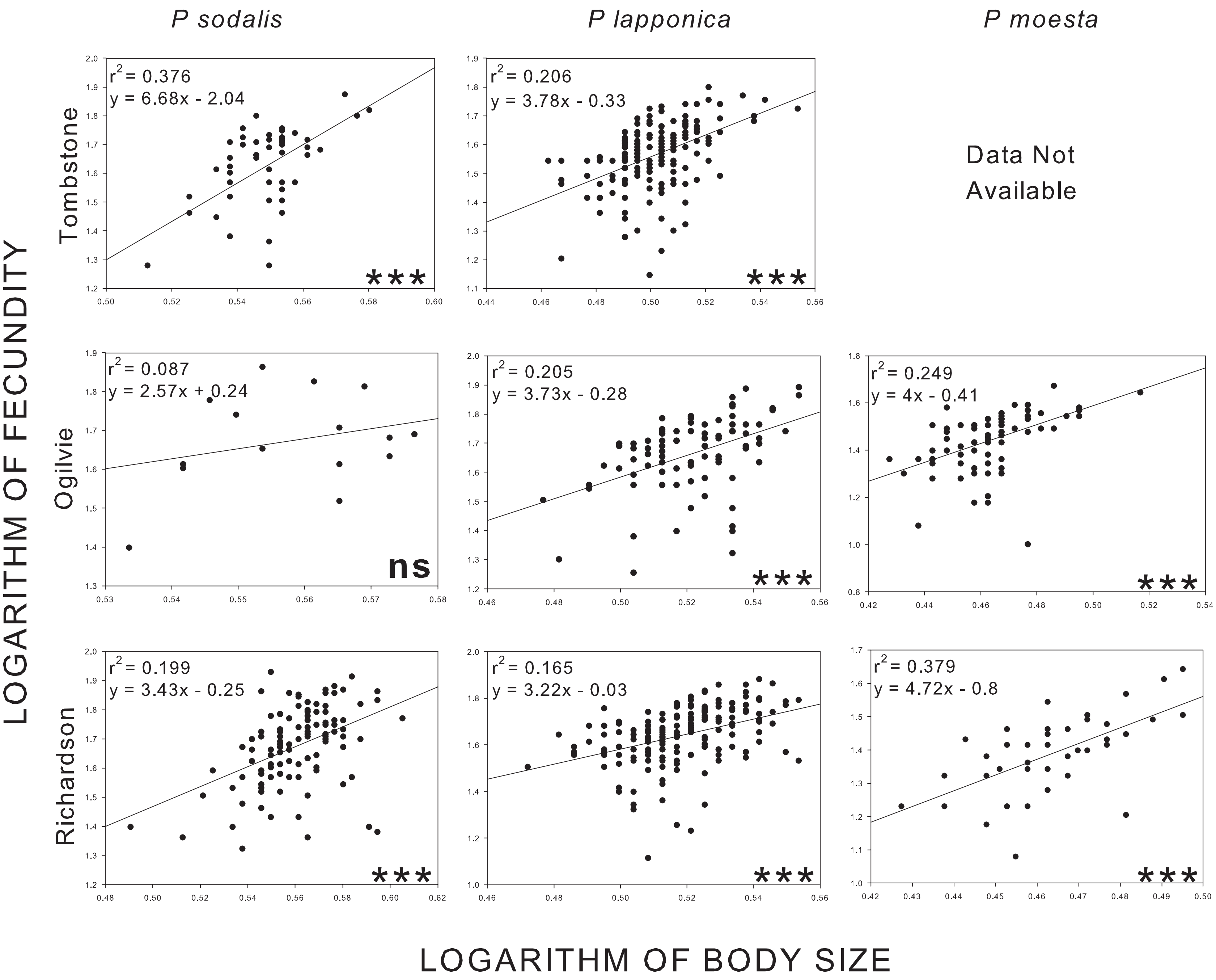
P sodalis
P lapponica
P moesta
LOGARITHM OF FECUNDITY
LOGARITHM OF BODY SIZE
Tombstone
Ogilvie
Richardson
r² = 0.376
y = 6.68x - 2.04
***
2.0 1.9 1.8 1.7 1.6 1.5 1.4 1.3 1.2
0.50 0.52 0.54 0.56 0.58 0.60
r² = 0.206
y = 3.78x - 0.33
***
1.9 1.8 1.7 1.6 1.5 1.4 1.3 1.2 1.1
0.44 0.46 0.48 0.50 0.52 0.54 0.56
Data Not Available
r² = 0.087
y = 2.57x + 0.24
ns
1.9 1.8 1.7 1.6 1.5 1.4 1.3
0.53 0.54 0.55 0.56 0.57 0.58
r² = 0.205
y = 3.73x - 0.28
***
2.0 1.9 1.8 1.7 1.6 1.5 1.4 1.3 1.2
0.46 0.48 0.50 0.52 0.54 0.56
r² = 0.249
y = 4x - 0.41
***
1.8 1.6 1.4 1.2 1.0 0.8
0.42 0.44 0.46 0.48 0.50 0.52 0.54
r² = 0.199
y = 3.43x - 0.25
***
2.0 1.9 1.8 1.7 1.6 1.5 1.4 1.3 1.2
0.48 0.50 0.52 0.54 0.56 0.58 0.60 0.62
r² = 0.165
y = 3.22x - 0.03
***
2.0 1.8 1.6 1.4 1.2 1.0
0.46 0.48 0.50 0.52 0.54 0.56
r² = 0.379
y = 4.72x - 0.8
***
1.7 1.6 1.5 1.4 1.3 1.2 1.1 1.0
0.42 0.43 0.44 0.45 0.46 0.47 0.48 0.49 0.50

Figure 4.2

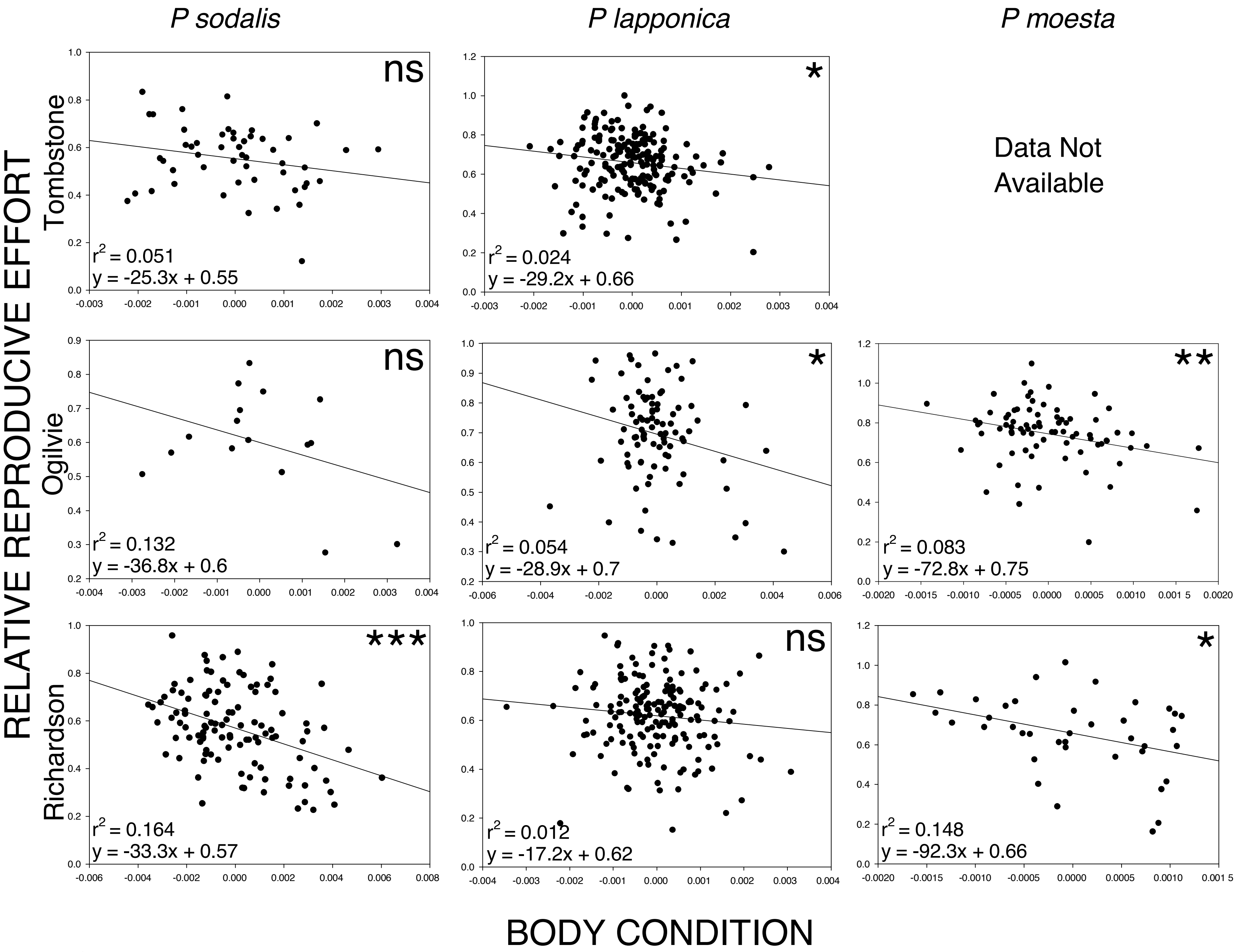
P sodalis
P lapponica
P moesta
RELATIVE REPRODUCIVE EFFORT
Tombstone
Ogilvie
Richardson
BODY CONDITION
ns
r² = 0.051
y = -25.3x + 0.55
*
r² = 0.024
y = -29.2x + 0.66
Data Not Available
ns
r² = 0.132
y = -36.8x + 0.6
*
r² = 0.054
y = -28.9x + 0.7
**
r² = 0.083
y = -72.8x + 0.75
***
r² = 0.164
y = -33.3x + 0.57
ns
r² = 0.012
y = -17.2x + 0.62
*
r² = 0.148
y = -92.3x + 0.66

Figure 4.3

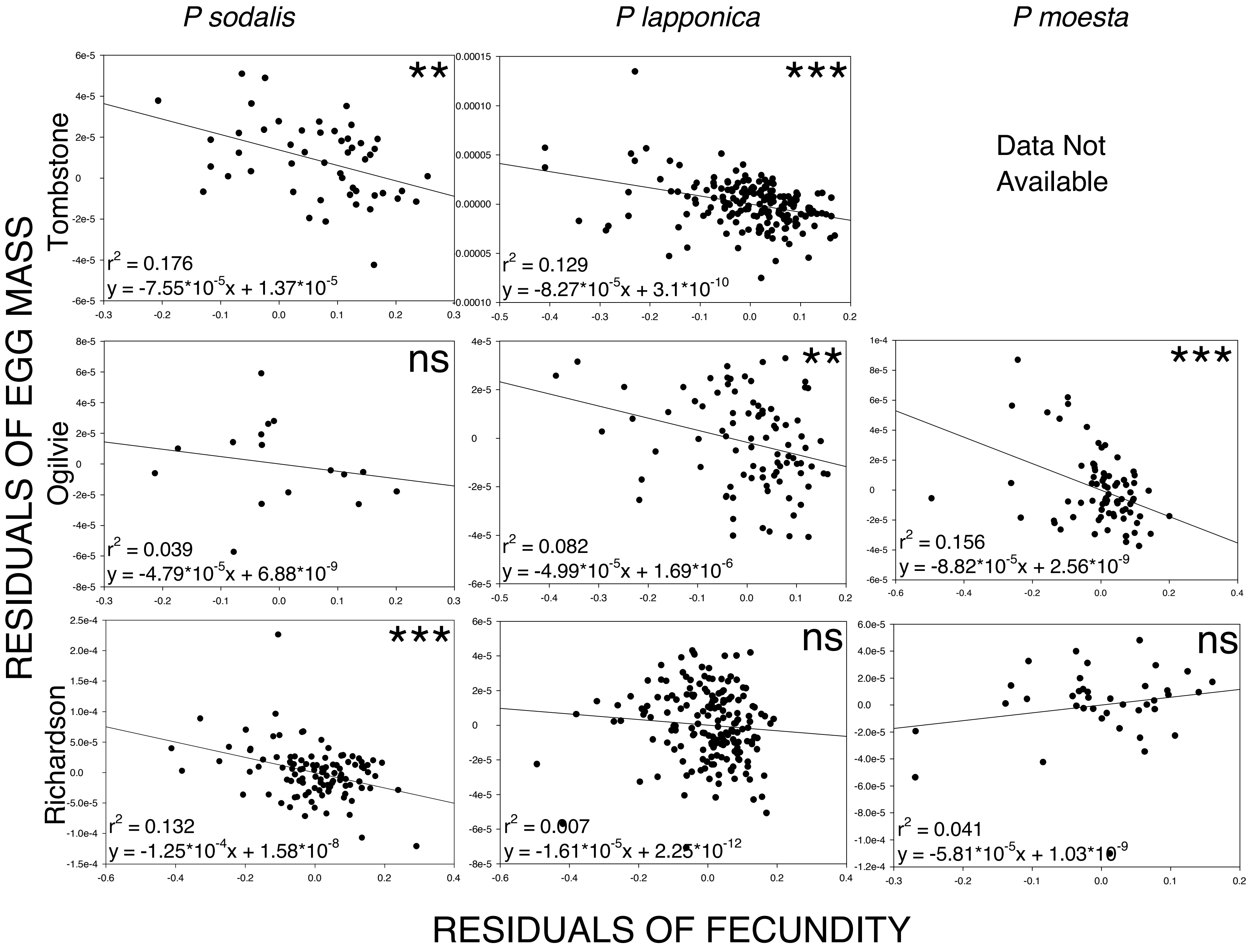
P sodalis
P lapponica
P moesta
RESIDUALS OF EGG MASS
RESIDUALS OF FECUNDITY
Tombstone
Ogilvie
Richardson
**
***
Data Not Available
r2 = 0.176
y = -7.55*10-5x + 1.37*10-5
r2 = 0.129
y = -8.27*10-5x + 3.1*10-10
ns
r2 = 0.039
y = -4.79*10-5x + 6.88*10-9
**
r2 = 0.082
y = -4.99*10-5x + 1.69*10-6
***
r2 = 0.156
y = -8.82*10-5x + 2.56*10-9
***
r2 = 0.132
y = -1.25*10-4x + 1.58*10-8
ns
r2 = 0.007
y = -1.61*10-5x + 2.25*10-12
ns
r2 = 0.041
y = -5.81*10-5x + 1.03*10-9

Figure 4.4

CHAPTER FIVE

Chapter 4 showed significant variation in life history traits in three species of wolf spiders, collected at three sites in the Yukon Territory. Chapter five is a natural extension of this work, and focuses on testing the effects of elevation on fecundity and body size. Elevation can be viewed as a natural gradient in resource availability and therefore serves well as a transect across which to examine changes in life history traits. I also test the prediction that patterns of body size differ between males and females in response to changes in elevation.

Fecundity and sexual size dimorphism of Arctic wolf spiders (Araneae: Lycosidae) along an elevational gradient

5.1. Abstract

The difference in body size between the sexes (sexual size dimorphism) varies among populations and among species. Because males and females are subject to different selection pressures they may be differentially affected by changes in environmental factors along spatial gradients. I tested whether variation in elevation affected body size and fecundity of three Arctic wolf spider species and whether male and female body size differed in response to the cline. My data show that female *Pardosa lapponica* and *Pardosa uintana* were four percent and five percent larger, respectively, than males. Males and females of *Alopecosa aculeata*, however, differed by less than one percent. I found a significant sex-elevation interaction for *P. lapponica*: females responded negatively to elevation compared to males. Males and females of *P. uintana* decreased significantly in size with elevation at a similar rate. *Alopecosa aculeata* males showed a significant positive response in body size to the gradient while females did not. *P. lapponica* females but not *P. uintana* females showed significant reduction in fecundity in response to elevation. These results may be due to species- and sex-specific responses to changes in resource availability or environmental factors along the elevational gradient and this could be related to alterations in selection (i.e., fecundity, sexual) for specific traits along the gradient.

5.2. Introduction

Arctic terrestrial arthropods are predicted to be affected significantly and rapidly by global climate changes (Callaghan et al. 2004a) and whether these changes occur *in situ* or due to shifts in range boundaries (Parmesan 2006), life history traits are thought to be important targets (e.g., Høye et al. 2009). Quantiative ecological data is required is required to make meaningful predictions about how climate change will affect Arctic arthropods (Høye et al. 2009); this is especially important given the rate at which climate change is occurring in northern regions (Hansen et al. 2006).

Changes in life history characteristics in response to recent climate change have been studied in some Arctic species (Meltofte et al. 2007, Høye et al. 2009). In these studies, traits such as phenology and body size have been shown to significantly vary in relation to the length of growing season in the Arctic (Meltofte et al. 2007, Høye et al. 2009). One primary concern in this context is phenological mismatch (Miller-Rushing et al. 2010) and alterations in other life history characteristics in response to climate change in the Arctic (Høye et al. 2009). For example, Miller-Rushing et al. (2010) suggest that changes in phenological cues (e.g., temperature, photoperiod) could disrupt the synchrony between a given species and the environment in which it lives and this could affect its population dynamics.

Strong environmental and spatial gradients represent model systems for studying variation in life history traits. Since many environmental factors vary in space they may reflect temporal changes and display the potential range of life history adaptation possible in a given species. Spatial gradients are often considered gradients in resource availability reflecting the harshness of local climate with increasing elevation (Hodkinson 2005).

Changes across elevation have yielded significant changes in life history characteristics of terrestrial arthropods (e.g., body size, fecundity, phenology) (Gutiérrez and Menéndez 1998, Karl et al. 2008, and reviewed in Hodkinson 2005). These studies have yielded mixed results with examples of positive and negative responses to such clines (Chown and Klok 2003, reviewed in Hodkinson 2005, Stillwell et al. 2007). Changes in body size associated with these clines are generally associated with developmental timing or local climate (Mousseau and Roff 1989, Chown and Klok 2003, Stillwell et al. 2007). Since the reproductive capacity of female arthropods is linked to body size and ultimately resource availability (Fox and Czesak 2000) one would expect changes along a gradient to be reflected in fecundity. Such geographical variation in body size has also been found to vary between the sexes (Stillwell et al. 2007, Høye and Hammel 2010).

Sexual size dimorphism (SSD) is the difference in mean body size between males and females of the same species, with males generally being relatively larger in the endotherms and females being relatively larger in ectotherms (Fairbairn 2007). Characters such as body size differences between the sexes and development time may have implications for life history evolution and fitness (Roff 2002). Differences in SSD have been detected among populations within species and the direction and strength of SSD and can be influenced by geographic variation (Blanckenhorn and Demont 2004, Schäuble 2004, Stillwell et al. 2007) in response to changes in biotic or abiotic factors (Foellmer and Moya-Laraño 2007, Stillwell et al. 2010). This can be due to differential responses driven by genetics or phenotypic plasticity of the sexes to various environmental variables (Stillwell and Fox 2007, Stillwell and Fox 2009). Variation in SSD over geographic clines has been detected in some groups, primarily at temperate and tropical latitudes (Schäuble 2004, Blanckenhorn et al 2006, but see Høye and Hammel

2010). Recently, Høye and Hammel (2010) showed that while female wolf spiders show a significant negative response in body size to increases in elevation, males generally do not change in Arctic Greenland. My research objectives were to test within species body size responses to elevation and especially whether there were significant body size differences between the sexes across elevation in Arctic wolf spiders. I also tested whether fecundity of female spiders changed with elevation independent of body size variation.

5.3. Materials and methods

From 14 June to 26 July 2006 ground-dwelling spiders were collected from three mountain ranges located in the Yukon Territory, Canada: the Tombstone Mountains (64.309N, 138.114W), Ogilvie Mountains (65.158N, 138.148W) and Richardson Mountains (66.725N, 136.114W). I sampled three mountains in each of the mountain ranges. The elevations in the Richardson Mountains ranged from 760 to 1060 meters, the Ogilvie Mountains ranged from 660 to 960 meters and the Tombstone Mountains ranged from 1060 to 1460 meters. Spiders were collected pitfall traps placed every 100 meters in elevation and all data were pooled by elevation. Additional details about our pitfall trapping methods and site descriptions can be found in Bowden and Buddle (2010*a*).

I selected three wolf spider species as model taxa for addressing my research objectives. These species were frequently collected at most of the study sites: *Pardosa lapponica* (Thorell), *Pardosa uintana* Gertsch and *Alopecosa aculeata* (Clerck). In general, past research has shown that these spiders are among the most dominant and broadly distributed species in the region (Bowden and Buddle 2010*a*, 2010*b*). They are also found across a broad range of elevations in high abundance making them good candidates with which to statistically test intraspecific life history changes across a spatial gradient.

I used carapace width as a measure of body size as this is the most common and accurate measure of size for spiders (Foellmer and Moya-Laraño 2007). All males and females were measured and the females' egg sacs dissected and contents counted using a Nikon® SMZ1000 stereoscopic microscope fitted with an ocular micrometer.

I tested for significant variation in male and female body size across elevation both within and among mountain ranges. I used analysis of covariance (ANCOVA) with elevation as a continuous variable and sex as a factor to test for main effects of sex and elevation and sex differences over elevation for body size. I used linear models with body size as a covariate to test for variation in fecundity with elevation in *P. lapponica* and *P. uintana* independent of body size. I was unable to test for changes in fecundity with elevation for *A. aculeata* due to low sample size (see Appendix 1 for summary of fecundity data). All analyses were conducted using the R environment (R Development Core Team 2010) for windows with the base package.

5.4. Results

I collected a regional dataset of 642 *P. lapponica*, 233 *P. uintana*, and 175 *A. aculeata* for analyses of body size and fecundity across elevation. Due to low abundances at some sites I used *P. lapponica* collected from the Tombstone and Richardson ranges, and *P. uintana* and *A. aculeata* collected from the Tombstone and Ogilvie mountain ranges. Females of *P. lapponica* and *P. uintana* were significantly larger than males

(Table 5.1). Males and females did not differ significantly in size for *A. aculeata*. I detected significant main effects of elevation on body size for *P. lapponica* and *P. uintana* but *A. aculeata* yielded no main effects in response to the elevational gradient. I found a significant sex-elevation interaction for *P. lapponica* but not for *P. uintana* or *A. aculeata*; the slopes for *P. uintana* males and females were similar (Table 5.2). Body size varied significantly in response to elevation for each sex within each species with the exception of *A. aculeata* females (Table 5.2). Females of *P. lapponica* decreased more strongly with increases in elevation than did males, while males of *A. aculeata* responded positively to increases in elevation. Females of *P. lapponica* were significantly larger than males at lower elevations but this trend disappeared at higher elevations (Figure 5.1). There was no significant variation within mountain range.

The females of *P. lapponica* produced fewer progeny at higher elevations independent of body size variation (Estimate = -0.014, p = 0.005). *Pardosa uintana* did not exhibit a significant relationship with elevation; however the two highest elevations at which gravid females were collected yielded the lowest number of eggs for this species (Appendix 1). Mean overall egg numbers for each species were 41.96 ± 1.01 eggs (mean ± SE) for *P. lapponica*, 40.92 ± 1.22 eggs for *P. uintana* and 94.5 ± 14.28 eggs for *A. aculeata*.

5.5. Discussion

There was significant effects of elevation on body size for two of the three species studied and one species (*P. lapponica*) displayed a significant sex-elevation interaction. *P. lapponica* and *P. uintana* also showed significant overall differences between the sexes whereas *A. aculeata* did not. I found a general decrease in fecundity with increasing elevation, independent of body size changes. Although many hypotheses have been proposed to explain the causes of SSD in spiders (Foellmer and Moya-Laraño 2007), in general, male biased SSD appears to arise from sexual selection (Stillwell et al. 2010) while fecundity selection supports larger females (Prenter 1999, Stillwell et al. 2010). However, SSD and selection for it can also be mediated by sex-specific differences in growth in response to external factors (Uhl et al. 2004, Fernández-Montreveta and Moya-Laraño 2007, Stillwell and Davidowitz 2010, reviewed in Stillwell et al. 2010). Stillwell et al. (2010) show that physiological difference between the sexes in plasticity of growth rate and development time can be ultimately responsible for differences in adult body size.

In this study, I found variation among the spider species examined and in the case of *Pardosa lapponica*, the sexes and populations across the elevational gradient. Høye and Hammel (2010) similarily found that males of two wolf spider species in Greenland did not change in body size in response to changes in elevation but females declined significantly in size. This is in agreement with the hypothesis that females are more plastic than males in response to environmental variation (Teder and Tammaru 2005; reviewed in Stillwell et al. 2010).

Numerous hypotheses exist for the existence of SSD and many in support of sexual selection keeping males small. Many of these hypotheses suggest that an advantage is conferred to males who mature earlier. For example, the protandry hypothesis posits thata male may sire more offspring if he is the first to mate with a given female. Also, in situations where male densities are low, inference competition may not select for large males. Furthermore, scramble competition may select for a morphology that begets finding females more efficiently and earlier than other males (Foellmer and Moya-Laraño 2007). Changes in density of these species across the elevational gradient (Bowden and Buddle 2010*a*) could give way to density-dependent selection on body size patterns.

The sexual cannibalism hypothesis suggests that sexual cannibalism is common in many spider species. This yields selection for smaller males that are more agile and thus more able to avoid being eaten by females prior to copulation (Foellmer and Moya-Laraño 2007). Since sexual cannibalism increases with body size in spiders (Wilder and Rypstra 2008) there could be consequences for future climate-induced body size alterations that yield changes in the local dynamics of populations and communities (De Roos et al. 2003), as well as species range shifts (Roy et al. 2001). There is, however, evidence that diet quality and/or quantity or other environmental factors (e.g., temperature) can produce sex-specific and species-specific differences in body size plasticity (Stillwell and Davidowitz 2010, Stillwell et al. 2010).The degree to which genetics or phenotypic plasticity regulates patterns in SSD is poorly understood and the studies are yet inconclusive (Stillwell and Fox 2009, Stillwell et al. 2010). This helps provide some insight into our finding that males and females of *P. uintana* exhibited the same response in body size to changes in elevation. Due to the low sample sizes of *A. aculeata* females it is difficult to make confident inferences about size changes and patterns of SSD in this species, but this is one of the only species that displays significant increases in abundance with elevation in the region (Bowden and Buddle 2010*a*). One explanation for the differences in SSD between the genera is that phylogenetic differences among taxa influence the expression of SSD (Prenter et al. 1999).

Arthropods are predicted to display a decline in fecundity in response to increases in elevation (Hodkinson 2005). This is not independent of reductions in body size which are highly related to fecundity in female spiders (Simpson 1993, Buddle 2000, and see Chapter 4). I found significant effects of elevation on fecundity for *P. lapponica* independent of body size. *Pardosa lapponica* may have to invest more in maintenance during adulthood at higher elevations where available resources decline. I did not find a significant relation between elevation and fecundity for *P. uintana* but at the highest two elevations they exhibited the lowest fecundity. It is possible that these females possess a higher threshold for resource limitation; hence they only display a decrease in fecundity at more extreme elevations. The more eggs that a given female produces, independent of body size, is often inversely related to the size of the individual offspring produced in Arctic wolf spiders (Simpson 1993, Chapter 4); so lower egg production at higher elevations could be explained by the production of larger offspring at higher elevations where resources are limiting (Roff 2002).

Future climate changes in the Arctic could have profound effects on life history adaptation in its fauna (Høye et al. 2009). Due to these forecasted changes to the Arctic environment (Callaghan et al. 2004a, Hansen et al. 2006) and the influence these changes will have on its fauna (e.g., Høye et al. 2009), it is important to obtain data on current life history traits in order to determine the effect size and the degree to which characters like SSD are widespread in the north.

5.6. Acknowledgements

I would like to thank Dr. Christopher M Buddle for his general supervision of this research, and comments on early drafts of the manuscript. I would also like to thank the Tetlit Gwitch'n, Nacho Nyak Dun, Vuntut Gwitch'n, Tr'ondëk Hwëch'in Han Nation and the Yukon Territorial Government. The authors would also like to thank Dan Brown for help with collection of specimens in the field. Financial support was provided by the Northern Scientific Training Program, the National Science and Engineering Research Council of Canada, and McGill University.

5.7. Literature Cited

Blanckenhorn, W. U. and Demont, M. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? Integrative and Comparative Biology 44: 413-424.

Blanckenhorn, W. U., Stillwell, R. C., Young, K. A., Fox, C. W. and Ashton, K. G. 2006. When Rensch meets Bergmann: Does sexual size dimorphism change systematically with latitude? Evolution 60: 2004-2011.

Bowden, J. J. and Buddle, C. M. 2010*a*. Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. Arctic 63: 26-272.

Bowden, J. J. and Buddle, C. M. 2010*b*. Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada. Écoscience 17: 287-297.

Buddle, C. M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28: 319-328.

Callaghan, T. V., Bjorn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G. and Henttonen, H. 2004. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. Ambio 33: 436-447.

Chown, S. L. and Klok, C. J. 2003. Altitudinal body size clines: latitudinal effects associated with changing seasonality. Ecography 26: 445-455.

De Roos, A. M., Persson, L. and McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6: 473-487.

Fairbairn, D. J. 2007. Introduction: the enigma of sexual size dimorphism. In: D. J. Fairbairn, et al. (eds), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, p. 266.

Foellmer, M. W. and Moya-Laraño, J. 2007. Sexual size dimorphism in spiders: patterns and processes. In: D. J. Fairbairn, et al. (eds), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, p. 266.

Fox, C. W. and M. E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45:341-369.

Gutierrez, D. and Menendez, R. 1998. Phenology of butterflies along an altitudinal gradient in northern Spain. Journal of Zoology 244: 249-264.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W. and Medina-Elizade, M. 2006. Global temperature change. Proceedings of the National Academy of Sciences of the United States of America 103: 14288-14293.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80: 489-513.

Høye, T. T., Hammel, J. U., Fuchs, T. and Toft, S. 2009. Climate change and sexual size dimorphism in an Arctic spider. Biology Letters 5: 542-544.

Høye, T. T. and Hammel, J. U. 2010. Climate change and altitudinal variation in sexual size dimorphism of arctic wolf spiders. Climate Research 41: 259-265.

Karl, I., Janowitz, S. A. and Fischer, K. 2008. Altitudinal life-history variation and thermal adaptation in the copper butterfly *Lycaena tityrus*. Oikos 117: 778-788.

Meltofte, H., Hoye, T. T., Schmidt, N. M. and Forchhammer, M. C. 2007. Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. Polar Biology 30: 601-606.

Miller-Rushing, A. J., Hoye, T. T., Inouye, D. W. and Post, E. 2010. The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B-Biological Sciences 365: 3177-3186.

Mousseau, T. A. and Roff, D. A. 1989. Adaptation to seasonality in a cricket: Patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. Evolution 43: 1483-1496.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37: 637-669.

Prenter, J., Elwood, R. W. and Montgomery, W. I. 1999. Sexual size dimorphism and reproductive investment by female spiders: A comparative analysis. Evolution 53: 1987-1994.

R Core Development Team. 2010. R: a language and environment for statistical computing. In: R Foundation for Statistical Computing.

Roff, D. A. 2002. Life History Evolution. Sinauer Associates, Inc.

Roy, K., Jablonski, D. and Valentine, J. W. 2001. Climate change, species range limits and body size in marine bivalves. Ecology Letters 4: 366-370.

Schäuble, C. S. 2004. Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L-peronii*. Biological Journal of the Linnean Society 82: 39-56.

Simpson, M. R. 1993. Reproduction in two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. Canadian Journal of Zoology 71: 451-457.

Stillwell, R. C. and Fox, C. W. 2007. Environmental effects on sexual size dimorphism of a seed-feeding beetle. Oecologia 153: 273-280.

Stillwell, R. C., Morse, G. E. and Fox, C. W. 2007. Geographic variation in body size and sexual size dimorphism of a seed-feeding beetle. American Naturalist 170: 358-369.

Stillwell, R. C. and Fox, C. W. 2009. Geographic variation in body size, sexual size dimorphism and fitness components of a seed beetle: local adaptation versus phenotypic plasticity. Oikos 118: 703-712.

Stillwell, R. C., Blanckenhorn, W. U., Teder, T., Davidowitz, G. and Fox, C. W. 2010. Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: From physiology to evolution. Annual Review of Entomology 55: 227-245.

Stillwell, R. C. and Davidowitz, G. 2010. A developmental perspective on the evolution of sexual size dimorphism of a moth. Proceedings of the Royal Society B-Biological Sciences 277: 2069-2074.

Teder, T. and Tammaru, T. 2005. Sexual size dimorphism within species increases with body size in insects. Oikos 108: 321-334.

Uhl, G., Schmitt, S., Schafer, M. A. and Blanckenhorn, W. 2004. Food and sex-specific growth strategies in a spider. Evolutionary Ecology Research 6: 523-540.

Wilder, S. M. and Rypstra, A. L. 2008. Sexual size dimorphism predicts the frequency of sexual cannibalism within and among species of spiders. American Naturalist 172: 431-440.

5.8. Tables and captions

Table 5.1 – Summary statistics of linear models showing the effects of sex elevation on body size (measured as carpace width) for each of the three wolf spider species in the Yukon Territory, Canada. ns – not significant, * - p-value < 0.05, *** - p-value < 0.001

		Intercept		Sex		Elevation		Sex:Elevation		Model			
Species	N	Estimate	p	Estimate	p	Estimate	P	Estimate	p	df	F-statistic	p	R^2_{Adj}
P. lapponica	642	2.488	***	-0.2965	***	-0.00026	***	0.000188	***	3,638	43.85	***	0.167
P. uintana	233	2.503	***	-0.1733	***	-0.0003	*	6.83E-05	ns	3,229	39.23	***	0.331
A. aculeata	175	3.216	***	0.2789	ns	0.000222	ns	0.0002	ns	3,171	11.76	***	0.157

Table 5.2 – Summary statistics of simple linear regressions of body size (measured as carapace width) on elevation for each sex of each wolf spider species from the Yukon Territory, Canada. ns – not significant, ** - p-value < 0.01, *** - p-value < 0.001

	b		F-statistic		Df		p		r^2_{Adj}	
Species	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
P. lapponica	-7.45E-05	-2.63E-04	10.07	24.25	1,434	1,204	**	***	0.02	0.102
P. uintana	-2.34E-04	-3.02E-04	32.27	27.14	1,116	1,113	***	***	0.211	0.187
A. aculeata	4.22E-04	2.00E-04	37.87	1.36	1,134	1,37	***	ns	0.215	0.01

5.9. Figure captions

Figure 5.1 – Variation in body size in response to elevation for male (open dots) and female (closed dots) wolf spiders from the Yukon Territory, Canada. Mean body size (carapace width) and 95% confidence intervals are shown for each sex of each species across the elevational gradient. Regression lines are shown for all significant relationships; males are shown by dotted lines and females by solid lines.

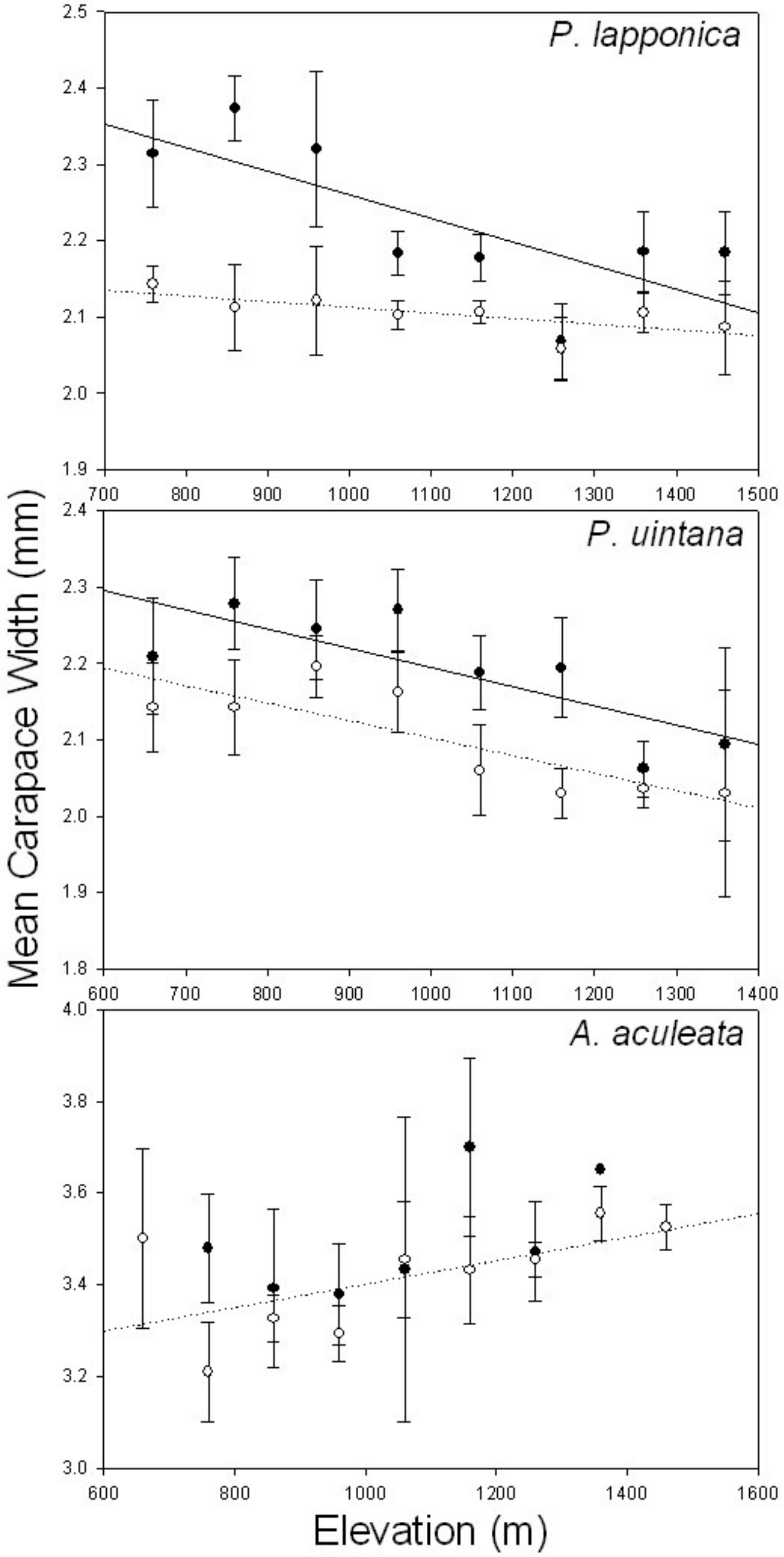
P. lapponica
P. uintana
A. aculeata
Mean Carapace Width (mm)
Elevation (m)
2.5
2.4
2.3
2.2
2.1
2.0
1.9
700
800
900
1000
1100
1200
1300
1400
1500
2.4
2.3
2.2
2.1
2.0
1.9
1.8
600
700
800
900
1000
1100
1200
1300
1400
4.0
3.8
3.6
3.4
3.2
3.0
600
800
1000
1200
1400
1600

Figure 5.1

Appendix 5.10.

Appendix 5.1 – Summary data of spiders collected for analysis of variation in sexual size dimorphism and fecundity across elevation.

* - indicates data not available/not applicable.

Species	Sex	Elevation m	Mountain Range	Mean Size mm (Range)	Mean Fecundity (Range)	Total Individuals	Gravid Females
P. lapponica	M	660	R	*	*	0	*
P. lapponica	F	660	R	*	*	0	0
P. uintana	M	660	O	2.14 (1.93-2.29)	*	16	*
P. uintana	F	660	O	2.21 (2.06-2.29)	46.75 (38-65)	9	8
A. aculeata	M	660	O	3.40 (3.20-3.50)	*	3	*
A. aculeata	F	660	O	*	*	0	0
P. lapponica	M	760	R	2.14 (1.90-2.35)	*	73	*
P. lapponica	F	760	R	2.31 (1.90-2.55)	54.50 (38-75)	22	10
P. uintana	M	760	O	2.14 (1.97-2.38)	*	14	*
P. uintana	F	760	O	2.28 (2.00-2.51)	43.67 (25-57)	17	9
A. aculeata	M	760	O	3.21 (3.10-3.40)	*	6	*
A. aculeata	F	760	O	3.48 (3.25-3.60)	74.67 (41-97)	5	3
P. lapponica	M	860	R	2.11 (1.97-2.19)	*	7	*
P. lapponica	F	860	R	2.37 (2.35-2.42)	45.33 (29-65)	3	3
P. uintana	M	860	O	2.20 (2.09-2.32)	*	12	*
P. uintana	F	860	O	2.24 (1.97-2.42)	41 (30-63)	15	12
A. aculeata	M	860	O	3.33 (3.15-3.45)	*	10	*
A. aculeata	F	860	O	3.39 (3-3.65)	90	7	1

P. lapponica	M	960	R	2.12 (2.06-2.29)	*	6	*
P. lapponica	F	960	R	2.32 (2.03-2.51)	46 (25-61)	8	7
P. uintana	M	960	O	2.16 (2.00-2.26)	*	10	*
P. uintana	F	960	O	2.27 (2.03-2.48)	42.64 (19-61)	22	14
A. aculeata	M	960	O	3.29 (3.05-3.75)	*	24	*
A. aculeata	F	960	O	3.38 (3.00-3.85)	126.5 (103-150)	14	2
P. lapponica	M	1060	T	2.10 (1.47-2.42)	*	98	*
P. lapponica	F	1060	T	2.18 (1.93-2.58)	40.53 (22-60)	69	36
P. uintana	M	1060	T	2.06 (1.87-2.26)	*	15	*
P. uintana	F	1060	T	2.19 (2.03-2.42)	43 (29-56)	19	13
A. aculeata	M	1060	T	3.46 (3.05-3.75)	*	10	*
A. aculeata	F	1060	T	3.43 (3.10-3.65)	*	3	0
P. lapponica	M	1160	T	2.11 (1.90-2.32)	*	149	*
P. lapponica	F	1160	T	2.18 (2.00-2.51)	42.83 (17-70)	53	42
P. uintana	M	1160	T	2.03 (1.93-2.22)	*	21	*
P. uintana	F	1160	T	2.19 (2.03-2.38)	43.1 (32-51)	11	10
A. aculeata	M	1160	T	3.43 (3.00-3.65)	*	13	*
A. aculeata	F	1160	T	3.70 (3.60-3.80)	*	2	0
P. lapponica	M	1260	T	2.06 (1.90-2.29)	*	23	*
P. lapponica	F	1260	T	2.07 (1.90-2.26)	34.2 (19-51)	17	10
P. uintana	M	1260	T	2.04 (1.93-2.22)	*	25	*
P. uintana	F	1260	T	2.06 (1.93-2.22)	28.1 (15-47)	19	10
A. aculeata	M	1260	T	3.45 (3.15-3.65)	*	50	*
A. aculeata	F	1260	T	3.47 (3.30-3.70)	*	7	0
P. lapponica	M	1360	T	2.11 (1.90-2.48)	*	64	*
P. lapponica	F	1360	T	2.19 (2.00-2.48)	37.69 (25-58)	29	16
P. uintana	M	1360	T	2.03 (1.93-2.29)	*	5	*

P. uintana	F	1360	T	2.09 (1.96-2.16)	24	3	1
A. aculeata	M	1360	T	3.56 (3.40-3.75)	*	18	*
A. aculeata	F	1360	T	3.65	*	1	0
P. lapponica	M	1460	T	2.09 (1.87-2.32)	*	16	*
P. lapponica	F	1460	T	2.18 (2.13-2.29)	35	5	1
P. uintana	M	1460	T	*	*	0	*
P. uintana	F	1460	T	*	*	0	0
A. aculeata	M	1460	T	3.53 (3.50-3.55)	*	2	*
A. aculeata	F	1460	T	*	*	0	0

CHAPTER SIX

Summary, Conclusions and Future Directions

6.1. Summary

Research on Arctic arthropods has historically been focused on general inventories and faunistics (Danks and Downes 1997) or adaptations to life in the relatively harsh environment (Danks 2004). Although these methods provide a wealth of descriptive data there is a need for quantitative data for future accurate comparison of changes in ecological structure or dynamics (e.g., population/community). The data in this thesis are also relevant in the context of future responses of spiders to climate change. In this thesis I present the first regional scale quantitative analyses of terrestrial arthropod assemblages in northern Canada and one of the few examinations of life history trait variation in Arctic spiders (see Simpson 1993; Høye et al. 2009 Høye and Hammel 2010).

Spiders served well as model organisms with which to evaluate hypotheses about large scale patterns of biodiversity and life history. Their abundance, richness, distribution, and biology make them good models for well replicated intra- and interspecific ecological studies across broad spatial scales, yielding the capacity for robust statistical analyses.

Chapter 2: Determinants of spider assemblage structure

The second Chapter of this thesis determined which of three complementary hypotheses best explained variation in spider assemblage structure across the boreal forest-tundra transition in the Yukon Territory, Canada. I hypothesized that vegetation and its associated structure would best explain the patterns due to past resesearch showing the importance of vegetation with many spider taxa. My results show that there are significant differences in spider composition between the boreal and tundra biomes, as well as the intermediate 'transition' sites of the northern Yukon Territory. Although overall ground-dwelling spider species richness does not differ significantly across the transition zone, abundance was highest in the tundra sites. We deduced that there were differences in the assemblage structure of spiders in the region, primarily due to spatially structured habitat changes. This conclusion is probably not independent of historical effects (e.g., glaciation) on the contemporary assemblages. This study was the first standardized large-scale collection of ground-dwelling arthropods in the region, yielding many new records (to Yukon Territory and North America) and possibly new species. I also show the habitat fidelity of many species, through the appendix and RDA biplot, of the species in the region.

Chapter 3: Spider assemblages across elevational gradients

In Chapter three I tested the effects of elevation and latitude on spider assemblage structure using multiple elevational transects as replicates. I was also interested in species-level and family-level responses to elevation in the region. I hypothesized that there would be significant differences among elevation and latitude in species composition, richness and abundance (measured as activity density) and predicted that species richness and abundance would decrease with increasing elevation and latitude. I detected significant differences in composition, richness and abundance, but there was a significant elevation-latitude interaction. There were also substantial changes in abundance within and among individual species across elevation. The proportion of families represented did not change across elevation. I concluded that within a given mountain range (latitude) individual mountains may be used as replicate transects for studies that seek to determine the structure of arthropod assemblages across elevation.

Chapter 4: Life history of Arctic wolf spiders

In Chapter four I investigated life history traits of the dominant wolf spider species in the region. I tested which morphometrics were the best predictors of fecundity and relative reproductive effort and I tested for a tradeoff between egg size and number in the female wolf spiders. I also examined the natural densities, in egg sac developmental timing and the incidence of parasitism in the study species. I predicted that body size would best explain variation in fecundity and that body condition would best explain variation in relative reproductive effort. I predicted that there would be a tradeoff between egg size and number. Overall, my predictions were supported, but the expression of a tradeoff varied among site. I found that densities of the spiders varied among site but they may be related to local incidence of parasitism. *Pardosa sodalis* Holm was the most frequently parasitized species overall with 52% and 49% of individuals being parasitized at two of the sites. *Pardosa sodalis* was also the earliest to develop into the first instar, despite being the species that reaches the largest adult size. I attribute these results to variation in the local environment, potentially related to local resource availability.

Chapter 5: Fecundity and sexual size dimorphism across elevation

Given the high variation in life history traits obtained from Chapter four I used a standardized elevational gradient to test for variation in life history traits. Using the individuals of three species collected for Chapter three I tested whether fecundity and sexual size dimorphism (SSD) varies with elevation. I found that fecundity changed significantly with elevation in *P. lapponica* (Thorell), but not in *P. uintana* Gertsch, however the lowest average number of eggs produced for *P. uintana* was at the two highest elevations. I also found that SSD differed overall between the sexes in the two Pardosa species but not in *Alopecosa aculeata* (Clerck). There was a significant sex-elevation interaction for *P. lapponica* but *P. uintana* males and females responded similarly to increases in elevation. SSD clearly varies among species with changes in environmental factors and is probably strongly influenced by phylogenetics (Prenter et al. 1999). More data across broader spatial and temporal scales would help to determine the degree to which there are differences in SSD temporally and spatially in the Arctic fauna.

6.2. Conclusions and Future Directions

My research on Arctic ground-dwelling spider assemblages in the Yukon Territory, Canada shows that the fauna is comprised of many unique species only found in restricted habitats in parts of northwestern North America and northeastern Siberia. These assemblages are structured primarily by vegetation characteristics and its associated spatial structure. This is a finding well supported in the literature about spider ecology from other environments (e.g., Uetz 1991; Rypstra et al. 1999, Jiménez-Valverde and Lobo 2007, Schaffers et al. 2008). I successfully described the spatial patterns and predictors of Arctic spider species diversity over a broad spatial scale and have illustrated numerous intraspecific patterns. I have also described numerous important life history trait relationships and related phenomena in the dominant species of the region. I have shown that the Arctic offers a unique system in which to study and evaluate hypotheses about biogeography, biodiversity and life history evolution, especially in the light of global climate change. I offer initial data on spider species diversity and life history in the region of the boreal forest-tundra transition; however, there are numerous opportunities and a need to study other patterns and processes in the Arctic fauna.

There are several areas in which future research can be directed in the context of Arctic arthropod research.

- It would be interesting to obtain a broader dataset of spider assemblages across the Arctic in order to examine longitudinal variation in composition, richness and abundance. It might be predicted that a latitudinal study of spider assemblages in the east would yield different results due to a different glacial history. However, if habitat is the most important factor in determining patterns of spider assemblages then the result should be similar to what I have concluded.
- A phylogeographic study of the species in the region would add support to the hypothesis that the patterns are due to historic adaptations to southern or northern refugia pre-glaciation.
- Physiological studies using resting metabolic rate or some direct physiological measure, for example, may help determine to what extent this mechanism has on the distribution/adaptation of individual species in the region.
- In the context of life history, direct tests of resource limitation may help explain some of the patterns and tradeoffs detected. It would also be interesting to determine the importance/degree of importance of egg sac parasitoids on/to life history evolution in Arctic wolf spiders.
- Recently, Høye et al. (2009) showed that changes in sexual size dimorphism in an Arctic wolf spider were related to long term alterations in season length; it would

be exciting and powerful to examine the degree to which this trend is widespread in the Arctic fauna.

- Finally, identifying life history traits of more species at numerous localities could help elucidate the importance of these traits and tradeoffs among them to local coexistence in the Arctic fauna.

Literature Cited

Almeida-Neto, M., Machado, G., Pinto-Da-Rocha, R., and Giaretta, A.A. 2006. Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: an alternative rescue effect to explain Rapoport's rule? Journal of Biogeography 33: 361-375.

Alsos, I. G., Engelskjøn, T., Gielly, L., Taberlet, P., and Brochmann, C. 2005. Impact of ice ages on circumpolar molecular diversity: insights from an ecological key species. Molecular Ecology 14: 2739-2753.

Andrew, N. R. and Hughes, L. 2004. Species diversity and structure of phytophagous beetle assemblages along a latitudinal gradient: predicting the potential impacts of climate change. Ecological Entomology 29: 527-542.

Andrew, N. R. and Hughes, L. 2005. Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. Austral Ecology 30: 281-297.

Balfour, R. A. and Rypstra, A. L. 1998. The influence of habitat structure on spider density in a no-till soybean agroecosystem. Journal of Arachnology 26: 221-226.

Baselga, A. 2008. Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography 31: 263-271.

Bates, D., and Maechler, M. 2009. lme4: Linear mixed-effects models using S4 classes. http://r-forge.r-project.org/projects/lme4/

Beals, M. L. 2006. Understanding community structure: a data-driven multivariate approach. Oecologia 150: 484-495.

Benton, M. J. and Uetz, G. W. 1986. Variation in life history characteristics over a clinal gradient in three populations of a communal orb-weaving spider. Oecologia 68: 395-399.

Blanckenhorn, W. U., Stillwell, R. C., Young, K. A., Fox, C. W. and Ashton, K. G. 2006. When Rensch meets Bergmann: Does sexual size dimorphism change systematically with latitude? Evolution 60: 2004-2011.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., and Sams, S. 1978. Relationships between Body Size and Some Life History Parameters. Oecologia 2: 257-272.

Bonsall, M. B., V. A. A. Jansen, and Hassell, M. P. 2004. Life history trade-offs assemble ecological guilds. Science 306:111-114.

Bonte, D., Criel, P., Van Thournout, I. and Maelfait, J. P. 2003. Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. Journal of Biogeography 30: 901-911.

Bonte, D., Baert, L., Lens, L. and Maelfait, J. P. 2004. Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. Ecography 27: 343-349.

Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principle coordinates of neighbour matrices. Ecological Modelling 153: 51-68.

Borcard, D., Legendre, P., Avois-Jacquet, C. and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826-1832.

Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045-1055.

Bowden, J. J. and Buddle, C. M. 2010a. Spider assemblages across elevational and latitudinal gradients in the Yukon Territory, Canada. Arctic. 63:261-272.

Bowden, J. J. and Buddle, C. M. 2010b. Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada. Écoscience. 17:287-297.

Brown, C. A., B. M. Sanford, and Swerdon, R. R. 2003. Clutch size and offspring size in the wolf spider *Pirata sedentarius* (Araneae, Lycosidae). Journal of Arachnology 31:285-296.

Buddle, C. M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. Journal of Arachnology 28:319-328.

Buddle, C. M. 2002. Interactions among young stages of the wolf spiders *Pardosa moesta* and *P. mackenziana* (Araneae : Lycosidae). Oikos 96: 130-136.

Buddle, C.M., and Draney, M.L. 2004. Phenology of linyphiids in an old-growth deciduous forest in central Alberta, Canada. Journal of Arachnology 32: 221-230.

Buddle, C. M., Spence, J. R. and Langor, D. W. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23: 424-436.

Buddle, C. M., Langor, D. W., Pohl, G. R. and Spence, J. R. 2006. Arthropod responses to harvesting and wildfire: Implications for emulation of natural disturbance in forest management. Biological Conservation 128: 346-357.

Buddle, C. M., Walker, S. E. and Rypstra, A. L. 2003. Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). Canadian Journal of Zoology 81: 1293-1297.

Bultman, T. L., Uetz, G. W. and Brady, A. R. 1982. A comparison of cursorial spider communities along a successional gradient. Journal of Arachnology 10: 23-33.

Callaghan, T.V., Bjorn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., et al. 2004a. Effects on the structure of arctic ecosystems in the short- and long-term perspectives. Ambio 33: 436-447.

Callaghan, T. V., Bjorn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E. and Zockler, C. 2004b. Biodiversity, distributions and adaptations of arctic species in the context of environmental change. Ambio 33: 404-417.

Cardelus, C.L., Colwell, R.K., and Watkins, J.E. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. Journal of Ecology 94: 144-156.

Cardillo, M. 2002. Body size and latitudinal gradients in regional diversity of New World birds. Global Ecology and Biogeography 11: 59-65.

Carrel, J. E. and Heathcote, R. D. 1976. Heart rate in spiders: Influence of body size and foraging energetics. Science 193: 148-150.

Case, T. J., Holt, R. D., McPeek, M. A., and Keitt, T. H. 2005. The community context of species' borders: ecological and evolutionary perspectives. Oikos 108: 28-46.

Chatzaki, M., Lymberakis, P., Markakis, G. and Mylonas, M. 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. Journal of Biogeography 32: 813-831.

Chown, S. L. and Klok, C. J. 2003. Altitudinal body size clines: latitudinal effects associated with changing seasonality. Ecography 26: 445-455.

Cobb, L. M., and Cobb, V. A. 2004. Occurence of parasitoid wasps, *Baeus* sp. and *Gelis* sp., in the egg sacs of the wolf spiders *Pardosa moesta* and *Pardosa sternalis* (Araneae, Lycosidae) in Southeastern Idaho. The Canadian Field Naturalist 118:122-123.

Colwell, R. K. 2006. EstimateS: Statistical estimation of species richness and shared species from samples, version 8. [Online] URL: http://viceroy.eeb.uconn.edu/EstimateS.

Colwell, R. K. and Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 345: 101-118.

Colwell, R. K. and Lees, D. C. 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution 15: 70-76.

Coulson, S. J., Hodkinson, I. D. and Webb, N. R. 2003. Microscale distribution patterns in high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. Ecography 26: 801-809.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E. and Turner, J. R. G. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7: 1121-1134.

Cushman, J. H., Lawton, J. H., and Manly, B. F. J. 1993. Latitudinal patterns in European ant assemblages: Variation in species richness and body size. Oecologia 95: 30-37.

Danks, H. V. 1981. Arctic Arthropods. A review of systematics and ecology with particular reference to the North American fauna. Entomological Society of Canada. Ottawa.

Danks, H. V. 1992. Arctic insects as indicators of environmental change. Arctic 45: 159-166.

Danks, H. V., Kukal, O. and Ring, R. A. 1994. Insect cold-hardiness: Insights from the Arctic. Arctic 47: 391-404.

Danks, H. V. and Downes, J. A. 1997. Insects of the Yukon. Museum of Nature, Ottawa.

Danks, H. V. 2004. Seasonal adaptations in Arctic insects. Integrative and Comparative Biology 44: 85-94.

Davis, D. H. S. 1936. A reconnaissance of the fauna of Akpatok Island, Ungava Bay. Journal of Animal Ecology 5: 319-332.

De Roos, A. M., Persson, L. and McCauley, E. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6: 473-487.

DeVito, J., Meik, J. M., Gerson, M. M. and Formanowicz, D. R. 2004. Physiological tolerances of three sympatric riparian wolf spiders (Araneae : Lycosidae) correspond with microhabitat distributions. Canadian Journal of Zoology 82: 1119-1125.

Dixon, A.F.G., Kindlmann, P., Leps, J., and Holman, J. 1987. Why there are so few species of aphids, especially in the Tropics. American Naturalist 129: 580-592.

Dondale, C., and Redner, J. 1990. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska. Canadian Government Publishing Centre, Ottawa.

Dondale, C., Redner, J. and Marusik, Y. M. 1997. Spiders (Araneae) of the Yukon. Pages 73-113 *in* H. V. Danks and J. A. Downes (eds), Insects of the Yukon. Canadian Museum of Nature, Ottawa.

Downie, I. S., Butterfield, J. E. L. and Coulson, J. C., 1995. Habitat preferences of sub-montane spiders in northern England. Ecography 18: 51-61.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345-366.

Drapela, T., Moser, D., Zaller, J. G. and Frank, T. 2008. Spider assemblages in winter oilseed rape affected by landscape and site factors. Ecography 31: 254-262.

Eason, R. R., W. B. Peck, and Whitcomb, W. H. 1967. Notes on spider parasites including a reference list. Journal of Kansas Entomological Society 40:422-434.

Edgar, W. D. 1971. Aspects of ecology and energetics of egg sac parasites of the wolf spider *Pardosa lugubris* (Walckenaer). Oecologia 7:155-163.

Enders, F. 1976. Clutch size related to hunting manner of spider species. Annals of the Entomological Society of America 69:991-998.

Environment Canada. 2011. National climate data and information archive. http://climate.weatheroffice.gc.ca

ESRI 2008, ArcGIS version 9.3: Environment systems, Research Institute Inc. Redlands, CA.

Fairbairn, D. J. 2007. Introduction: the enigma of sexual size dimorphism. In: D. J. Fairbairn, et al. (eds), Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, p. 266.

Foellmer, M. W. and Moya-Laraño, J. 2007. Sexual size dimorphism in spiders: patterns and processes. In: D. J. Fairbairn, et al. (eds), Sex, Size and Gender Roles:

Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, p. 266.

Finch, O. D., Blick, T. and Schuldt, A. 2008. Macroecological patterns of spider species richness across Europe. Biodiversity and Conservation 17: 2849-2868.

Foelix, R. F. 1996. Biology of spiders, 2nd ed. Oxford University Press, New York.

Fox, C. W., and Czesak, M. E. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45:341-369.

Gaston, K. J. and Spicer, J. I. 2004. Biodiversity: an introduction, 2nd ed. Blackwell Science, Ltd. Malden.

Gobbi, M., Fontaneto, D., and De Bernardi, F. 2006. Influence of climate changes on animal communities in space and time: the case of spider assemblages along an alpine glacier foreland. Global Change Biology 12: 1985-1992.

Gotelli, N. J. and Ellison, A. M. 2002. Biogeography at a regional scale: Determinants of ant species density in New England bogs and forests. Ecology, 83: 1604-1609.

Gutierrez, D. and Menendez, R. 1998. Phenology of butterflies along an altitudinal gradient in northern Spain. Journal of Zoology 244: 249-264.

Greenstone, M. H. 1984. Determinants of web spider species diversity: Vegetation structural diversity vs prey availability. Oecologia 62: 299-304.

Halaj, J., Ross, D. W. and Moldenke, A. R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90: 139-152.

Hansell, R. I. C., Malcolm, J. R., Welch, H., Jefferies, R. L. and Scott, P. A. 1998. Atmospheric change and biodiversity in the Arctic. Environmental Monitoring and Assessment 49: 303-325.

Hansen, J., M. Sato, R. Ruedy, K. Lo, D. W. Lea, and Medina-Elizade, M. 2006. Global temperature change. Proceedings of the National Academy of Sciences of the United States of America 103:14288-14293.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J. F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E. and Turner, J. R. G. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84: 3105-3117.

Hawkins, B. A., and Porter, E. E. 2003. Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. Global Ecology and Biogeography 12: 475-481.

Hendrickx, F., and Maelfait, J. P. 2003. Life cycle, reproductive patterns and their year-to-year variation in a field population of the wolf spider *Pirata piraticus* (Araneae, Lycosidae). Journal of Arachnology 31:331-339.

Hendrickx, F., Maelfait, J. P., Speelmans, M. and Van Straalen, N. M. 2003. Adaptive reproductive variation along a pollution gradient in a wolf spider. Oecologia 134: 189-194.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. and Jarvis, A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965-1978.

Hodkinson, I. D., Webb, N. R., Bale, J. S., Block, W., Coulson, S. J. and Strathdee, A. T. 1998. Global change and Arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. Arctic and Alpine Research. 30: 306-313.

Hodkinson, I. D., Coulson, S. J. and Webb, N. R. 2004. Invertebrate community assembly along proglacial chronosequences in the high Arctic. Journal of Animal Ecology. 73: 556-568.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80: 489-513.

Høye, T. T., and Forchhammer, M. C. 2008. Phenology of high-arctic arthropods: effects of climate on spatial, seasonal and inter-annual variation. Advances in Ecological Research 40: 299-324.

Høye, T. T., Hammel, J. U., Fuchs, T. and Toft, S. 2009. Climate change and sexual size dimorphism in an Arctic spider. Biology Letters 5:542-544.

Høye, T. T. and Hammel, J. U. 2010. Climate change and altitudinal variation in sexual size dimorphism of arctic wolf spiders. Climate Research 41: 259-265.

Hurd, L. E. and Fagan, W. F. 1992. Cursorial spiders and succession: Age or habitat structure? Oecologia 92: 215-221.

Jakob, E. M., S. D. Marshall, and Uetz, G. W. 1996. Estimating fitness: A comparison of body condition indices. Oikos 77:61-67.

Jia, G. S., Epstein, H. E. and Walker, D. A. 2006. Spatial heterogeneity of tundra vegetation response to recent temperature changes. Global Change Biology 12: 42-55.

Jimenez-Valverde, A. and Lobo, J. M. 2007. Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. Ecological Entomology 32: 113-122.

Karl, I., Janowitz, S. A. and Fischer, K. 2008. Altitudinal life-history variation and thermal adaptation in the copper butterfly *Lycaena tityrus*. Oikos 117: 778-788.

Kaufmann, R. 2001. Invertebrate succession on an alpine glacier foreland. Ecology 82: 2261-2278.

Kessler, A. 1971. Relation between egg production and food consumption in species of genus *Pardosa* (Lycosidae, Araneae) under experimental conditions of food-abundance and food-shortage. Oecologia 8:93-109.

Koponen, S. 1987. Communities of ground-living spiders in six habitats on a mountain in Québec, Canada. Holarctic Ecology 10: 278-285.

Koponen, S. 1999. Common ground-living spiders in old taiga forests of Finland. The Journal of Arachnology 27: 201-204.

Koponen, S., Vygandes, R. and Dapkus, D. 2001. Changes in structure of ground-living spider (Araneae) communities on peatbogs along a transect from Lithuania to Lapland. Norweigian Journal of Entomology 48: 167-174.

Kotwicki, L., Szymelfenig, M., De Troch, M., Urban-Malinga., and Węsławski, J.M. 2005. Latitudinal biodiversity patterns of meiofauna from sandy littoral beeches. Biodiversity and Conservation 14: 461-474.

Kouki, J., Niemelä, P., and Viitasaari, M. 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). Annales Zoologici Fennici 31: 83-88.

Kruskal, J. 1964. Nonmetric multidimensional scaling: a numerical method. . Psychometrika 29: 115-129.

Larrivée, M. and Buddle, C. M. 2009. Diversity of canopy and understorey spiders in north-temperate hardwood forests. Agricultural and Forest Entomology 11: 225-237.

Lawrence, K.L., and Wise, D.H., 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44: 33-39.

Leech, R. E. 1966. The spiders (Araneida) of Hazen Camp 81° 49’ N, 71° 18’ W. Quaestiones Entomologicae 2: 153-212.

Leech, R. E. and Ryan, J. K. 1972. Notes on Canadian Arctic spiders (Araneida), mainly from Devon Island, NWT. Canadian Entomologist. 104: 1787-1791.

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Elsevier, Amsterdam.

Legendre, P. and Gallagher, E. D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271-280.

Legendre, P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. Journal of Plant Ecology 1: 3-8.

Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P. and Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320: 1768-1771.

Lepš, J. and Šmilauer, P. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. Ecology 73: 1943-1967.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10: 3-13.

Lomolino, M. 2006. Biogeography. Sinauer Associates, Sunderland.

Lowrie, D. C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology 29: 334-351.

Lyons, S.K., and Willig, M. R. 2002. Species richness, latitude, and scale-sensitivity. Ecology 83: 47-58.

Magurran, A. 2004. Measuring biological diversity. Wiley-Blackwell, Malden.

Mani, M. S. 1968. Ecology and biogeography of high altitude insects. The Hague: Dr. W. Junk Publishers.

Marusik, Y.M., and Koponen, S. 2002. Diversity of spiders in boreal and arctic zones. Journal of Arachnology 30: 205-210.

Marusik, Y., Koponen, S., Vinokurov, N. and Nogovitsyna, S. 2001. Spiders (Araneae) from northernmost forest-tundra of northesatern Yakutia (70^{O}35'N, 134^{O}34'E) with description of three new species. Arthropoda Selecta 10: 351-370.

Marshall, S. D., and Gittleman, J. L. 1994. Clutch size in spiders: Is more better? Functional Ecology 8:118-124.

McCoy, E.D. 1990. The distribution of insects along elevational gradients. Oikos 58: 313-322.

McCune, B., and Grace, J. 2002. Analysis of ecological communities*,* Glenedan Beach, OR, MjM Software Design.

McCune, B., and Mefford, M. 1999. PC-ORD 4: Multivariate analysis of ecological data. MjM Software, Glenedan Beach, OR.

Meltofte, H., Hoye, T. T., Schmidt, N. M. and Forchhammer, M. C. 2007. Differences in food abundance cause inter-annual variation in the breeding phenology of high Arctic waders. Polar Biology 30: 601-606.

Menge, B. A. and Olson, A. M. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5: 52-57.

Messina, F. J., and Fox, C. W. 2001. Offspring size and number. Page 452 in Evolutionary Ecology: Concepts and Case Studies (C. W. Fox, D. A. Roff, and D. J. Fairbairn, Eds.). Oxford University Press, New York.

Mielke, P., and Berry, K. 2001. Permutation Methods: A distance function approach, New York, Springer-Verlag.

Miller-Rushing, A. J., Hoye, T. T., Inouye, D. W. and Post, E. 2010. The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society B-Biological Sciences 365: 3177-3186.

Moring, J. B. and Stewart, K. W. 1994. Habitat partitioning by the wolf spider (Araneae, Lycosidae) guild in streamside and riparian vegetation zones of the Conejos River. Colorado. Journal of Arachnology 22: 205-217.

Mousseau, T. A. and Roff, D. A. 1989. Adaptation to seasonality in a cricket: Patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. Evolution 43: 1483-1496.

Muff, P., Kropf, C., Frick, H., Nentwig, W. and Schmidt-Entling, M. H. 2009. Co-existence of divergent communities at natural boundaries: spider (Arachnida: Araneae) diversity across an alpine timberline. Insect Conservation and Diversity 2: 36-44.

Niemelä, J., Pajunen, T., Haila, Y., Punttila, P. and Halme, E. 1994. Seasonal activity of boreal forest-floor spiders (Araneae). Journal of Arachnology 22: 23-31.

Oksanen, J. 2009. Vegan: R functions for vegetation ecologists. http://cc.oulu.fi/~jarioksa/softhelp/vegan.html

Olson, D. M. 1994. The distribution of leaf-litter invertebrates along a Neotropical altitudinal gradient. Journal of Tropical Ecology 10: 129-150.

Otto, C., and Svensson, B.S. 1982. Structure of communities of ground-living spiders along altitudinal gradients. Holarctic Ecology 5(1): 35-47.

Owen, D. and Owen, J. 1974. Species diversity in temperate and tropical Ichneumonidae. Nature 249: 583-584.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics 37: 637-669.

Payette, S., Fortin, M. J. and Gamache, I. 2001. The subarctic forest-tundra: the structure of a biome in a changing climate. Bioscience 51: 709-718.

Peres-Neto, P. R. 2006. VarCan: Variation Estimation and Partitioning in Canonical Analysis. [Online] URL: http://esapubs.org/archive/ecol/E087/158/Guide.pdf

Peres-Neto, P. R., Legendre, P., Dray, S. and Borcard, D. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. Ecology 87: 2614-2625.

Pfeiffer, M., Chimedregzen, L. and Ulykpan, K. 2003. Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. Journal of Biogeography 30: 1921-1935.

Pickavance, J.R. 2006. The spiders of East Bay, Southampton Island, Nunavut, Canada. Arctic 59: 276-282.

Plaistow, S. J. and Benton, T. G. 2009. The influence of context-dependent maternal effects on population dynamics: an experimental test. Philosophical Transactions of the Royal Society B-Biological Sciences 364: 1049-1058.

Platnick, N. 2009. The World Spider Catalog Online, version 10.0. American Museum of Natural History, New York, New York.

Post, E. and Forchhammer, M. C. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B-Biological Sciences 363: 2367-2373.

Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Høye, T. T., Ims, R. A., Jeppesen, E., Klein, D. R., Madsen, J., McGuire, A. D., Rysgaard, S., Schindler, D. E., Stirling, I., Tamstorf, M. P., Tyler, N. J. C., van der Wal, R., Welker, J., Wookey, P. A., Schmidt, N. M. and Aastrup, P. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science 325: 1355-1358.

Prenter, J., Elwood, R. W. and Montgomery, W. I. 1999. Sexual size dimorphism and reproductive investment by female spiders: A comparative analysis. Evolution 53: 1987-1994.

Qian, H., Badgley, C., and Fox, D.L. 2009. The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. Global Ecology and Biogeography 18: 111-122.

R Core Development Team. 2009. R: a language and environment for statistical computing, version 2.9.0. R Foundation for Statistical Computing. Vienna, Austria.

Rahbek, C. 1995. The elevational gradient of species richness: A uniform pattern? Ecography 18: 200-205.

Rao, C. 1964. The use and interpretation of principal component analysis in applied research Sankhyā 26: 329-358.

Reed, D. H., and Nicholas, A. C. 2008. Spatial and temporal variation in a suite of life-history traits in two species of wolf spider. Ecological Entomology 33:488-496.

Reynolds, J. D. 2003. Life histories and extinction risk. Page 464 in Macroecology: Concepts and Consequences (T. M. Blackburn, and K. J. Gaston, eds.). British Ecological Society, Malden.

Ricklefs, R. 1987. Community diversity: Relative roles of local and regional processes. Science 235: 167-171.

Ricklefs, R. and Schluter, D. 1993. Speceis diversity in ecological communities. The University of Chicago Press, Chicago.

Ries, L., Fletcher, R. J., Battin, J. and Sisk, T. D. 2004. Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology Evolution and Systematics 35: 491-522.

Rodriguero, M. S. and Gorla, D. E. 2004. Latitudinal gradient in species richness of the New World Triatominae (Reduviidae). Global Ecology and Biogeography 13: 75-84.

Roff, D. A. 2002. Life History Evolution. Sinauer Associates, Inc., Sunderland.

Rohde, K. 1992. Latitudinal Gradients in Species-Diversity - the Search for the Primary Cause. Oikos 65: 514-527.

Roininen, H., Danell, K., Zinojev, A., Vikberg, V. and Virtanen, R. 2002. Community structure, survival and mortality factors in arctic populations on Eupontania leaf gallers. Polar Biology 25: 605-611.

Roy, K., Jablonski, D. and Valentine, J. W. 2001. Climate change, species range limits and body size in marine bivalves. Ecology Letters 4: 366-370.

Ruggiero, A., and Hawkins, B.A. 2008. Why do mountains support so many species of birds? Ecography 31: 306-315.

Rushton, S.P., and Eyre, M.D. 1992. Grassland spider habitats in north-east England. Journal of Biogeography 19: 99-108.

Rypstra, A. L., Carter, P. E., Balfour, R. A. and Marshall, S. D. 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. Journal of Arachnology 27: 371-377.

Rypstra, A. L. and Samu, F. 2005. Size dependent intraguild predation and cannibalism in coexisting wolf spiders (Araneae: Lycosidae). Journal of Arachnology 33: 390-397.

Samu, F., Toft, S. and Kiss, B. 1999. Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). Behavioural Ecology and Sociobiology 45: 349-354.

Sanders, N. J. Elevational gradients in ant species richness: area, geometry and Rapoport's rule. Ecography 25: 25-32.

Sanders, N. J., Moss, J. and Wagner, D. 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Global Ecology and Biogeography 12: 93-102.

Schaffers, A. P., Raemakers, I. P., Sykora, K. V. and Ter Braak, C. J. F. 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89: 782-794.

Schäuble, C. S. 2004. Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L-peronii*. Biological Journal of the Linnean Society 82: 39-56.

Schmoller, R. 1970. Life histories of alpine tundra arachnids in Colorado. American Midland Naturalist 83:119-133.

Schweger, C. 1997. Late Quaternary Paleoecology of the Yukon: A Review. Pages 59-72 *in* H. Danks and J. Downes (eds), Insects of the Yukon. Biological Survey of Canada, Ottawa.

Scudder, G. 1997. Environment of the Yukon. In: H. Danks and J. Downes (eds), Insects of the Yukon. Canadian Museum of Nature, pp. 14-57.

Simpson, M. R. 1993. Reproduction in two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. Canadian Journal of Zoology 71:451-457.

Simpson, M. R. 1995. Covariation of Spider Egg and Clutch Size - the Influence of Foraging and Parental Care. Ecology 76:795-800.

Smith, C. C., and Fretwell, S. D. 1974. Optimal Balance between Size and Number of Offspring. American Naturalist 108:499-506.

Spence, J. R., M. Zimmermann, and Wojcicki, J. P. 1996. Effects of food limitation and sexual cannibalism on reproductive output of the nursery web spider *Dolomedes triton* (Araneae: Pisauridae). Oikos 75:373-382.

SPSS for Windows, Evaluation Version 15.0. 2006. SPSS Inc., Chicago IL.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. Functional Ecology 3:259-268.

Sturm, M., C. Racine, and Tape, K. 2001. Climate change - Increasing shrub abundance in the Arctic. Nature 411:546-547.

Strathdee, A.T., and Bale, J.S. 1998. Life on the edge: Insect ecology in arctic environments. Annual Review of Entomology 43: 85-106.

Stillwell, R. C. and Fox, C. W. 2007. Environmental effects on sexual size dimorphism of a seed-feeding beetle. Oecologia 153: 273-280.

Stillwell, R. C., Morse, G. E. and Fox, C. W. 2007. Geographic variation in body size and sexual size dimorphism of a seed-feeding beetle. American Naturalist 170: 358-369.

Stillwell, R. C. and Fox, C. W. 2009. Geographic variation in body size, sexual size dimorphism and fitness components of a seed beetle: local adaptation versus phenotypic plasticity. Oikos 118: 703-712.

Stillwell, R. C., Blanckenhorn, W. U., Teder, T., Davidowitz, G. and Fox, C. W. 2010. Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: From Physiology to Evolution. Annual Review of Entomology 55: 227-245.

Stillwell, R. C. and Davidowitz, G. 2010. A developmental perspective on the evolution of sexual size dimorphism of a moth. Proceedings of the Royal Society B-Biological Sciences 277: 2069-2074.

ter Braak, C. J. F. and Šmilauer, P. 2002. Canoco for Windows, version 4.5. Biometris: Plant Research International. Wageningen, The Netherlands.

Teder, T. and Tammaru, T. 2005. Sexual size dimorphism within species increases with body size in insects. Oikos 108: 321-334.

Tilman, D., and Pacala, S. 1993. The maintenance of species richness in plant communities. In: Ricklefs, R. and Schluter, D. (eds.) Speceis Diversity in Ecological Communities. The University of Chicago Press, Chicago, pp. 24-25.

Tokeshi, M. 1999. Species Coexistence: Ecological and Evolutionary Perspectives. Blackwell Science Ltd., Malden.

Turnbull, A. L. 1973. Ecology of true spiders (Araneomorphae). Annual Review of Entomology 18: 305-348.

Ubick, D., Paquin, P., Cushing, P., and Roth, V. 2005. Spiders of North America: An identification manual, American Arachnological Society.

Uetz, G. 1991. Habitat structure and spider foraging. Pages 325-348 *in* S. S. Bell, E. D. McCoy, H. R. Mushinsky. (eds), Habitat Structure: The physical arrangement of objects in space. Chapman and Hall, London.

Uhl, G., Schmitt, S., Schafer, M. A. and Blanckenhorn, W. 2004. Food and sex-specific growth strategies in a spider. Evolutionary Ecology Research 6: 523-540.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P. and Parmenter, R. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30: 257-300.

Walker, S. E., A. L. Rypstra, and Marshall, S. D. 2003. The relationship between offspring size and performance in the wolf spider *Hogna helluo* (Araneae : Lycosidae). Evolutionary Ecology Research 5:19-28.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jonsdottir, I. S., Klein, J. A., Magnusson, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen, A., Totland, O., Turner, P. L., Tweedie, C. E., Webber, P. J. and Wookey, P. A. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103: 1342-1346.

Wedell, N. and Karlsson, B. 2003. Paternal investment directly affects female reproductive effort in an insect. Proceedings of the Royal Society B-Biological Sciences 270: 2065-2071.

Weeks, R. D. and Holtzer, T. O. 2000. Habitat and season in structuring ground-dwelling spider (Araneae) communities in a shortgrass steppe ecosystem. Environmental Entomology 29: 1164-1172.

Whitehouse, M. E. A., Hardwick, S., Scholz, B. C. G., Annells, A. J., Ward, A., Grundy, P. R. and Harden, S. 2009. Evidence of a latitudinal gradient in spider diversity in Australian cotton. Austral Ecology 34: 10-23.

Wilder, S. M. and Rypstra, A. L. 2008. Sexual size dimorphism predicts the frequency of sexual cannibalism within and among species of spiders. American Naturalist 172: 431-440.

Willig, M. R., and Bloch, C. P. 2006. Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. Oikos 112: 163-173.

Willig, M. R., Kaufman, D. M., and Stevens, R. D. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annual Review of Ecology Evolution and Systematics 34: 273-309.

Willis, K. J. and Whittaker, R. J. 2002. Species diversity: Scale matters. Science 295: 1245-1248.

Wise, D. H. 1979. Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species (Araneae, Araneidae). Oecologia 41:289-300.

Wise, D. 1993. Spiders in Ecological Webs. Cambridge University Press, Cambridge.

Wise, D. H. 2004. Wandering spiders limit densities of a major microbi-detritivore in the forest-floor food web. Pedobiologia 48: 181-188.

Wise, D. H. 2006. Cannibalism, food limitation, intraspecific competition and the regulation of spider populations. Annual Review of Entomology 51: 441-465.