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Spider communities in boreal mixed-wood forests of Alberta: succession, species interactions and habitat utilization

by

Christopher Martin Buddle ©

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

in

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Spider communities in boreal mixed-wood forests of Alberta: succession, species interactions and habitat utilization** submitted by Christopher Martin Buddle in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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I dedicate this thesis to my wife,
Rebecca Stone, for her love and support,
my son Evan for showing me joy, and my
parents for teaching me the
value of wilderness

Abstract

Spiders (Araneae) are important and ubiquitous predators in terrestrial ecosystems, and they are an ideal taxon for assessing the impact of forest harvesting on the biota of boreal forests. I investigated how spider succession differs following wildfire and clear-cutting in a chronosequence study of aspen-dominated stands in north-central Alberta, Canada. Such comparisons support insights into how harvesting may alter natural succession in fire-driven ecosystems. Results showed that spiders recovered rapidly from both disturbances, and by 30 years after disturbance, there was a faunal recovery and general convergence toward pre-disturbance community structure. There were, however, some important differences between the two disturbances in that wildfire stands harboured a more diverse spider fauna and certain species appeared dependent on some of the conditions associated with wildfire.

Wolf spiders (Lycosidae) were dominant in most of the study sites in the chronosequence study. Experiments in a mixed-wood forest in central Alberta revealed that two species, *Pardosa moesta* Banks and *P. mackenziana* (Keyserling), had nearly identical biennial life-cycles, and young stages of these species have the potential to interact in the leaf-litter. A competition experiment, however, showed that exploitative competition did not govern populations of *P. moesta* and *P. mackenziana*, and suggested that mortality factors such as intraguild predation and cannibalism play important roles in their survival.

Knowledge from the competition and life-history experiments served to explain patterns in the occurrence of *Pardosa* species throughout north-central Alberta.

The chronosequence study also suggested that fallen logs, or downed woody material (DWM), was an important habitat for spiders. This was tested by trapping spiders directly on the surface of fallen logs and by manipulating the volume of DWM on the forest floor and tracking changes in spider assemblages. Results showed that a diverse spider fauna uses the surface of DWM, and that some species are dependent on the habitat complexity of fallen logs. Manipulating the volume of DWM on the forest floor, however, had few short-term effects on spider assemblages, except that diversity tended to increase when DWM was augmented on the forest floor.

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1. Introduction

Background and rationale

> *"If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering"* – Aldo Leopold, 1949

Not only is keeping all parts of an ecosystem vital to the future health and well-being of our planet, it is the responsibility of the natural sciences to understand how the cogs and wheels work. Most scientists would agree that we are in a sixth great extinction, due primarily to human encroachment on already taxed ecosystems (Wilson, 1992; Chapin *et al.*, 2000). We are not immune to these problems in Canada as there are immense pressures on our land base resulting from industrial practices such as forest harvesting (Pratt & Urquart, 1994; May, 1998).

The impact of these changes on ecosystems must be understood, especially given the importance of biological diversity, or biodiversity, to the maintenance of ecological services (Chapin *et al.*, 2000). Biodiversity is here defined as the variation in life forms, across all levels of biological organization, from within species to the array of species themselves and to living communities of ecosystems (Wilson, 1994). Although the links between biological diversity and ecosystem stability remain controversial (e.g., Johnson *et al.*, 1996; Tilman, 1999; McCann, 2000), few deny that anthropogenic changes to biodiversity have the potential for detrimental effects on ecosystems (Ehrlich & Wilson, 1991; Wilson, 1992; Chapin *et al.*, 2000). One theory, as E. O. Wilson (1992) states, is that ecosystems are designed with redundancies and various species can fill empty niches when they become vacated (e.g., from extinction); however, with a continual loss of species, eventually ecosystems will not be resilient to imposed pressures and thus collapse.

Biodiversity has become a phenomenon in ecology (Haila & Kouki, 1994), evident by the increased interest in biodiversity in prominent scientific journals (e.g., Naeem & Li, 1997; Lawton *et al.*, 1998; Chapin *et al.*, 2000; McCann, 2000). Although interest in biological diversity is nothing new (Hutchinson, 1959), the recent resurgence has resulted in heightened awareness of the issues surrounding land management and ecological "integrity" or "health". Despite semantic issues, the emergence of these concepts serve to illustrate that properly functioning ecosystems do depend on the correct biotic components (i.e., species) being in place.

One role of ecologists is to apply knowledge of various taxa to current applied problems of societal and economic importance. In Alberta, one of the current issues is how best to manage forest resources to ensure economic vitality without significant long-term impact on the biota. Managing forests with consideration of biodiversity issues can and should be done (Boyle, 1991; Probst & Crow, 1991; Burton *et al.*, 1992), and foresters must work with ecologists in ways that satisfy the demands of ecological sustainability (Perry, 1998).

One method of forest harvesting that shows promise falls under the umbrella of "ecosystem management" (Perry, 1998) and is led by the natural disturbance paradigm. Given that the boreal forests have been under the influence of wildfires for centuries (Bonan & Shugart, 1989), some suggest one way to manage forests in an ecologically sound manner is to harvest in a way that best emulates the ecologically significant features of disturbance by fire (Hunter, 1993; DeLong & Tanner, 1996; Angelstam, 1998). In other words, it may be possible to cut forests with a periodicity and pattern that match a natural disturbance regime (Hunter, 1993; Angelstam, 1998).

The natural disturbance hypothesis, however, still needs to be empirically tested, especially in relation to invertebrates. Not only do invertebrates account for upwards of 80% of global diversity (Wilson, 1992), they perform countless vital services to both ecosystems (e.g., pollination, nutrient cycling, litter decomposition, soil formation) and to humankind (e.g., pollination of food plants, pharmaceutical advances, biological control, etc.) [reviewed by Wilson (1992)]. Furthermore, because wildfire and harvesting are not functionally equivalent (Perry, 1998), there may be deleterious effects of forestry on invertebrates (e.g., Spence *et al.*, 1996a; Niemelä, 1997), and invertebrates may respond differently to wildfire than to forest harvesting (e.g., Muona & Rutanen, 1994). Research in Fennoscandia, for example, has illustrated that natural forests often have higher diversity of invertebrates than managed forests, and this has implications for highly prized vertebrates such as passerine birds (Pettersson *et al.*, 1995). In North America, similar patterns have been revealed for ground beetles (Coleoptera: Carabidae); forestry activities can change the distribution, and abundance of many species, including losses of species dependent on older forests (Niemelä *et al.*, 1993; Spence *et al.*, 1996a). Data required to test fully the natural disturbance paradigm, however, remains scarce. Quantitative research investigating differences in invertebrate communities between wildfire and harvested areas may guide us toward more ecologically sound forest management.

Beyond understanding general patterns in diversity and abundance of invertebrates in relation to processes such as harvesting and wildfire, identifying key habitat features of forested landscapes will also provide useful information for ecologists and forest managers. Coarse woody debris (CWD), in the form of standing dead trees (snags) and fallen trees (downed woody material, DWM) represents one habitat that is altered by forestry (Duvall & Grigal, 1999; Siitonen *et al.*, 2000) and important for biodiversity. CWD provides habitat for numerous taxa including highly valued birds and vertebrates (Mannan *et al.*, 1980; Harmon *et al.*, 1986; Bowman *et al.*, 2000) and lesser understood or valued organisms such as fungi (Amaranthus *et al.*, 1994) and invertebrates (e.g., Harmon *et al.*, 1986; Siitonen & Martikainen, 1994; Hammond, 1997). After a single logging rotation, CWD can be reduced as much as 80% on the land-base (Angelstam, 1997), and this has the potential for deleterious effects on the forest biota.

The importance of CWD to invertebrates has primarily focused on taxa that require dead wood to complete their life cycles [e.g., saproxylic invertebrates (Speight, 1989; Hammond, 1997)]. Mainly, this research deals with beetles associated with CWD and illuminates the risks associated with losses of CWD in managed forests (e.g., Siitonen & Martikainen, 1994; Martikainen *et al.*, 1999). However, there is a gap in our understanding of the extent to which other forest-dwelling invertebrates may utilize CWD, and virtually nothing is known of the effect that changes in CWD may have on these taxa.

Properly addressing applied ecological problems also requires knowledge about how biological communities are organized. Understanding factors governing populations and communities will aid in interpreting large-scale patterns and small-scale habitat use. Research on the natural history of species, and experimental studies on species interactions may shed light on why certain species may be affected by forest management. An example of such an approach comes from research on ground beetles inhabiting deciduous leaf-litter experimentally placed in coniferous stands (Koivula *et al.*, 1999). Deciduous leaf-litter is a rare habitat in the boreal forest of Finland since intensive forest management has drastically reduced the deciduous component of the forests. Koivula *et al.* (1999) provided information on potential competitive interactions between beetle species and between ants and carabid beetles, and such information helped explain their data about local distributions of carabid beetles. This provides a more comprehensive understanding of the larger applied problem.

Ecologists have the tools to understand Leopold's cogs and wheels and to address the central theme of E.O. Wilson's (1992) treatise. Facing ecological problems of societal importance requires identifying the problems, observing patterns, determining key components, and understanding the factors driving the overall system. My doctoral dissertation applied this approach by first using a "natural experiment" (Hairston, 1989) that investigated the effect of wildfire and harvesting on spider assemblages (Arthropoda: Araneae). Although this natural experiment cannot be used for direct hypothesis testing (Hairston, 1989), it did generate patterns and testable predictions about the importance of DWM, as a key habitat feature, for spider assemblages, and about the role of competition as a factor governing populations of certain spiders. Field experiments were then used to unravel some of the complexity of these ecological questions.

Spiders: A model study taxon

> *"The spider has a bad name: to most of us, she represents an odious, noxious animal, which every one hastens to crush under foot. Against this summary verdict the observer sets the beast's industry, its talent as a weaver, its wiliness in the chase, its tragic nuptials and other characteristics of great interest. Yes, the spider is well worth studying"*
>
> -J. Henri Fabre, 1916

After 400 million years of evolution (Platnick, 1995), spiders remain among the dominant arthropod predators in most terrestrial ecosystems [reviewed in Turnbull (1973)]. Bristowe (1958) estimated five million spiders could be found per ha in an abandoned old field in England, and Turnbull (1973) reported spider densities between 0.64 to 842 m^{-2}. Because of their abundance and predatory habits, spiders consume vast numbers of invertebrate prey, and are important in the energy dynamics of ecosystems. Moulder & Reichle (1972) report that spiders consume 44% of the annual crop of ground-dwelling invertebrates, and van Hook (1971) suggested wolf spiders in grasslands consume 20% of the total net herbivore and omnivore production. More recently, Lawrence & Wise (2000) showed that spiders may eat enough Collembola to affect rates of litter decomposition.

As voracious predators, spiders also have the potential to reduce populations of pest insect species. In agricultural systems, Riechert & Bishop (1990) showed that manipulating habitat to favour spiders can result in decreased abundance of pest insects. In a forestry setting, spiders eat many economically important forest pests such as western spruce budworm, *Choristoneura occidentalis* Freeman (Mason *et al.*, 1997). Given their generalist predatory behaviour, spiders seldom track pest insect outbreaks in a density dependent fashion (Riechert & Lockley, 1984); it is argued, however, that the overall spider community can provide background predation pressure that naturally resists outbreaks of certain pest insects (Nyffeler & Benz, 1987; Riechert & Bishop, 1990; Wise, 1993).

In the ecological literature, spiders have often been the focus of studies on intra- and interspecific competition (Horton & Wise, 1983; Reichert & Cady, 1983; Spiller, 1984; Toft, 1990; Wise & Wagner, 1992; Wise, 1993), cannibalism (Spence *et al.*, 1996b; Wagner & Wise, 1996; Samu *et al.*, 1999), and intraguild predation (IGP)(Polis & McCormick, 1986; Halaj *et al.*, 1997; Wise & Chen, 1999). Results have generally shown that exploitative competition may be rare among web-building spider species [reviewed by Wise (1993)], but hunting spiders (i.e., those not relying on webs to capture prey) have seldom been studied. One exception is research on the wolf spider genus *Schizocosa* (Wise & Wagner, 1992). In concert with exploitative intraspecific competition, cannibalism and IGP play a large role in governing populations of *Schizocosa* (Wagner & Wise, 1996; Wise & Chen, 1999).

There is also a large amount of life-history information on various spider species (e.g., Dondale, 1961; Vlijm *et al.*, 1963; Edgar, 1971; Oraze *et al.*, 1989; Zimmermann & Spence, 1998), and a basis for understanding the factors governing life history traits and reproductive potential (Kessler, 1971; Beck & Conner, 1982; Marshall & Gittleman, 1994; Zimmermann & Spence, 1998). This work has provided the foundation for understanding spider ecology.

Spiders are sensitive to changes in their habitat. Web-building species depend on the complex architecture of their surroundings (Robinson, 1981; Greenstone, 1984; Riechert & Gillespie, 1986). Changes in the architecture, such as needle-loss in coniferous trees, can result in lower densities of certain spiders (Gunnarsson, 1988). Web-building species on the forest floor (e.g., species from the family Linyphiidae) typically build sheet-webs within the complex microhabitats of the leaf-litter (Huhta, 1971), and changes to this habitat can have profound effects on these species (Huhta, 1971; McIver *et al.*, 1992). Hunting spiders are also dependent on the complexity of the leaf-litter (Uetz, 1991) and changes in their abundance can often be attributed to changes in leaf-litter complexity and depth (Bultman & Uetz, 1982). In a forestry context, spiders have proven to be exceptional indicators of large-scale habitat change (Huhta, 1971; Coyle, 1981; McIver *et al.*, 1992; Pajunen *et al.*, 1995). Open habitat species, typically found in regions of low litter depth and complexity, tend to dominate clear-cut forest stands (Coyle, 1981; Pajunen *et al.*, 1995). In contrast, many web-building species show affinities towards mature, closed-canopy forests (Huhta, 1971; McIver *et al.*, 1992).

Spiders, the order Araneae, rank seventh in global diversity [*ca.* 36,000 described species (Platnick, 1995)], after the insect orders Coleoptera, Hymenoptera, Lepidoptera, Diptera and Hemiptera, and the Arachnid order Acari (Coddington & Levi, 1991). North America is thought to have approximately 4000 spider species (Coddington & Levi, 1991), and Canada is estimated to harbour 1500 species (Bennett, 1999). The taxonomy of spiders in North America is well known as an estimated 80% of our fauna has been described (Coddington & Levi, 1991). With the exception of the family Linyphiidae, taxonomic keys available allow for accurate species determinations (e.g., Dondale & Redner, 1990).

Spiders, therefore, meet many of the suggested criteria for selecting a taxon to indicate environmental, ecological, or biodiversity change (McGeoch, 1998). Spiders are abundant, diverse, taxonomically well known, easily sampled, stored, and identified. They are widely distributed, sensitive to habitat change, represent a critical component of ecosystems, and are ecologically and economically important as generalist predators. There is also good base-line data on the biology and natural history of spiders. This foundation make spiders an ideal taxon to experimentally test general ecological theories (e.g., competition, life-history traits and tradeoffs, life-cycle regulation, biological control, the role of IGP, etc.) (Wise, 1993). Thus, spiders represent a model study taxon for ecologists studying a wide range of ecological problems.

Structure of Thesis

The first objective of my thesis research is to understand how the succession of spider assemblages differs between wildfire and harvesting in the boreal mixed-wood forest. Chapter 2 summarizes the results of a large-scale survey of 12 forest stands throughout north-central Alberta and compares the spider fauna of young stands of trembling aspen (*Populus tremuloides* Michx.) (i.e., < 30 yr) that were initiated by either wildfire or clear-cutting. This work aimed to test directly the basis of the natural disturbance paradigm by asking whether, over time, spiders converge on similar species assemblages following the natural disturbance of wildfire compared to anthropogenic disturbance of harvesting. Chapter 3 is a continuation of Chapter 2, and asks if spider assemblages from young successional *Populus* stands begin to resemble the fauna of mature (> 70 yr) and old (>140 yr) stands that are representative of a pre-disturbance state. This chapter is focused on the recovery of spiders in the boreal mixed-wood after disturbance by wildfire and harvest.

Chapters 4 and 5 represent a shift in focus from the large to the small-scale. These chapters aim to understand the natural history and interactions between dominant spider species found in boreal mixed-wood forests of Alberta. Results from Chapter 2 indicated that two species of wolf spiders [*Pardosa moesta* Banks and *P. mackenziana* (Keyserling)] were numerically dominant, and coexist, in most deciduous forest stands throughout north-central Alberta. Although these species are widely distributed in Canada (Dondale & Redner, 1990), virtually nothing is known of their natural history. Chapter 4 focuses on understanding the life-history of *P. moesta* and *P. mackenziana*. The objectives were to ascertain the natural densities of these species, their life-cycles, and to determine if female size affects fecundity. Chapter 5 asks whether intra- or inter-specific exploitative competition govern populations of these species: this work was done by stocking different densities of the two species in a series of field enclosures.

The third theme of my thesis evaluates the importance of fallen logs (DWM) to the spider fauna of a deciduous mixed-wood forest stand. Virtually nothing is known of how generalist predators, such as spiders, may depend on DWM in a forest, and results from Chapter 2 suggested that the variation in spider assemblages in certain stands may be partially explained by the habitat complexity provided by DWM. The experiment outlined in Chapter 6 involved using a novel trapping technique of my own design to assess quantitatively what spider species actively use the surface of DWM. To assess further whether spiders may be dependent on the habitat complexity of fallen logs, catches on wooden telephone poles, which mimicked the coarse structure of natural logs, were compared to collections of spiders on logs with and without bark.

Chapter 7 continues with a focus on DWM and discusses a large manipulative experiment that altered the volume of DWM on the forest floor and followed changes in the spider fauna before and after the experimental treatments were applied. The general objective of this work was to ask whether spider assemblages changed in relation to the addition or removal of DWM on the forest floor.

My dissertation research is varied and addresses a range of ecological questions at different scales. It begins with a large-scale community survey (Chapters 2 and 3), and this work led me to study life-history and competition between two *Pardosa* species (Chapters 4 and 5) and to study the importance of DWM to spiders (Chapter 6 and 7). Chapter 8 attempts to synthesize these three themes and summarize what has been learned of spider assemblages in boreal mixed-wood forests. It points to some of the major findings and greatest contributions my work has made towards the discipline of terrestrial ecology. I also present some ideas on where future research should be directed.

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2. Succession of boreal forest spider assemblages following wildfire and harvesting*

Introduction

Wildfire is a major component of the natural disturbance regime that structures the boreal forest (Rowe & Scotter, 1973; Johnson, 1992) resulting in a mosaic of stand types and stand ages (Bonan & Shugart, 1989; Stelfox, 1995). However, extensive forest harvesting now rivals or surpasses fire as an agent of stand renewal in the boreal mixed-wood ecoregion of northern Alberta where trembling aspen (*Populus tremuloides* Michx.) is being cut at an unprecedented rate (Peterson & Peterson, 1992; Pratt & Urquhart, 1994). These developments in industrial forestry raise questions about the long-term sustainability and productivity of forests, and about conservation of the forest biota.

Some suggest that wildfires can act as a template for more ecologically sound forest management (Hunter, 1993; Bunnell, 1995; DeLong & Tanner, 1996). However, fire and harvesting may not be functionally equivalent, and thus harvesting could promote deleterious ecological changes in developing stands. This concern is especially relevant with respect to invertebrate communities (Zackrisson, 1977; Muona & Rutanen, 1994; Spence *et al.*, 1996). Conservation of biodiversity is now considered an important and necessary part of resource management (Burton *et al.*, 1992; Probst & Crow, 1991), and since invertebrates represent over 80% of the world's described species (Wilson, 1992) and perform numerous vital roles in forest ecosystems, we seek to understand how fire and

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harvesting affect invertebrate communities over the course of succession.

We chose spiders (Araneae) as a model taxon for study. Spiders are significant predators in forest ecosystems (Clarke & Grant, 1968; Moulder & Reichle, 1972; Turnbull, 1973), and contribute to the dynamics of soil litter communities (Petersen & Luxton, 1982). Arboreal spiders help reduce economically important forest insect pest populations (Mason *et al.*, 1997) and provide an important food source for wintering birds (Jansson & Brömssen, 1981). Spiders are also sensitive to habitat change (Robinson, 1981; Riechert & Gillespie, 1986; Uetz, 1991), have a relatively stable taxonomy (Coddington & Levi, 1991), well understood life history characteristics (Wise, 1993), occupy a wide breadth of habitats (Turnbull, 1973), and are easily sampled and identified. Taken together, these factors satisfy many of the suggested criteria for taxa indicating biodiversity and ecosystem change (McGeogh, 1998).

Spider assemblages show clear responses to both forest harvesting (Coyle, 1981; Jennings *et al.*, 1988; McIver *et al.*, 1992; Pajunen *et al.*, 1995; Pettersson, 1996) and wildfire (Schaefer, 1980; Koponen, 1993; Aitchison-Benell, 1994; Johnson, 1995; Collins *et al.*, 1996). However, with the exception of work by Huhta (1971) there is little basis for understanding how changes in spider assemblages following wildfires compare to changes following harvesting. We addressed these questions in aspen-dominated stands in north-central Alberta, predicting that recent fire- and harvest-origin stands will harbour distinct spider assemblages because recently burned stands are structurally different than young clear-cuts. Our aim was to quantify these differences and understand how long they persist by asking the following questions in a chronosequence study: 1) how does the diversity and abundance of spiders compare between fire- and harvest-origin stands in the early successional stages of aspen dominated forests?; 2) is there a convergence in the trajectories of spider re-colonization following harvesting and wildfire after *ca.* 30 years of forest growth?; and 3) are certain spider species dependent on pyrogenic stands?

Materials and methods

Study Area

All study sites were in the mid-boreal mixed-wood ecoregion of Alberta (Strong & Leggat, 1992) and were bounded by N55°11' to N56°31' and by W111°46' to W115°52' (Fig. 2-1). Forests in this region are dominated by trembling aspen; other overstory trees include balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss), and white birch (*Betula papyrifera* Marsh). The understory vegetation of the study stands was dominated by grasses, wild rose (*Rosa acicularis* Lindl.), mooseberry (*Viburnum edule* [Michx.] Raf.), fireweed (*Epilobium angustifolium* L.), dewberry (*Rubus pubescens* Raf.), and mosses. Study sites were chosen to be dominated by trembling aspen (> 90% of stems), and all stands were > 30 ha in size. Six of the study stands originated after wildfire and six represent natural regeneration after harvest. We studied stands originating in *ca.* 1995, 1982 or 1968 as representative of early succession in mixed-wood forests (Fig. 2-1). The resulting design therefore has two treatment types (disturbance type and age class) with two stands for each treatment combination. Aspen harvesting is a relatively recent practice in Alberta and harvested stands > 30 years old were not available for study. The general limited availability of harvested stands > 10 years old restricted the overall sample size for our comparisons.

Sampling

Litter and ground-dwelling spiders were sampled using continuous pitfall trapping from 3 June – 24 September in 1996 and from 5 May – 23 September in 1997. Six traps, placed *ca.* 50 m apart to reduce trap-to-trap interference (Digweed *et al.*, 1995), were set out in a linear arrangement in each stand. Traps were white plastic containers 10 cm in diameter, containing 2 - 3 cm of ethylene glycol and covered with a 15 x 15 cm elevated plywood roof [see Spence & Niemelä (1994) for details]. Traps were emptied at 10 - 15 day intervals throughout the collection period.

Spiders living in the understory vegetation were sampled using a sweep net (46 cm diameter) in 1997. Weather permitting, 10 sweeps of the vegetation at breast height were completed along transects extending from three randomly chosen pitfall trap locations in each stand. The same transects were used throughout the sampling period (June - August 1997). To minimize collecting biases, one person (CMB) was responsible for all sweep-net collections.

All adult spiders were identified to species, and classification followed Platnick (1993, 1997). Accurate species determinations are not possible with most immature spiders; however, juvenile and penultimate stages were identified to the generic level when possible. Voucher specimens for all taxa are deposited in the Canadian Forest Service arthropod collection at the Northern Forestry Centre, Edmonton, Alberta, Canada.

In the summer of 1997, vegetation was assessed by estimating the percent ground cover by plant type for a 5 x 5 m grid around each pitfall trap [see Niemelä & Spence (1994) for details and procedure]. The shade coverage for each grid was estimated as a percentage at a height of 0.5 m. Litter characteristics (i.e., of "litter layers", LFH) including depth (cm) and biomass (dried, from 0.25 x 0.25 m sample) were also measured at each pitfall trap location. Coarse woody debris (CWD) estimates, including volume of downed woody material (DWM, m^3 ha^{-1}) and snag densities (standing dead trees, number ha^{-1}) were obtained for each study stand from P. Lee at the Alberta Research Council, Vegreville, Alberta. We sought to correlate vegetation, shade, litter, and CWD parameters with variation in spider assemblages among treatments.

Analyses

Differences in the relative numbers of spiders caught (pooled data from all six traps in a stand) were tested using a 2-factor ANOVA with stand disturbance (fire- or harvest-origin) and stand age (originating in 1995, 1982, or 1968) as main effects. Mature and immature spiders were used for comparisons of relative abundance; all other analyses excluded immature specimens. Sampling effort varied among stands, as some traps were flooded or disturbed by mammals.

Therefore, comparisons of relative abundance were based on catches standardized to 500 trap-days (number of traps x number of undisturbed trap-days). Sweep-net samples were also standardized to 200 sweeps per stand, as it was not possible to complete the same number of sweeps for each stand due to varying weather conditions. The SAS statistical package (SAS Institute Inc., Cary, NC) was used for all ANOVA tests.

To compare species richness among stands, the data were adjusted by rarefaction to compensate for varying sample sizes (Simberloff, 1978). The resulting value can be interpreted as a diversity index as both species richness and relative abundance are taken together. The Berger-Parker index was adopted (calculated as the inverse of the proportion of the most abundant species in a sample) to assess the dominance structure of the spider assemblages by stand type. This index has the virtue of having a low sensitivity to sample size and being intuitively and mathematically tractable (May, 1975; Magurran, 1988).

Correlation analysis was used on pitfall trap data to test whether spider species richness, relative abundance, and numbers of the 10 most commonly collected spider species responded to the following measured environmental parameters: total plant species richness (herbaceous plants and shrubs), average percent cover of common plants (average cover > 1%) typically found in mesic habitats (Corns & Annas, 1986; Johnson *et al.*, 1995), snag density, volume of DWM, average litter biomass, average litter depth, and average shade cover. Correlations were calculated and analyzed at the stand level ($n = 12$).

Log-transformed data from standardized catches (800 trap-days) were used for cluster analyses to group stand types based on the similarity of the spider assemblages. Pair-wise similarities were based on the Bray-Curtis Index for percent similarity (Bray & Curtis, 1957) and clusters were formed using unweighted arithmetic averaging [internet-based software provided by Brzustowski (2000)]. Species represented by one individual were removed from the analysis before dendrograms were produced to reduce the likelihood of including non-resident species in the analysis.

Cluster analysis was also used to group environmental variables by stand type. The resulting dendrograms were compared to dendrograms based on spider assemblages to examine whether succession of the vegetation and abiotic stand characteristics (litter depth, biomass, shade cover, and 40 plant species with an average abundance > 1% of the total cover) corresponded with succession of spider assemblages. Cover classes approximated a log scale and were not adjusted before analysis; all other measurements were log transformed.

Dendrograms were tested for their sensitivity to particular species through an iterative process that constructed a dendrogram *n* times (*n* = number of species in analysis), with a different species removed from the analysis at each iteration. The shape of the resulting dendrograms were compared to the dendrogram without species removed. The number of times each sample (and its corresponding node) in the dendrogram changed position was noted and assigned a "node stability" value, defined as the number of times the samples from a particular node did not change position divided by the total number of iterations (*n*). For example, samples and their corresponding nodes that did not change position over all iterations were given a value of 1, suggesting their position is insensitive to species removal in the analysis. A similar analysis was done for environmental data. Although these node stability measures are not formal statistical tests, they are useful descriptors that provide a measure of the degree of confidence in the placement of samples in a dendrogram.

Pitfall trap data were numerous enough to further analyze with detrended correspondence analysis (DCA), which is a useful technique for examining patterns in community structure and assessing sources of variation in ecological data (Hill & Gauch, 1980; ter Braak, 1990, 1995). Data from 11 pitfall traps which experienced frequent disturbance and had < 75 trapping days each were removed from the analysis. Additionally, species represented by one individual were excluded from the DCA.

Spider species can be placed in two distinct foraging guilds based on their primary mode of prey capture. Hunting species do not rely on silk for prey capture while web-building species rely on various kinds of webs to capture prey.

Rank abundance plots of the dominant species from each guild were compared by stand type.

Results

Abundance and diversity

A total of 127 species and over 8400 mature and immature specimens from 15 families was collected in 1996 - 1997 by pitfall traps and sweep-netting (Table 2-1, Appendix 1). In pitfall traps, wolf spiders (Lycosidae) were numerically dominant, representing 44% of the total catch, followed by Linyphiidae (30%) and Amaurobiidae (14%). Linyphiidae was the most diverse family with 45 species collected in pitfall traps. Sweep net samples were also dominated by the linyphiids with 7 species representing 60% of the total catch of mature specimens.

Many spider species collected were uncommon or rare. For instance, of the 105 species collected by pitfall traps, 31 were represented by one individual and 8 species were represented by two individuals. Similarly, 12 of the 29 species collected by sweeping were represented by one individual and 3 by two individuals.

More spiders were collected by pitfall traps in 1997 than in 1996, likely due to a longer sampling period and a warmer, drier summer in 1997 (Table 2-2A,B). Immature specimens accounted for < 7% of the total pitfall trap catch and 56% of the sweep-net collection (Table 2-2). The fewest spiders were caught by pitfall trapping in 1995 fire-origin stands (1996 collection) and the most were caught in 1982 harvest-origin stands (1997 collection) (Table 2-2A,B); sweep-netting captured the most mature specimens in 1968 harvest-origin stands, and the fewest were collected in 1995 harvest-origin stands (Table 2-2C).

The total relative abundance of spiders from pooled pitfall trap collections from 1996 and 1997 did not differ significantly among stand ages or between disturbance types; however, some significant patterns were apparent among species and families (Table 2-3A). Stand age significantly affected wolf spiders

(Lycosidae), as more were caught in stands originating in 1995 than in those originating in 1968 (Tukey's test, $p < 0.05$). Sheet-web spiders (Linyphiidae) were more frequently captured in harvest-origin stands than in fire-origin stands. Of the ten species most commonly collected by pitfall trapping, the linyphiids *Allomengea dentisetis* (Grube) and *Lepthyphantes intricatus* (Emerton) were significantly more abundant in catches from harvest-origin than from fire-origin stands, and the liocranid *Agroeca ornata* Banks was more frequently collected in 1968 stands as compared to 1995 stands (Tukey's test, $p < 0.05$). A significant interaction between disturbance type and age was noted for the lycosid *Pardosa moesta* Banks and the amaurobiid *Amaurobius borealis* Emerton. *Pardosa moesta* showed a higher relative abundance in 1995 harvest-origin stands compared to other stand types, and *A. borealis* was most commonly collected in 1982 harvest-origin stands. Significantly more spiders (both mature and immature specimens) were collected by sweeping the vegetation in fire-origin stands compared to harvest-origin stands (Table 2-3B).

In pitfall trap collections in 1996, species richness was highest in 1995 harvest-origin stands and in 1997 in 1982 harvest-origin stands (Table 2-2A,B). Species richness, however, is influenced by sampling effort which varied among stands. Results from rarefaction analysis (standardized to 280 individuals) reveal few significant differences in species richness by stand origin or age and few significant differences between collection years (Fig. 2-2A). The only notable differences are the high expected number of species from the 1982 fire-origin stands sampled in 1997 and the decrease in the expected number of species in 1968 fire-origin stands from 1996 to 1997. The sweep-net samples show a different pattern as the highest species richness was in 1995 fire-origin stands (Table 2-2C), and this is confirmed by rarefaction results (Fig. 2-2B). In seven of nine comparisons among stands of equivalent age, the estimates from rarefaction show that fire-origin stands have a higher expected species richness than harvest-origin stands.

The dominance structure of the spider assemblages, as evaluated with the Berger-Parker index, differed by age, disturbance type and collection technique.

With the exception of the first year after fire (1995 fire-origin stand, 1996 pitfall trap collection) the spider assemblages from pitfall traps became more evenly distributed as the stands aged (Table 2-2A,B). One year following wildfire, the spider assemblages from pitfall traps had a low dominance structure suggesting a remarkably even distribution of spider species. By the second year of pitfall trapping in 1995 fire-origin stands, however, the dominance structure more closely resembled that of the 1995 harvest-origin stands. Spiders collected by sweeping showed an opposite pattern in dominance structure with the 1995 fire- and harvest-origin stands supporting more even distributions of species than older stands (Table 2-2C).

Environmental variables

The vegetation survey revealed some differences in dominant plant species by disturbance types. For example, many species associated with wet habitats [e.g., mosses, horsetail species (*Equisetum* sp.), coltsfoot (*Petasites palmatus* (Ait.) A. Gray), bunchberry (*Cornus canadensis* L.), and tall lungwort (*Mertensia paniculata* (Ait.) G. Don.)] (Corns & Annas, 1986; Johnson *et al.*, 1995) were more common following wildfire (Fig. 2-3). Volume of DWM was higher in 1982 and 1968 fire-origin stands than in harvested stands of the same age, and snag densities were greater in 1995 and 1982 fire-origin stands than in comparable harvested stands (Fig. 2-3).

In general, few environmental variables were correlated with spider species richness, total number of spiders collected, and the relative abundance of the most abundant 10 species collected in 1996 and 1997 (pitfall trap samples) (Table 2-4). Plant species richness was positively correlated to average spider species richness, abundance of linyphiid spiders, and abundance of four species of spiders [*L. intricatus*, *Amaurobius borealis*, *Bathyphantes pallidus* (Banks), and *Agroeca ornata*]. These spider species and *Cybaeopsis euopla* (Bishop & Crosby) were also positively correlated with the average ground cover by plants associated with moist (mesic) environments. Linyphiids were positively correlated, and lycosids were negatively correlated with average cover of plants commonly associated with mesic sites. Litter biomass did not correlate with any of the measured variables. Litter depth was negatively correlated to the relative abundance of *P. moesta* and positively to *Trochosa terricola* Thorell. *Pardosa mackenziana* (Keyserling) and *T. terricola* were both negatively correlated with shade. Snag density was negatively correlated with the relative abundance of linyphiids and *A. dentisetis*, and positively correlated with *P. xerampelina* (Keyserling). There was a positive correlation between *T. terricola* and volume of DWM.

Succession and community patterns

Because sampling period differed between 1996 and 1997 and there were relatively few differences in diversity across years, community-level analyses were completed on pooled data from 1996 and 1997. Cluster analyses show that spider assemblages from the 1968 fire-origin stands were most similar to those from the 1968 harvest-origin stands (clustering at 82% similarity for pitfall trap samples and 76% similarity for sweep net samples), and these nodes were very stable (Figs. 2-4, 2-5). The 1982 harvest-origin stands clustered closer to the 1968 stands than to 1982 fire-origin stands and both 1995 stands and this topology was also stable. Positions of the 1982 fire-origin stands and the 1995 fire- and harvest-origin stands were more sensitive to the removal of species from the analysis (lower node stability), suggesting that interpretations about the placement of these stand types should be approached with caution (Figs. 2-4, 2-5).

The dendrogram produced from clustering the environmental data had high stability measures at all nodes which suggests that plants and abiotic measures provide a relatively homogeneous pattern (Fig. 2-4). As with the spider data, 1995 fire-origin stands were most variable based on environmental data. However, in contrast to the spider communities, vegetation and abiotic site conditions from the 1982 and 1968 stands cluster according to disturbance type, suggesting environmental site conditions are more sensitive to disturbance type than are spider communities.

Results from the DCA ordination using pooled pitfall trap data from 1996 and 1997 support many of the findings from the cluster analyses. Plotting sample scores from each pitfall trap suggests that 1995 fire-origin stands have a different community composition than 1995 harvest-origin stands. These separate mainly on axis 2 and show high variation across axis 1 (Fig. 2-6). In this ordination, axis 1 separates stands mainly on age. Sample scores from 1968 stands all fall within the same region of the ordination space and show less variation in sample scores than younger stands. This suggests a convergence in the spider fauna after *ca.* 30 years of forest growth. The community composition of 1982 fire-origin stands is distinct showing high variation along both axis 1 and 2 and wide separation from other stand types. Sample scores from the 1982 harvest-origin stands fall closer to the scores from 1968 harvest and fire-origin stands than do the 1982 fire-origin stands to the 1968 stands.

Hunting spiders tended to show a preference for the youngest stands (Figs. 2-7, 2-8), and their relative abundance decreased in older stand age-classes. In contrast, the web-building guild increased in relative abundance in older stands and 1968 stands were dominated by web-building species.

Focussing on the pitfall trap data, stands originating in 1982 support a transitional fauna, including both hunting species common to younger stands and web-building species dominant in older stands (Fig. 2-7). Harvest-origin stands originating in 1995 were primarily dominated by the wolf spider *P. moesta.* In 1982 and 1968 stands, *P. moesta* was much less abundant suggesting that these populations were relicts of higher density populations characteristic of stands shortly after disturbance. *Pardosa moesta* was captured more frequently in harvest-origin compared to fire-origin stands. *Pardosa xerampelina*, the most commonly collected species in 1997, also showed a trend of decreasing relative abundance with increasing stand age. This species was most commonly caught in sampling dates from May and early June. Because sampling did not commence until June in 1996, we cannot establish how this species responded immediately to disturbance by fire and harvesting. Populations of at least three species of linyphiids collected by pitfall traps were strongly reduced by wildfire:

Allomengea dentisetis, *L. intricatus*, and *B. pallidus*. Although these species were initially slow to recover after disturbance by wildfire, they were abundant in both 1968 fire- and harvest-origin stands.

Spiders collected by sweeping the vegetation were primarily web-builders (Fig. 2-8). One linyphiid species, *Helophora insignis* (Blackwall), dominated sweep-net collections, representing 34% of the total catch. This species was most commonly collected in stands originating in 1968.

Species associated with stand conditions following wildfire

Among the species restricted to one stand type, the Linyphiidae was usually the dominant family represented, with the exception of young (1995) stands where wolf spiders (Lycosidae) dominated. Most of the restricted species were represented by 1 - 2 individuals, which precludes confident use of these taxa as indicators of stand preference. However, two more abundant species more clearly exhibited stand preference; *Gnaphosa borea* Kulczyński (20 individuals captured) was collected exclusively in fire-origin stands, and *Arctosa alpigena* (Doleschall) was collected only in 1995 stands, with 15 of the 16 specimens collected in fire-origin stands. Several other lycosid species [*P. hyperborea* (Thorell), *P. uintana* Gertsch, and *Pirata bryantae* Kurata] also showed strong preferences for 1995 fire-origin stands, even though they were not restricted to that stand type.

Discussion

Abundance and diversity

The dominant spider families responded differently to disturbance type and stand age. Lycosids were more commonly collected in young compared to older stands. These hunting spiders are active on the forest floor, and many species are strongly associated with open habitats, especially following forest harvesting (Huhta, 1971; Coyle, 1981; McIver *et al.*,1992; Pajunen *et al.*, 1995). Linyphiids were more abundant in harvested than in burned stands, mainly reflecting a dramatic population increase in the youngest harvested stand age class studied. Linyphiids inhabit complex microhabitats in the leaf litter and soil of forests (Huhta, 1971), and many species in this family are commonly associated with mature or old boreal forests (Koponen, 1995; Pajunen *et al.*, 1995). We suggest that linyphiids may survive harvesting by moving deep into the litter or upper soil layer, whereas an intense, hot wildfire will likely destroy linyphiids and their habitat within the leaf/litter matrix. Our data suggest that it takes 15 - 30 years for populations of some linyphiid species to recover from wildfire.

Spiders collected by sweeping were also more abundant following wildfire than after harvesting. At this point we cannot distinguish between the possibilities that fire-origin stands provide more structural complexity due to presence of high snag densities and DWM, or that prey abundance is differentially affected by the two disturbances. It was observed, however, that webs of the large orb-weaver *Araneus marmoreus* Clerck were frequently placed between adjacent snags in 1995 fire-origin stands.

Fire-origin stands tend to have more diverse spider assemblages than harvest-origin stands. Furthermore, recently burned stands support more even distributions of spiders compared to other stands of the same age, a finding similar to that reported by Collins *et al.* (1996). High evenness may be partially explained by viewing a recent burn as essentially a neutral landscape which initially offers all colonizing spider species a similar chance for survival (i.e., no existing competitors). Although wildfire can completely destroy populations of most spiders (Huhta, 1971; Schaefer, 1980), spiders can rapidly re-colonize via long-distance dispersal (ballooning) or short-distance dispersal (e.g., from unburned forest patches or fire-skips). Over time, however, those unable to survive or reproduce will disappear through a combination of local extinction and movement. Young harvested stands do not support even distributions of spider species as several species (e.g., *P. moesta*) rapidly colonized, and dominated clear-cuts immediately following disturbance. This may partially reflect a landscape effect since overall cut-block size was small in comparison to burned areas, and species such as *P. moesta* may quickly re-colonize open clear-cuts through short-distance dispersal from adjacent forests or cut-blocks whereas re-colonization of large burns would be delayed.

Succession and community patterns

There is convergence in the spider fauna after *ca.* 30 years of forest growth following wildfire and harvesting, but the trajectories of re-colonization depend on disturbance type. Succession of spiders following wildfire lags behind and differs in some important ways from that following harvest. A suite of open-habitat specialists (e.g., *P. moesta*) quickly exploit young clear-cut blocks, and many linyphiid species presumed to be present in the forest before harvesting rapidly re-establish populations in young clear-cuts (e.g., *A. dentisetis*). After *ca.* 15 years of forest growth, the fauna became increasingly dominated by web-building species characteristic of older forests. This coincided with succession of the forest toward canopy closure as suggested by previous studies (Huhta, 1971; McIver *et al.*, 1992).

The 1995 fire-origin stands have vegetation, abiotic conditions and a spider fauna that are most dissimilar to all other stand types (Fig. 2-4). However, successional pathways of spiders and vegetation apparently then diverge. Disturbance type appears to be driving the development of vegetation and abiotic characteristics in 1982 and 1968 stands, whereas stand age is more important for spider assemblages. Thus, spider populations may actually recover faster following wildfire and harvesting than do the vegetation and abiotic elements of the forests.

Certain vegetation characteristics, such as plant species richness, and the presence of mesic plants, appear important for some elements of the spider fauna. Stand conditions that promote plant species richness and favour plants with high moisture requirements also promote linyphiid abundance and to a lesser degree, spider species richness and the abundance of several common species. Surprisingly, there were few correlations between spider data and litter characteristics and shade cover (Table 2-4). This is contrary to past research which demonstrated links between vegetation type or structure and spider communities (Robinson, 1981; Riechert & Gillespie, 1986), and between epigaeic spiders and litter depth and complexity [see Uetz (1991) and references therein].

Our results suggest that it takes forest-dwelling species (primarily in the family Linyphiidae) longer to recover following a wildfire than after harvest. Epigaeic spider populations are destroyed by fire; even *ca.* 15 years after fire, recovery lags behind that in harvested stands of comparable age. In coniferous forests of Europe, Huhta (1971) suggested that spider communities began resembling those of an old pine/spruce forest between 7 and 13 years after prescribed burning and clear-cutting, and in a western coniferous forest McIver *et al.* (1992) reported a recovery by 30 years after clear-cutting. The situation in northern aspen-dominated stands appears to be similar.

Ordination analyses using DCA suggest that spider communities vary more (i.e., greater separation along DCA axis 1) following wildfire than harvest, perhaps in response to the presence of a wider range of microhabitats available for spiders after fire. The young burned stands were substantially wetter than young harvested stands, and pond or bog-associated species, such as *Pirata bryantae* [see Dondale & Redner (1990)], were common in 1995 fire-origin stands. This pattern was also evident from the vegetation survey as many plant species associated with wet forest types were present two years following wildfire, yet were absent or rare two years following harvesting.

Spider assemblages of the1982 fire-origin stands were also more variable than those of the 1982 harvested stands. The latter were closer in species composition to the 1968 stands than to the 1982 fire-origin stands. The habitat in the 1982 fire-origin stands was more variable and more structurally complex than in the 1982 harvest-origin stands. This is due in part to the greater amount of DWM (Fig. 2-3), which increases the habitat heterogeneity and structural diversity on the forest floor in fire-origin stands (Franklin *et al.*, 1987). For example, Lowrie (1948) suggested that fallen logs are important habitats for certain species, and the wolf spiders *P. mackenziana* and *P. xerampelina* have been observed utilizing this habitat for foraging, shelter, and sunning egg sacs (C.M. Buddle, unpubl.).

Species associated with stand conditions following wildfire

Some spider species may require the high habitat heterogeneity of fire-origin stands. For example, the twenty individuals of *G. borea* were collected exclusively from fire-origin stands. This species is relatively rare in Canada, and has been collected under stones, on moss, from wet or marshy areas, and in sphagnum bogs (Platnick & Dondale, 1992; Koponen, 1994). It appears that the usual habitat for *G. borea* is among the wet, moist, complex litter of boreal forests, and this type of habitat may be more plentiful following wildfire than harvest. Similarly, *Pirata bryantae* requires wet habitats and showed a strong preference for young burned stands.

The lycosid species *Arctosa alpigena* was collected only from 1995 stands and the majority of specimens (15 out of 16 individuals) were collected from fire-origin stands. This species has previously been noted as showing a preference for recently burned stands after a wildfire in the boreal forests of northern Quebec (Koponen, 1993), and its typical habitat is reported to be sphagnum bogs, tundra, or in pine or spruce forests (Dondale & Redner, 1990).

A smaller species of wolf spider, *P. hyperborea*, was also most commonly collected in young fire-origin stands (83 out of 108 individuals were collected in 1995 fire-origin stands). The usual habitats for *P. hyperborea* include sphagnum bogs, low-lying spruce forests, rocky hillsides, alpine and arctic tundra, on needle mats in coniferous forests, and in recently burned habitats (Dondale & Redner, 1990; Koponen, 1993; Aitchison-Benell, 1994). Neither *P. hyperborea* nor *A. alpigena* is typically found in aspen forests, and they may have moved into recently burned stands from adjacent coniferous fire-skips. Residual, unburned patches may be similar to the old growth boreal swamp forests of Sweden that are reported to be biodiversity hotspots (Ohlson *et al.*, 1997; Hörnberg *et al.*, 1998), and these fire-skips may also act as source habitats for spider species that re-colonize a burned landscape.

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Table 2-1 Spider families, total number collected (adult specimens only), and number of genera and species collected by pitfall traps (1996 and 1997) and sweep-netting (1997) in three age-classes of aspen stands originating in fire and harvest.

Family	Total number collected	Number of genera	Number of species
Lycosidae	3232	5	14
Linyphiidae	2335	32*	46*
Amaurobiidae	1065	3	3
Liocranidae	316	1	1
Thomisidae	270	3	10
Gnaphosidae	205	7	14
Clubionidae	51	1	5
Theridiidae	37	4	7
Agelenidae	36	1	1
Salticidae	24	4	5
Araneidae	19	5	5
Philodromidae	10	3	5
Tetragnathidae	6	1	4
Hahniidae	3	2	2
Mimetidae	1	1	1

* 4 Linyphiidae species are currently undetermined and not included here.

Table 2-2 Relative abundance, species richness, and dominance measures of spiders in fire- and harvest-origin aspen stands of three ages in north-central Alberta.

	Fire			Harvest			
Year of stand origin:	1995	1982	1968	1995	1982	1968	Total
A) 1996 pitfall traps							
No. mature spiders	288	316	318	740	351	397	2410
No. immature spiders	17	38	12	23	21	17	128
Species richness	30	37	36	41	37	35	76
Berger-Parker dominance	6.1	4.5	5.8	2.3	3.5	3.6	
B) 1997 pitfall traps							
No. mature spiders	719	549	649	1015	1173	872	4977
No. immature spiders	113	76	27	87	79	29	411
Species richness	41	48	37	45	52	50	88
Berger-Parker dominance	2.6	4.5	4.3	3.1	6.8	5.9	
C) 1997 sweep-net							
No. mature spiders	41	32	43	21	39	47	223
No. immature spiders	62	69	69	24	24	31	279
Species richness	16	11	12	9	8	13	29
Berger-Parker dominance	5.8	2.5	1.7	5.2	2.1	1.8	

Table 2-3 Two factor (disturbance type, stand age) ANOVA results for relative abundance of Lycosidae and Linyphiidae families, and 5 species collected by pitfall traps (data pooled for 1996 and 1997). Data are standardized to 500 trap-days or 200 sweeps. NS indicates non-significance at $p > 0.05$. Total catch, and number of *Pardosa mackenziana*, *P. xerampelina*, *Cybaeopsis euopla*, *Bathyphantes pallidus*, and *Trochosa terricola* (pitfall trap samples) NS for disturbance type, stand age, and interaction (disturbance x age).

	Disturbance type	Stand age	Disturbance x Age
A) Pitfall traps			
Lycosidae	NS	$F_{2,6}=5.28$, $p=0.048$	NS
Linyphiidae	$F_{1,6}=7.1$, $p=0.037$	NS	NS
Pardosa moesta	-	-	$F_{2,6}=7.34$, $p=0.024$
Allomengea dentisetis	$F_{1,6}=7.2$, $p=0.036$	NS	NS
Lepthyphantes intricatus	$F_{1,6}=9.13$, $p=0.023$	NS	NS
Amaurobius borealis	-	-	$F_{2,6}=21.5$, $p=0.002$
Agroeca ornata	NS	$F_{2,6}=10.2$, $p=0.012$	NS
B) Sweep-net			
Total number collected	$F_{1,6}=15.8$, $p=0.007$	NS	NS

Table 2-4 Correlation coefficients between environmental variables and spider species richness, total number collected, and relative abundance of Lycosidae, Linyphiidae, and 10 most commonly collected species (pitfall trap data, pooled for 1996 and 1997). Data are standardized to 500 trap-days per stand (n = 12 stands). Significance indicated at * (p < 0.05), ** (p < 0.01), and *** (p < 0.001).

	Plant species richness	Mesic plants	Snags (ha^{-1})	DWM (m^3ha^{-1})	Litter biomass	Litter depth	Shade
Spider species richness	0.59*	0.29	-0.30	-0.35	-0.38	0.24	0.16
Total number collected	0.22	0.04	-0.07	-0.23	0.02	-0.43	0.11
Number of Lycosidae	-0.53	-0.64*	0.48	-0.22	0.37	-0.43	-0.08
Number of Linyphiidae	0.77*	0.63*	-0.61*	-0.14	-0.35	0.01	0.35
Pardosa moesta	-0.04	-0.41	-0.21	-0.21	-0.21	-0.67*	0.46
Allomengea dentisetis	0.37	0.14	-0.60*	-0.06	-0.11	-0.24	0.46
P. mackenziana	-0.34	-0.50	0.03	0.53	0.17	0.26	-0.58*
P. xerampelina	-0.57	-0.44	0.75**	-0.43	0.53	-0.31	-0.04
Cybaeopsis euopla	0.51	0.79**	-0.36	0.02	-0.31	-0.08	0.26
Lepthyphantes intricatus	0.86***	0.77**	-0.54	-0.09	-0.46	-0.06	0.36
Amaurobius borealis	0.86***	0.66*	-0.49	-0.06	-0.40	0.08	0.21
Bathyphantes pallidus	0.81**	0.70*	-0.42	-0.29	-0.38	0.16	0.20
Agroeca ornata	0.67*	0.81**	-0.38	0.41	-0.42	0.24	-0.20
Trochosa terricola	0.13	0.05	-0.24	0.58*	0.14	0.64*	-0.78**

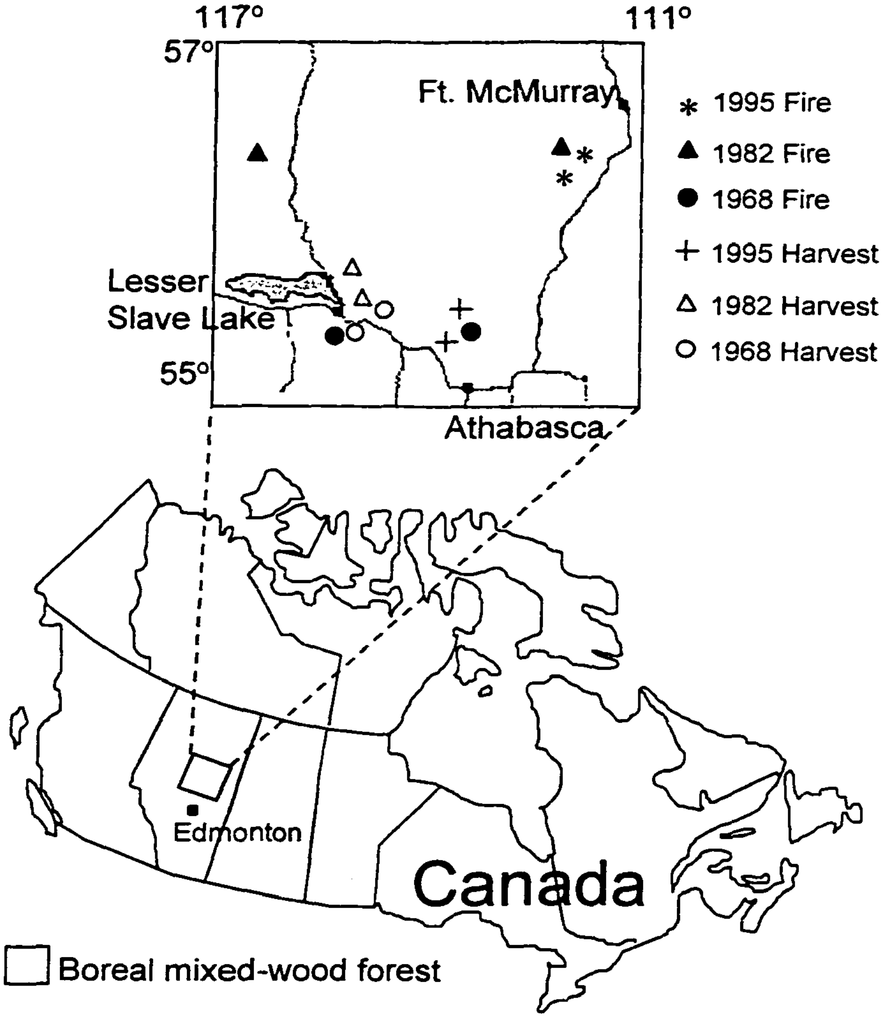

Figure 2-1 Location of study sites in Alberta, Canada.

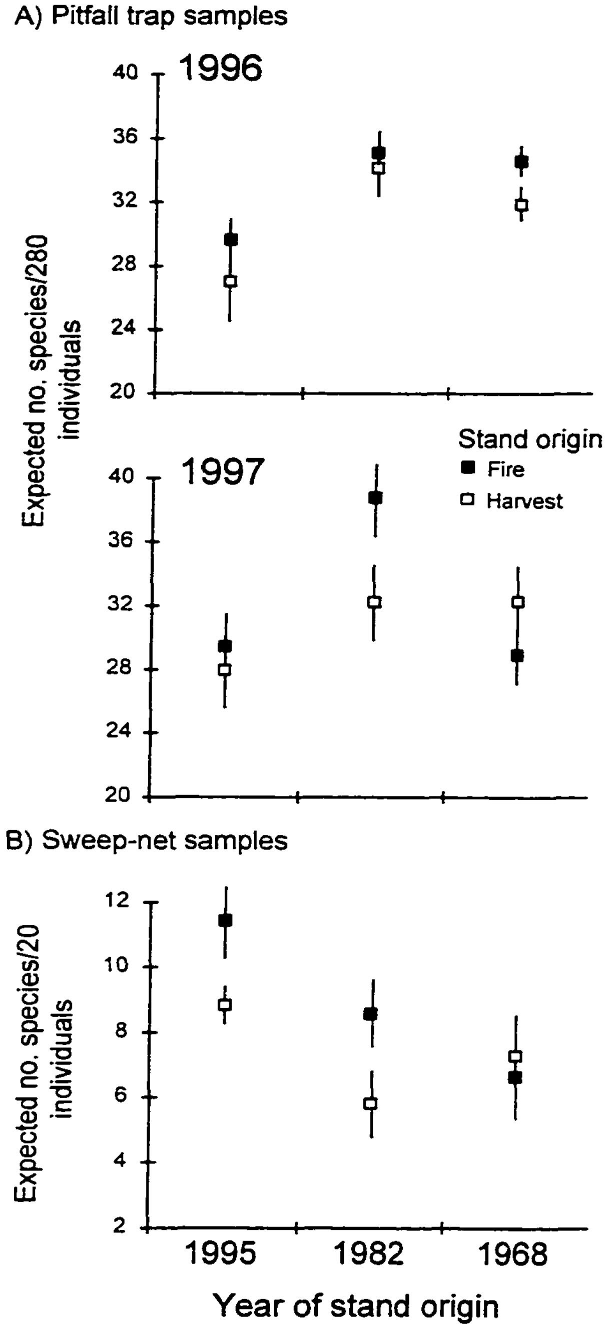

Figure 2-2 Rarefaction estimates of spider diversity in three age-classes of stands originating from fire and harvest. Error bars are 1 standard deviation.

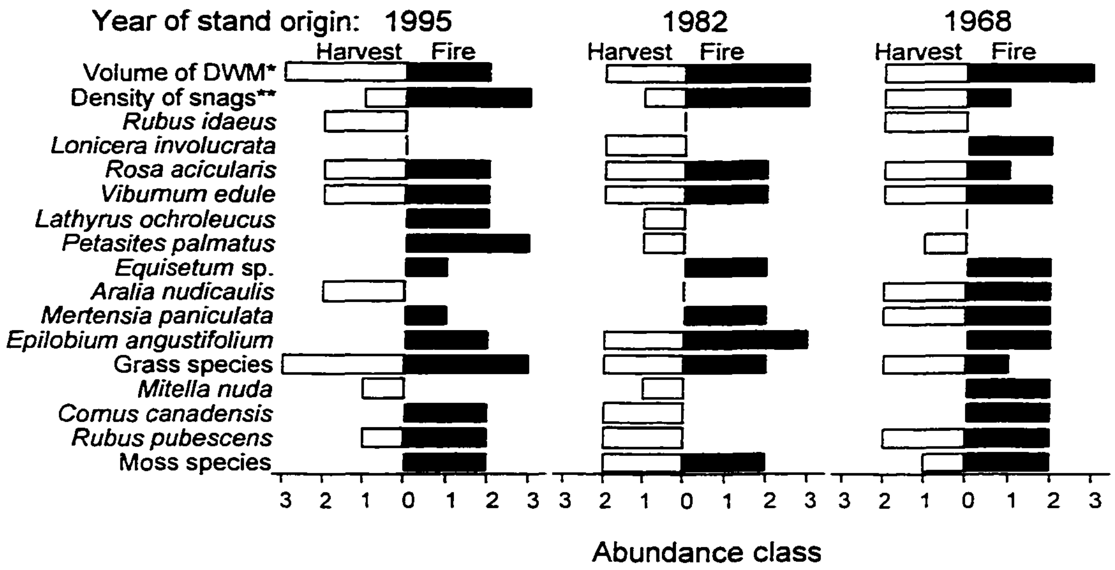

Figure 2-3 Abundance of fifteen dominant plant species, volume of downed woody material (DWM), and snag densities by stand age and origin. Abundance classes (modes from 12 pitfall traps per stand type presented) for vegetation: 0-absent, 1 - <1% cover, 2 - 1% to 20% cover, 3 - >20% cover. *DWM volume classes: 1 - <40 $m^3 ha^{-1}$, 2 - 40 to 80 $m^3 ha^{-1}$, 3 - >80 $m^3 ha^{-1}$. **Snag density classes: 1 - <40 snags ha^{-1}, 2 - 40 to 80 snags ha^{-1}, 3 - >80 snags ha^{-1} (snag and DWM estimates at the stand level).

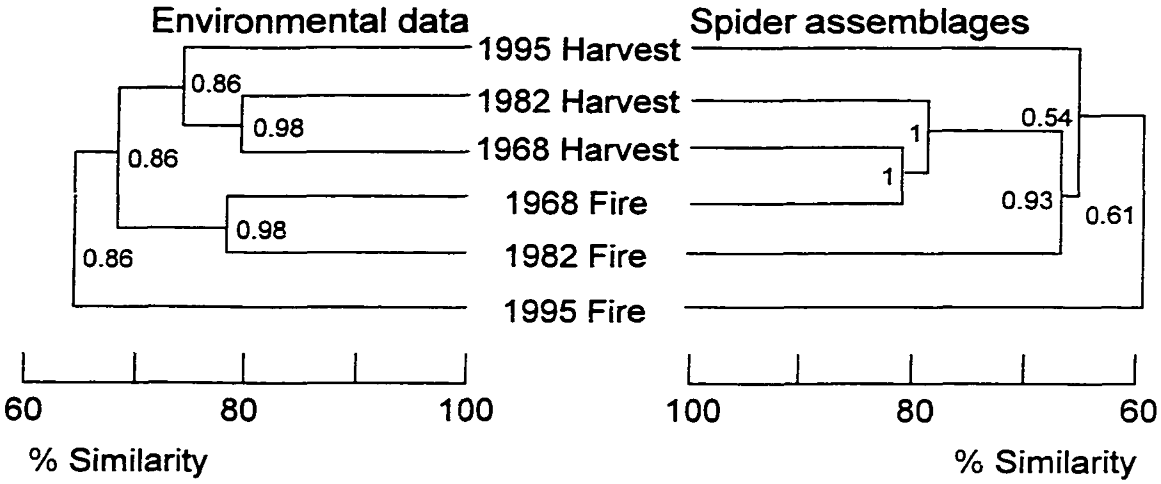

Figure 2-4 Cluster analysis of Bray-Curtis measures of percent similarity for 74 species of spiders from pitfall traps and environmental data. Numbers at each node indicate node stability (74 iterations for spider data, 43 iterations for environmental variables).

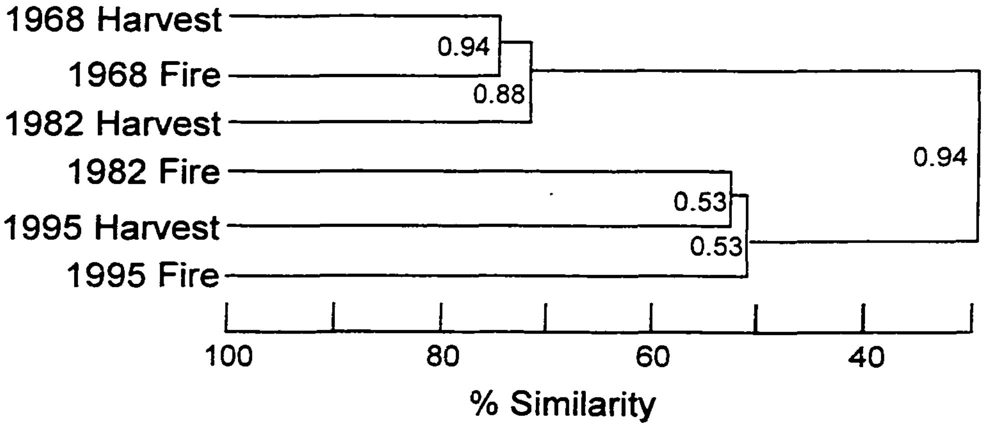

Figure 2-5 Cluster analysis of Bray-Curtis measures of percent similarity for 17 species of spiders from sweep-net collections. Numbers at each node indicate node stability (17 iterations).

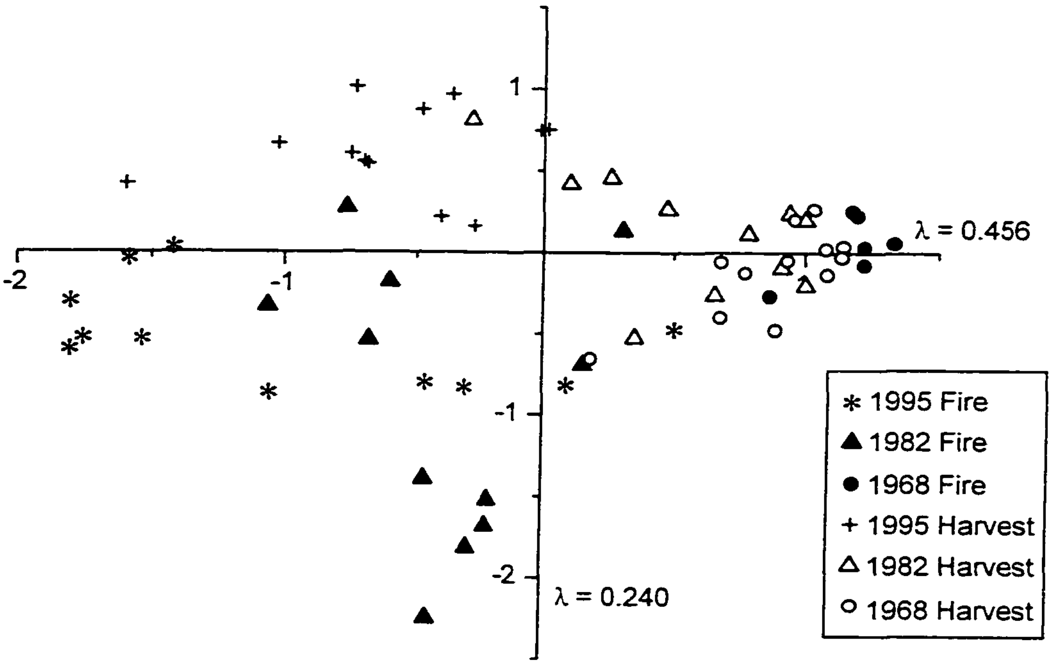

Figure 2-6 Sample scores from DCA ordination (axis 1 and 2) derived from 63 pitfall trap samples and 74 spider species.

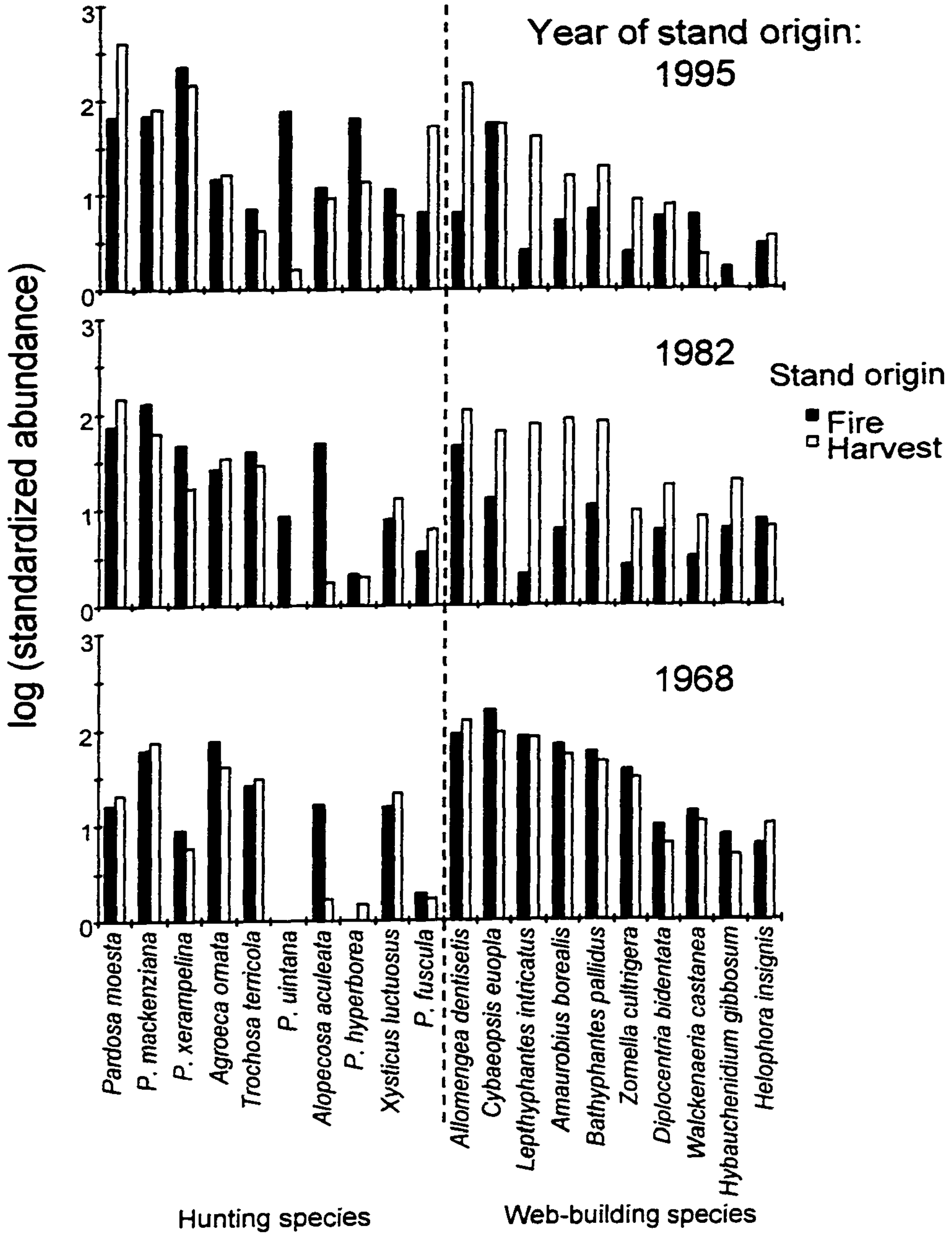

Figure 2-7 Log (standardized abundance) of the most abundant 10 hunting and 10 web-building spider species collected by pitfall traps. These 20 species account for 89% of total abundance.

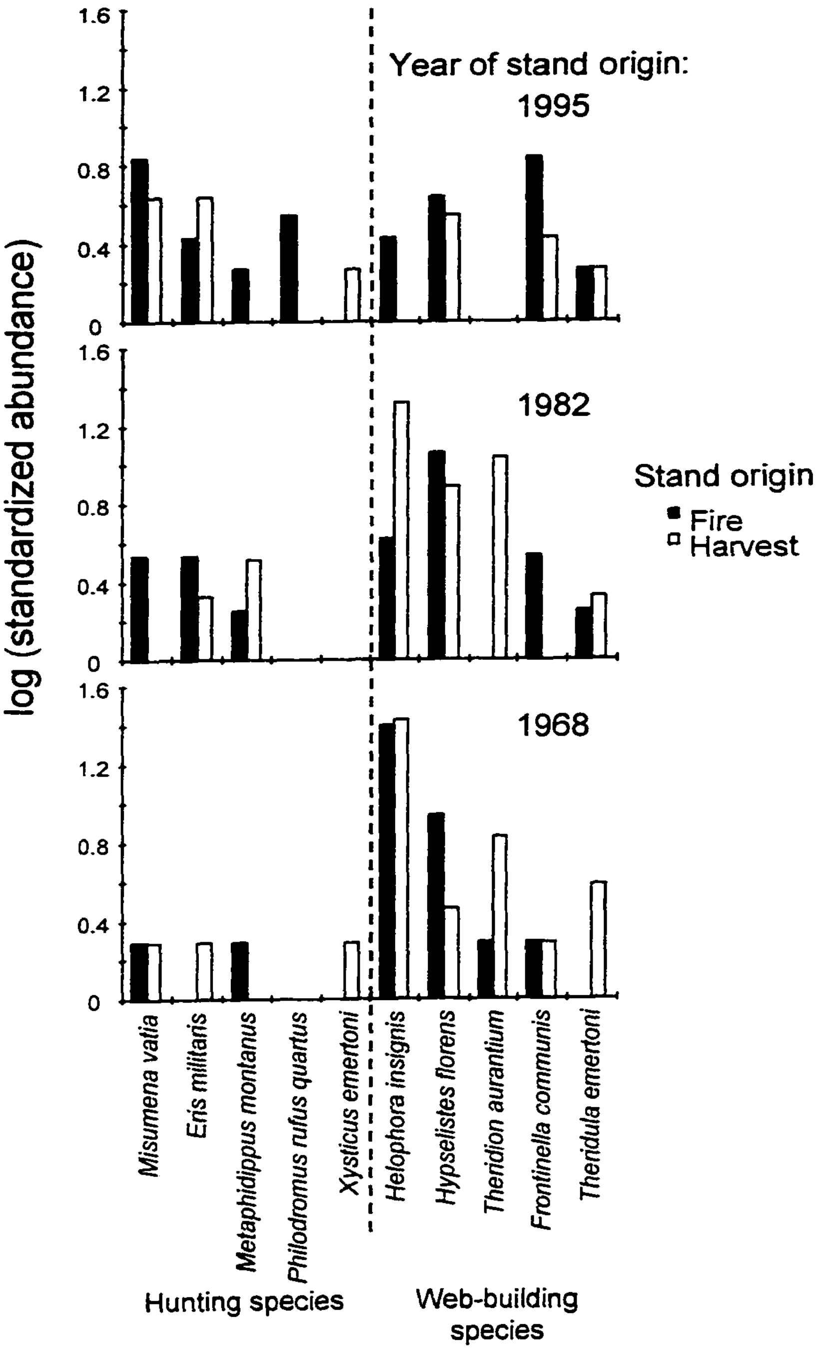

Figure 2-8 Log (standardized abundance) of the most abundant 5 hunting and 5 web-building spider species collected by sweep-net. These 10 species account for 84% of total abundance.

3. The recovery of boreal forest spider assemblages following wildfire and harvesting

Introduction

Previous research has established that ground-dwelling spiders (Araneae) converge on similar species assemblages *ca.* 30 years following disturbance by wildfire and harvesting in *Populus*-dominated boreal forests (Buddle *et al.*, 2000). Immediately post-disturbance, however, the spider fauna differed in some important ways between wildfire- and harvest-origin stands. For example, many web-building species (especially in the family Linyphiidae), presumably present in the forest before disturbance, were slow to recover following wildfire, yet these species persisted following harvest. In general, young forests were dominated by hunting spiders (i.e., wolf spiders, Lycosidae) that showed affinities towards open habitats. By 30 years after disturbance, however, the fauna was dominated by web-building species more characteristic of older forests (Huhta, 1971; Koponen, 1995; Pajunen *et al.*, 1995).

Although there was a strong faunal convergence following the two disturbance types, the study by Buddle *et al.* (2000) failed to address whether or not the ground-dwelling spider fauna recovered to levels characteristic of a pre-disturbance state. This question is of great importance given the increased harvesting demands on hardwood forests in the province of Alberta (Peterson & Peterson, 1992; Pratt & Urquhart, 1994). If the spider fauna does not recover towards levels found in old-growth forests, current harvesting practices may be detrimental to ground-dwelling spider assemblages; the two-pass logging system may not leave enough time between cuts to ensure recovery of species into the original clear-cuts, and aspen is harvested under a short rotation time (i.e., 40 - 70 yr). Ground-dwelling spider assemblages from old and mature mixed-wood stands were therefore compared to spider assemblages from young harvest and wildfire stands [data from Buddle *et al.* (2000)] to assess whether the fauna showed recovery after 30 years post-disturbance.

Methods

The one mature (*ca.* 70 yr) and one old (> 140 yr) mixed-wood stands were sampled in 1992 and 1993 as part of a study on arthropod assemblages in aspen-dominated stands of various ages (Spence *et al.*, 1997). The mature and old stands were located in the same general geographic region as the stands studied by Buddle *et al.* (2000); they were both within a *ca.*13 km radius of the town of Slave Lake, Alberta and located in the mid-boreal ecoregion of Alberta (Strong & Leggat, 1992). The stands studied by Buddle *et al.* (2000) represented three age classes: origin in 1995, 1982, and 1968. Each age class was represented by four forest stands, two with a wildfire origin and two with an origin from clear-cutting. These 12 stands, all > 30 ha in size, were sampled for spiders in 1996 (between 3 June – 24 September) and in 1997 (between 5 May – 23 September). The forest stands used by Buddle *et al.* (2000) were all dominated by *Populus* trees (i.e., trembling aspen *Populus tremuloides* Michx. and balsam poplar *Populus balsamifera* L.); the old and mature forest stands originated in wildfire, were also > 30 ha, and *Populus*-dominated, but contained a slightly higher proportion of coniferous trees [i.e., white spruce *Picea glauca* (Moench) Voss].

Arthropods were sampled using pitfall traps; pitfall traps were 1 L white plastic containers (10 cm diameter) containing a 0.5 L inner sampling cup with 2 - 3 cm of ethylene glycol that acted as a preservative. Traps were covered by an elevated 15 x 15 cm plywood roof to prevent flooding and trap disturbance. Six pitfall traps were placed in each stand and were arranged in a linear arrangement *ca.* 50 m apart, as described by Buddle *et al.* (2000). Trapping in old and mature stands was between 13 May – 12 October in 1992 and between 15 May – 6

October in 1993; on average, traps were emptied every 17 days in 1992 and every 21 days in 1993. With the exception of immature and damaged specimens, all spiders were identified to species; a voucher collection is housed in the Canadian Forest Service arthropod collection at the Northern Forestry Center, in Edmonton Alberta.

To assess the recovery of ground-dwelling spider assemblages following wildfire or harvesting, the data from the old and mature stands were compared to data from Buddle *et al.* (2000). Data were pooled across the two years of sampling and catches standardized to 2000 trap-days (i.e., number of traps days per stand type over two sampling years). Data standardization was necessary because of unequal sampling effort among stands. Rarefaction analysis was used to compare spider diversity in the different stand 'types'. Ordination, using detrended correspondence analysis (DCA), was done on individual trap data, with traps experiencing frequent disturbance removed prior to analysis (Buddle *et al.*, 2000). Trap disturbances were low in the old and mature forest stands and hence all data were used in the DCA. Additionally, rank abundance plots were compared between the different disturbance types, and were separated on the basis of the primary mode of prey capture for the dominant spider species collected (i.e., hunting and web-building species). The 10 most common hunting and web-building species were ranked based on their abundance in samples from old and mature forest stands and this ranking was compared with the rank abundance of species collected in the younger forest age classes.

Results and Discussion

A total of 1833 spiders representing 47 species was collected in the old and mature forest stands (Appendix 1). Of the 110 species collected over both studies, only 5 species were caught exclusively in the old and mature stands (Appendix 1). Four of these species were represented by fewer than 6 individuals;

the crab spider *Xysticus obscurus* Collett by 18 individuals. The presence of *X. obscurus* in these forests is likely a function of habitat rather than forest age as this species is usually collected in coniferous forests (Dondale & Redner, 1978), and the old and mature stands had more white spruce than the younger stand age classes.

The fauna of the old and mature stands consisted largely of web-building species in the family Linyphiidae (50% of the total catch), and wolf spiders (family Lycosidae) accounted for 13% of the total catch. In contrast, younger age-classes of forests were numerically dominated by lycosids (44%), and linyphiids represented 30% of the total catch (Buddle *et al.*, 2000). The differences between the two data-sets largely reflect the very high capture of lycosids in the youngest wildfire and harvest stands studied (Buddle *et al.*, 2000).

The four most common linyphiids, *Allomengea dentisetis* (Grube), *Lepthyphantes intricatus* (Emerton), *Helophora insignis* (Blackwall), and *Bathyphantes pallidus* (Banks) accounted for 48% of the total catch in old and mature stands. Although linyphiids typically dominate old-growth forests (Koponen, 1995, 1999), the common linyphiids collected cannot be classified as old-growth dependent since they were also frequently collected in younger stand age-classes (Buddle *et al.*, 2000). This finding is consistent with research in boreal forests of Finland, as Pajunen *et al.* (1995) also suggest few spider species in these forests can be considered dependent on older stands. Only one lycosid, *Pardosa mackenziana* (Keyserling), was commonly collected in old and mature forest stands (229 individuals), reflecting the ubiquity of this species in a wide range of forest types (Dondale & Redner, 1990; Buddle *et al.*, 2000).

When the rank abundance of hunting and web-building species are compared among the different stand types, it is evident that by *ca.* 30 years after wildfire and harvest, the dominant spider species are approaching abundance typical of old and mature forests (Fig. 3-1). The hunting spiders that were numerically dominant immediately following disturbance [e.g., *Pardosa moesta* Banks and *P. xerampelina* (Keyserling)] are still above levels found in old and mature forests, but show a trend towards decreased abundance in the older forest age-classes. Other hunting species such as *P. mackenziana* and *Agroeca ornata* Banks show an almost complete recovery *ca.* 30 years post-disturbance (Fig. 3-1). With the exception of the linyphiid *H. insignis*, most web-building species also show similar catches in 30-year old forests compared to old and mature forests (Fig. 3-1). The web-building species that were originally slow to recover following wildfire (e.g., *A. dentisetis*, *L. intricatus*, and *B. pallidus*) had recovered to levels typical of old and mature forests by *ca.* 30 years post-disturbance.

At a sub-sample size of 860 individuals, the rarefaction estimates show that the diversity of spiders in the old and mature stands was significantly lower than in the younger stand age-classes (Fig. 3-2). The 30 year old stands (stand origin in 1968) supported a higher diversity than old and mature stands, largely reflecting that the fauna in these stands is still in transition. Together with web-building species characteristic of older forests, many open-habitat species such as *P. moesta* and *P. xerampelina* still maintain populations in 30 year old stands, possibly relicts of their high populations in young, open-canopy forests (Buddle *et al.*, 2000). Pre-climax *Populus* forests therefore have more diverse spider assemblages than old and mature mixed-wood stands and also harbour most of the species found in older stands.

Ordination results from the DCA reveal little variation between pitfall traps placed in old and mature stands compared to other stand types (Fig. 3-3), and these pitfall traps occupy a similar space in the ordination with traps from 30 year (i.e., origin in 1968) wildfire and harvest stands. As previously noted by Buddle *et al.* (2000), the youngest wildfire and harvest stands showed the highest variation in pitfall trap catches, possibly reflecting the higher habitat heterogeneity present immediately following disturbance. These results suggest that not only is the ground-dwelling spider fauna from old and mature stands homogeneous, it is also virtually indistinguishable from the overall community composition in 30 yr old wildfire and harvest stands.

A DCA using only the 30 year old stands and the old and mature stands was also done to evaluate how the ordination using all stands may be influenced by the younger stand age-classes. This ordination (Fig. 3-4) poorly explains variation within the pitfall trap data, as indicated by the low eigenvalues for axis 1 and 2 and the low total inertia [i.e., total variance of species data (ter Braak, 1990)] of 0.944. This further supports the hypothesis that closed-canopy forests have a relatively homogeneous spider fauna. However, this analysis also suggests that the spider fauna from old and mature stands does differ from the assemblage of spiders from 30 year harvest and wildfire stands, as most of the samples from old and mature stands occupy a different space in the ordination from 1968 wildfire and harvest stands (Fig. 3-4).

After 30 years of forest growth, ground-dwelling spider assemblages show a strong faunal convergence following wildfire and harvest, and show some degree of recovery to levels typical for pre-disturbance forests. In general, current forest harvesting practices may have few detrimental effects on ground-dwelling spiders. These conclusions, however, are limited by the scope of the research in design (i.e., only two stands were studied for each age-class) and by the nature of a chronosequence study. The only way to truly assess the recovery of the spider fauna would be to sample the stands used by Buddle *et al.* (2000) over a longer time period. Even after 30 years post-disturbance, there were still some elements of the spider fauna that differed between wildfire and harvest (Buddle *et al.*, 2000), and between the old and mature fauna and the fauna from younger age-classes. Diversity, for example, was much lower in the old and mature stands, and the overall assemblage in old and mature forests was more homogeneous than the younger stands. Ordinations of the 30 year stands and the old and mature stands also suggest the fauna has not fully recovered following disturbance by wildfire and harvest.

Conclusions from the study are also limited by the study taxon. Inclusion of other arthropod groups may provide different results. Beetles (Coleoptera: Carabidae and Staphylinidae) were also collected and identified from the study stands and preliminary analysis of the full data-set (i.e., using 223 species of spiders and beetles) suggest a faunal convergence occurs by *ca.* 30 years after wildfire and harvesting, but a recovery is not apparent (Buddle, C.M., J.S. Spence, D.W. Langor, & G.R. Pohl, unpublished). Although spiders show a rapid recovery following disturbance, beetles appear to differ dramatically in their successional trajectories. Providing guidelines for management must take into account variation among taxa, and when possible, should include results from as many taxa as possible.

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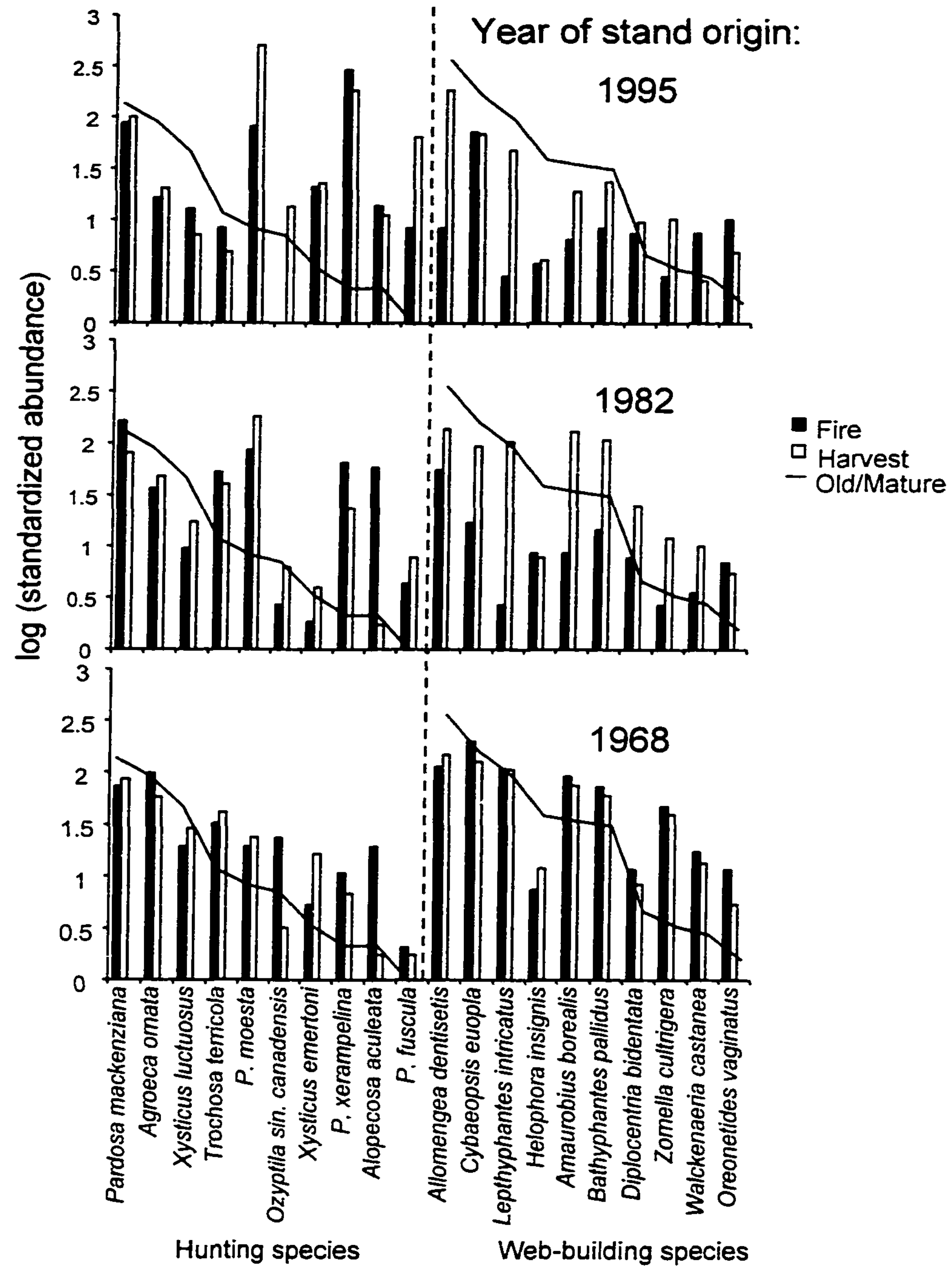

Figure 3-1 Log (standardized abundance) of the most abundant 10 hunting and 10 web-building spider species collected by pitfall traps in younger stand age-classes (stand origin in 1995, 1982, and 1968) originating by wildfire and clear-cutting and in old and mature forest stands. Species are ranked by their abundance in old and mature stands.

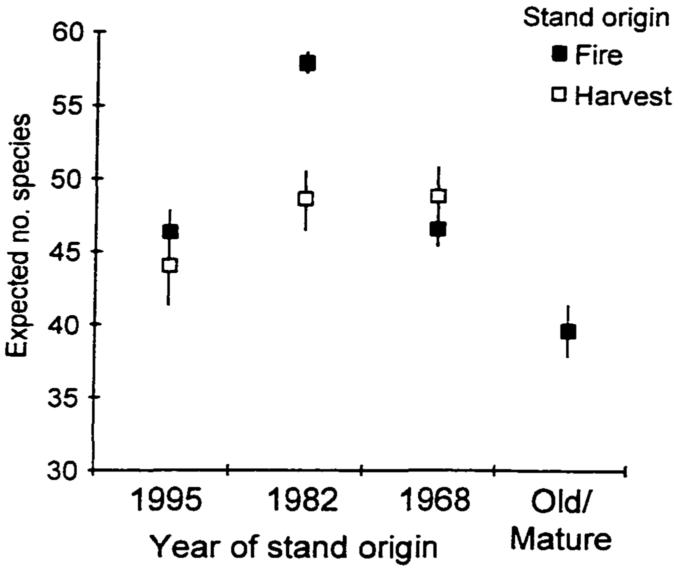

Figure 3-2 Rarefaction estimates of spider diversity in four age-classes of stands (originating in 1995, 1982, 1968, by fire and harvest, and old and mature stands) at a sample size of 860 individuals. Error bars are 1 standard deviation.

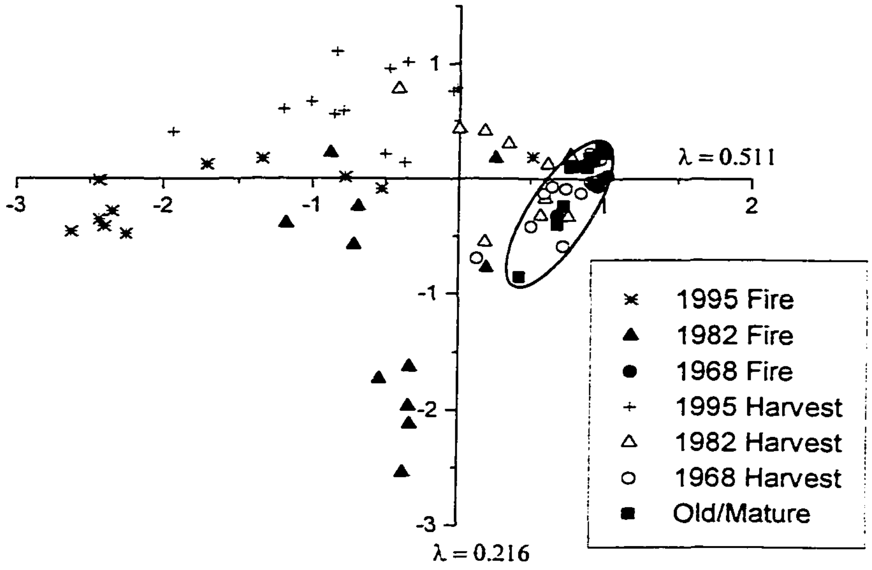

Figure 3-3 Sample scores (pitfall traps) from DCA ordination (axes 1 and 2) for 110 spider species collected in four stand age classes [originating in 1995, 1982, 1968, by fire and harvest, and old and mature stands (enclosed by ellipse)].

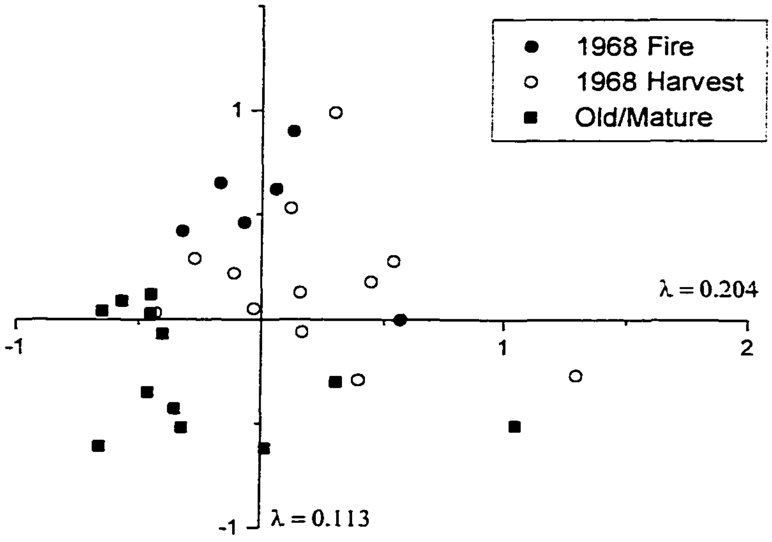

Figure 3-4 Sample scores (pitfall traps) from DCA ordination (axes 1 and 2) for 73 spider species collected in 1968 fire- and harvest-origin stands, and old and mature stands.

4. Life history of *Pardosa moesta* and *P. mackenziana* in central Alberta*

Introduction

Wolf spiders in the genus *Pardosa* C.L. Koch are among the most conspicuous and abundant of the ground-dwelling spiders. However, little is known about the life history of many northern species of this genus in North America, even though 46 species are found in Canada, at least 8 of which are distributed widely across the country (Dondale & Redner, 1990). Two of these species, *Pardosa moesta* Banks and *Pardosa mackenziana* (Keyserling), have been noted as being among the most abundant wolf spiders collected in deciduous forests of north-central Alberta (Buddle *et al.*, 2000).

Significant progress has been made in understanding the ecology and biology of many *Pardosa* species in Europe, Japan, and southern latitudes in North America (e.g., Hallander, 1967; Vlijm & Kessler-Geschiere, 1967; Miyashita, 1968, 1969; Edgar, 1971, 1972; Dondale, 1977; Greenstone, 1980; Oraze *et al.*, 1989; Samu *et al.*, 1998). It is commonly thought that most spiders living in temperate zones have annual life-cycles (Gertsch, 1979), and this is true for many *Pardosa* from various regions including Europe, southern Canada, and the United States (Vlijm & Kessler-Geschiere, 1967; Schmoller, 1970; Dondale, 1977; Oraze *et al.*, 1989). However, several *Pardosa* species studied from high altitudes, northern latitudes, and under cooler conditions require more than one

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* A version of this chapter has been published. Buddle, C.M. (2000) *Journal of Arachnology*, **28,** 319-328.

year to complete their development (Leech, 1966; Schmoller, 1970; Edgar, 1971b).

Other characteristics such as natural densities of *Pardosa* species and estimates of clutch size are known for many species in the United States and some regions in Canada (e.g., Eason, 1969; Schmoller, 1970; Dondale, 1977; Lowrie & Dondale, 1981), and various species from Europe (e.g., Edgar, 1971b; Kessler, 1971). For example, Dondale (1977) reported densities of *P. saxatilis* (Hentz) between 0.8 to 4.4 m^{-2} in southern Ontario, and as part of a detailed study of *P. lugubris* (Walckenaer) in Scotland, Edgar (1971b) reported densities of various life stages between 1.7 and 6.2 m^{-2}. There are also a variety of published records on the average clutch size for many *Pardosa* species, and these range from as low as 25.5 eggs per female for the small species *P. saxatilis* to a high of 82.0 eggs per female for the larger *P. amentata* (Clerck) (Marshall & Gittleman, 1994).

During 1998 and 1999 I studied life history characteristics of *P. moesta* and *P. mackenziana*. The objectives were to determine the natural densities of these species, establish their clutch sizes and assess whether the number of offspring is determined by female size, and to ascertain the life cycles of *P. moesta* and *P. mackenziana* in deciduous forests of central Alberta, Canada.

Methods

Study site and species descriptions

This work was done at the George Lake Field Site located 75 km northwest of Edmonton, Alberta (ca. 53°57'N, 114°06'W). There are approximately 180 ha of continuous deciduous forest at the field site, which is surrounded by agricultural land to the south and west, a lake to the east, and more than 500 ha of continuous deciduous forest to the north. Dominant tree species include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), birches [*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)], and patches of white and black spruce [*Picea glauca* (Moench) Voss and *P.*

mariana (Mill.) BSP]. The study area for this research was a 2.2 ha area of upland aspen forest (Niemelä *et al.*, 1992).

Pardosa moesta and *P. mackenziana* are among the most abundant wolf spiders found on the forest floor at George Lake; other *Pardosa* species encountered less frequently include *P. xerampelina* (Keyserling), *P. fuscula* (Thorell), *P. distincta* (Blackwall) and *P. ontariensis* Gertsch. *Pardosa moesta* has general habitat affinities including meadows, hayfields, marshes, bogs, lawns, gravel pits, clear-cuts, rocky shores, and deciduous forests (Wolff, 1981; Dondale & Redner, 1990; Buddle *et al.*, 2000). Lowrie (1973) has suggested that western populations of *P. moesta* occur more often in wet habitats from various elevations. *Pardosa mackenziana* is usually associated with coniferous forests although known to inhabit salt marshes, bogs, beaches, and deciduous forests (Lowrie, 1973; Dondale & Redner, 1990; Buddle *et al.*, 2000).

In a study of spider assemblages in north-central Alberta, Buddle *et al.* (2000) found that *P. moesta* and *P. mackenziana* co-occur in a variety of different age-classes of deciduous forest stands. The proportions of the two species, however, differed depending on whether the forest stand had a closed canopy. In open stands, 67.3% of the total catch of the two species was *P. moesta*. In closed canopy stands the situation was reversed as 67.8% of the total catch of the two species was *P. mackenziana*.

Pardosa moesta and *P. mackenziana* are easily distinguished in the field based on their size and coloration. *Pardosa moesta* is the smaller of the two species, with an average body length of 4.95 mm for males and 5.64 mm for females, whereas the average length for *P. mackenziana* is 5.91 mm for males and 6.85 mm for females (Dondale & Redner, 1990). Adult and sub-adult male *P. moesta* have a dark, shiny carapace in contrast to the lighter brown carapace with its lighter median band on male and female *P. mackenziana*. Female *P. moesta* have a dark carapace with faint median and submarginal bands. It is also possible to distinguish between immature stages of the two species based on subtle difference in the coloration and patterns on the carapace; immature *P.*

mackenziana have distinct white setae that outline a V-pattern on the median region of the carapace. The white setae on the carapace of immature *P. moesta* are arranged in a more scattered pattern on the carapace. Additionally, the carapace of immature *P. mackenziana* is a deeper brown colour than the carapace of immature *P. moesta*. Voucher specimens of both species are deposited in the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, Canada.

Density estimates

Densities of *Pardosa* were estimated by haphazardly placing an upright bucket (28 cm diameter, 23 cm height) with its bottom removed on the forest floor. After the bucket was firmly placed on the forest floor the enclosed leaf-litter was searched for wolf spiders [similar to quadrat sampling used by Edgar (1971)]. Individual *Pardosa* were identified, counted, and brought to the laboratory. This procedure was repeated 241 separate times between 23 April – 15 June 1999. Three different life-stages were classified for both species: immatures, sub-adults, males, and females. Results from the bucket estimates were extrapolated to the number of *Pardosa* of different life stages per m^2 of forest floor, separated into three sampling periods of approximately equal lengths (23 April – 10 May, 11 May – 27 May, and 28 May – 15 June).

Fecundity

Female *P. moesta* and *P. mackenziana* carrying egg sacs, or those appearing to be gravid (i.e., found with swollen abdomens), were collected on an opportunistic basis (i. e., when they were seen during other field work and/or during specific searches for *Pardosa*) during the spring of 1998 and 1999 in order to assess fecundity and relationships between female size and clutch size. Many *Pardosa* species are known to produce more than one egg sac in a given season (Miyashita, 1969; Edgar, 1971b; Wolff, 1981). However, all collections were made early in the season, ensuring that catches did not contain females with second egg sacs, which are known to contain fewer eggs (Miyashita, 1969; Edgar, 1971a). Data about size and fecundity were collected for a total of 66 *P. moesta* and 73 *P. mackenziana*. Live females were gently held between a piece of soft foam and a clear plastic petri dish and their carapace width (CW) was measured to the nearest 0.01 mm using an ocular micrometer. CW is easily measured and thought to be a good indicator of overall spider size, as has been shown for both web-building and hunting spiders (Hagstrum, 1971; Spiller & Schoener, 1990; Wise & Wagner, 1992; Zimmermann & Spence, 1992). Spiders were held at 25°C under long-day photoperiod (16 hr light: 8 hr dark) in clear film canisters with moistened plaster-of-paris on the bottom to maintain humidity [similar to the procedure outlined by Wise & Wagner (1992)]. Many females produced egg sacs in captivity, and for most female spiders, spiderlings were allowed to hatch to determine clutch size. Due to time constraints, however, some of the specimens were placed immediately in 70% ethanol, and egg sacs were later dissected for measures of clutch size. Linear regression was used to assess the relationships between female size and number of offspring produced for each species.

Life cycle

Adult population dynamics

The activity of adult wolf spiders can be assessed by using a sampling technique such as pitfall trapping. Pitfall trap catches depend on spider activity so absolute density estimates, for example, are not possible with such data. However, pitfall trap data can be used to infer the peak reproductive period for spiders as during this time male and female spider activity increases. In the present study, data generated from live-trapping and mark recapture using pitfall traps are used only to assess the activity of adult *Pardosa*, the peak reproductive period, and the duration of female survival. This work was completed from May to August 1998 using enclosures previously used for experiments with ground beetles [see Niemelä *et al.* (1997)]. Enclosures were located 50 - 60 m from the area where density estimates were obtained. Three sets of enclosures measuring 4 x 24 m in length (subdivided into six compartments per enclosure, each measuring 4 x 4 m) were made in 1989 by sinking 3/4" (*ca.* 2.0 cm) plywood 30 cm into the ground, leaving 40 - 45 cm above ground. All seams were sealed with caulking and a strip of aluminium flashing 10 cm wide was screwed or nailed to the top part of the walls. Experiments were designed based on the assumption that *Pardosa* species would be unable to move between compartments. However, both *P. moesta* and *P. mackenziana* were observed climbing between compartments; nevertheless, it was still possible to monitor the population dynamics of adult wolf spiders within the enclosures and to assess the length of female survival.

Eight pitfall traps without preservative were placed in each of the 18 compartments. Traps were 1 L plastic containers sunk into the ground so that the trap lip was flush with the substrate. Funnels were placed in the traps to prevent spiders from escaping. Traps were opened and monitored three to four times per week from early May until mid-July and about once per week until the end of August. I recorded the sex of captured *P. moesta* and *P. mackenziana*, and recorded whether females carried egg sacs.

Sixty *P. moesta* and 48 *P. mackenziana* females carrying egg sacs were marked and released on 16 June into the aforementioned compartments. Spiders were marked with a small dot of enamel paint on the carapace. A small hole was drilled into a petri dish that was placed over the spider being gently held on a piece of foam; females were manoeuvred on the foam pad so their carapace was directly below the hole and a toothpick dipped in paint was inserted through the hole to place paint on the carapace. Marked females were monitored along with other live trap catches in the compartments to estimate how long individual *P. moesta* and *P. mackenziana* females survive in the field.

Juvenile growth and development

Understanding population dynamics of adult spiders is insufficient for an adequate understanding of life-cycles; additionally, it is essential to determine the growth of juvenile spiders through the course of the summer, and to establish the overwintering stage. As part of an experiment investigating the competitive interactions between *P. moesta* and *P. mackenziana*, a number of newly dispersed spiderlings were released into small arenas. The arenas were white buckets with the bottoms removed, measuring 28 cm in diameter and 23 cm in height. The buckets were sunk 5 - 7 cm into the ground on 8 July 1998 and covered with fine mesh to prevent immigration and emigration. Newly dispersed spiderlings were obtained from female *P. moesta* and *P. mackenziana* used for fecundity estimates. Spiderlings from more than 10 females of each species were bulk weighed in groups of ten. A total of 237 *P. moesta* and 234 *P. mackenziana* was placed in 12 arenas between 13 July – 21 July 1998. In September 1998, the leaf litter from within the arenas was sifted and searched for *Pardosa* specimens. These were weighed and then immediately returned to the arenas. As soon as the snow melted in the spring of 1999, the litter within the arenas was searched a final time and *Pardosa* were counted and weighed.

Spring cohorts

To better understand what life-stages of *P. moesta* and *P. mackenziana* overwinter in central Alberta, the specimens retained from the density estimates were weighed to the nearest mg. Some additional specimens were collected on an opportunistic basis through until 30 June 1999 to increase the sample size for these estimates. It was assumed that if these species are annual, only one weight class of individuals would be present following the overwintering period. Species requiring two years to complete development should show two size classes of individuals at the time of spring emergence, and three size classes of individuals during the reproductive period (Dondale, 1961; Edgar, 1972).

Results

Density estimates

A total of 117 *P. moesta* and *P. mackenziana* was counted during the 241 density estimate samplings. Immature *Pardosa* represented the most frequently encountered spiders, and had the highest density estimates during most sampling periods (Table 4-1). Densities of sub-adults were highest between 23 April – 27 May and decreased in the final sampling period; adults increased in density in the last two sampling periods (Table 4-1). Males of both species were encountered infrequently during the survey and thus their density estimates were low in comparison to other life stages (Table 4-1). Female densities averaged 0.88 m^{-2} for *P. moesta* and 0.60 m^{-2} for *P. mackenziana.*

Fecundity

Pardosa moesta was the smaller of the two species with a mean (± SE) CW of 2.1 ± 0.02 mm, and its average clutch size was 33.1 ± 1.29 eggs or spiderlings per egg sac. *Pardosa mackenziana* had an average CW of 2.7 ± 0.02 mm and a mean clutch size of 48.4 ± 1.67. Both species showed a significantly positive relationship between female size and clutch size using linear regression (Fig. 4-1). However, very little of the variation in clutch size was explained by female size as indicated by the low R^2 values [especially for *P. mackenziana* (Fig. 4-1B)].

Life cycle

Adult population dynamics

Live-trapping data show that male and female *P. moesta* were most active in mid-May and early June (Fig. 4-2A). Peak activity of *P. mackenziana* males and females was slightly later; they were most frequently caught between late May and mid-June (Fig. 4-2B). Spider activity is known to vary with temperature (Dondale & Binns, 1977). The high variation in live catches of adult *Pardosa* in

May and June was partially explained by variation in the mean daily temperatures during the spring (temperatures were obtained from a weather station at Sion, Alberta, 14 km south-west of the George Lake Field Site); warm days often corresponded to peaks in adult *Pardosa* activity (Fig. 4-2).

Females carrying egg sacs were caught from 3 June – 25 August for *P. moesta* and from 21 May – 25 August for *P. mackenziana* (Fig. 4-2). Therefore, spiderlings could be active from late spring and into the autumn months for both species. The late season catches of females carrying egg sacs likely corresponded to the production of a second or third egg sac.

Marked females were released on 16 June and individuals of both species were re-captured at various times throughout the summer (Fig. 4-2). Two marked *P. moesta* were re-captured on 11 August, showing that females live at least 56 days in the field after being collected, marked and returned to the enclosures on 16 June. Female *P. mackenziana* were not found in the enclosures as long as *P. moesta*; the latest re-capture for *P. mackenziana* was 21 July, 35 days after release.

Juvenile growth and development

Spiderlings released into arenas at the beginning of this experiment (13 July – 21 July) had an average weight of 0.45 ± 0.022 mg for *P. moesta* and 0.58 ± 0.028 mg for *P. mackenziana*. Weights in September were 1.32 ± 0.200 mg for *P. moesta* ($n = 29$), and 1.28 ± 0.103 mg for *P. mackenziana* ($n = 34$). Thus, *Pardosa moesta* spiderlings gained on average 2.9 times their weight, and *P. mackenziana* 2.2 times their weight between mid-July and September, 1998. Leaf-litter from the arenas was sifted and searched again on 23 April 1999; four *P. moesta* with an average weight of 1.25 ± 0.289 mg and five *P. mackenziana* with an average weight of 1.40 ± 0.274 mg overwintered in the arenas. Although the arenas only approximated natural conditions, some spiders survived the winter and did not gain weight between September 1998 and April 1999.

Spring cohorts

Spider weights from individuals retained from the density estimates indicate that two life stages, and a few larger individuals, were present immediately following winter (23 April – 13 May) (Fig. 4-3). During the peak reproductive period (13 May – 30 June), three life stages were present for both species (Fig. 4-3). The majority of specimens collected fell below the average weight of adult specimens (Fig. 4-3). Although adult *P. moesta* and *P. mackenziana* showed a peak in activity from mid-May until late June, which would correspond to the reproductive period (Fig. 4-2.), many smaller instars (i.e. < 5 mg in size) of both species were also present on the forest floor during this time (Fig. 4-3).

Taken together, results from the population dynamics of adults, juvenile growth and development, and from the weight classes of spring cohorts suggest *P. moesta* and *P. mackenziana* take two years to complete development in central Alberta. Both species have the same generalized life-cycle (Fig. 4-4); the only notable difference in life-cycles between the two species is that *P. moesta* has an earlier reproductive period than *P. mackenziana* (Fig. 4-2). Both species appear to have at least two overwintering periods: one as immatures and one as sub-adults (Fig. 4-4).

Discussion

Density

Densities of sub-adult and adult *P. moesta* and *P. mackenziana* were below 2.0 m^{-2} during all sampling periods and immature densities were all below 3.0 m^{-2}; these estimates were lower than has been reported for other species of *Pardosa*. In Scotland, for example, Edgar (1971b) reported immature *P. lugubris* densities as high as 6.2 m^{-2} for shaded areas in the spring. However, immature *P. lugubris* were also found to have low densities in clearings (Edgar, 1971b); different life-stages of *Pardosa* may use different habitats and their densities would thus vary depending on habitat type. Immature *P. lugubris* move from clearings to overwintering areas in the autumn, and female *P. lugubris* carrying egg sacs may search for open areas in which to sun their egg sacs and deposit their young (Edgar, 1971). Adult *P. moesta* are known to attain high populations in open, grassy regions (e.g., Dondale & Redner, 1990; Buddle *et al.*, 2000), which are common in the agricultural landscape within 100 - 200 m of the George Lake study area. Although *P. moesta* can certainly maintain populations in a closed canopy deciduous forest, densities of this species may be higher in more open habitats. Similarly, *P. mackenziana* may have higher densities in coniferous forests where this species is reported to be most commonly collected (Dondale & Render, 1990).

Although densities of immature *P. moesta* and *P. mackenziana* remained between 1.29 and 2.99 m^{-2} during all three sampling periods at George Lake, sub-adult and adult densities varied more dramatically by sampling period. Sub-adult densities of both species decreased as spring progressed as sub-adults moulted to sexually mature adults during the peak reproductive period from mid-May to late June. Male densities were low for both species, which may reflect their higher mobility; males may have been better able to escape when the bucket was placed on the forest floor.

Fecundity

Measures of both female spider size and fecundity varied considerably in *P. moesta* and *P. mackenziana*. Overall, however, both species were substantially larger than the average for Canada. *Pardosa moesta* has previously been reported as having an average CW (± 1 SD) of 1.91 ± 0.14 mm ($n = 20$) and the average CW for *P. mackenziana* has been reported as 2.55 ± 0.17 mm ($n = 136$) (Lowrie & Dondale, 1981; Dondale & Redner, 1990). Clutch size of 48.4 for *P. mackenziana* is close to the estimate of 50 reported by Lowrie & Dondale (1981) but was substantially lower than the estimate of 57.5 provided by Schmoller (1970) for alpine populations in Colorado.

In general, the average female size of a spider species is positively correlated with average clutch size (Marshall & Gittleman, 1994). Using data from Schmoller (1970), Lowrie & Dondale (1981), Marshall & Gittleman (1994), and my unpublished data for *P. xerampelina*, I used linear regression to assess the strength of this relationship for *Pardosa* species. Using data for 14 species of *Pardosa*, there is a positive relationship between species size and clutch size, and close to two-thirds of the variation in clutch size is explained by species size ($R^2 = 0.62$, Fig. 4-5). Clutch size for *P. moesta* at George Lake is close to what can be expected based on its size alone. However, the estimates for *P. mackenziana* from George Lake fell farther below what was expected, and out of the 95% confidence limits for the regression line (Fig. 4-5). Thus, understanding variation in fecundity demands more than simply an understanding of size.

Within a species, however, there are strong relationships between female size and fecundity for both web-building and hunting spiders (e.g., Wise, 1979, 1993; Enders, 1976; Beck & Conner, 1992; Simpson, 1995). Although positive relationships characterized both *P. moesta* and *P. mackenziana*, female size is clearly not the only determinant of fecundity. Kessler (1971) showed that food shortages can affect the number of eggs in two species of *Pardosa*. Furthermore, in a study of food limitation on the reproductive output of the pisaurid *Dolomedes triton* Walckenaer, Spence *et al.* (1996) also showed that food limitation may be important in determining clutch size, but that these effects may vary with female size. Clutch size is dependent on the individual condition of the female and this will vary depending on various factors such as environmental conditions, prey availability, and habitat type.

Life cycle

The population dynamics of adult *P. moesta* and *P. mackenziana* were inferred from live pitfall trapping, a technique that depends on the activity of individual spiders. Focussing on this data, it appears that *P. moesta* and *P. mackenziana* follow a pattern typical for life histories of *Pardosa* in temperate zones: sub-adults must overwinter since mating occurs early in the spring, males die shortly after the reproductive period, and females carry egg sacs into the summer months (Turnbull, 1966; Edgar, 1971a). There were only two notable differences in adult activity between the two species: female *P. moesta* may live longer than female *P. mackenziana*, and the reproductive period for *P. moesta* is slightly earlier than for *P. mackenziana*, a finding also noted by Wolff (1981).

By itself, the phenological data for adult populations could be interpreted to mean that both species have annual life-cycles. However, data about juvenile growth and development and weight classes of spring cohorts establish that more than one year is required for these species to mature. The numerous small (i.e., < 5 mg) individuals of *P. moesta* and *P. mackenziana* found in the early spring would require at least one more year to complete their development. Also, *P. moesta* and *P. mackenziana* spiderlings held in outdoor arenas did not reach the sub-adult stage in their first growing season and would require an additional overwintering period to complete their development.

During the period of spring emergence, weights of immature *Pardosa* specimens did not fall into a single weight class but were spread over several weight classes (Fig. 4-3). This may reflect the different cohorts produced from early (i.e., mid-May until June) compared to mid-season (i.e., late June until July) egg sacs from the previous summer. Spiderlings dispersing from mid-season egg sacs would not have the same potential for growth and development before the onset of cooler conditions compared to spiderlings dispersing from early season egg sacs. This suggests that overwintering for immature *P. moesta* and *P. mackenziana* may be facultative rather than obligatory; immature spiderlings may overwinter at different stages in their development. However, the reproductive period for both species is early in the spring, suggesting that the second overwintering stage primarily consists of sub-adults.

To ensure synchrony of the mating period, spiderlings from mid-season egg sacs would have to gain proportionally more size during their second summer compared to those from early season egg sacs. *Pardosa* may accomplish this by altering the number of instars to reach maturity, as instar number is flexible in many spider species (e.g., Miyashita, 1968; Edgar, 1972; Toft, 1976; Zimmermann & Spence, 1998). Edgar (1971a) also showed that although the second egg sacs of *P. lugubris* had fewer eggs, the eggs themselves were heavier, possibly in preparation for cooler winter conditions.

A small number of female *P. moesta* and *P. mackenziana* carry egg sacs much later in the season than the majority of the populations (i.e., late August, Fig. 4-2). Since spiderlings emerging from these egg sacs would be substantially smaller in size than those emerging earlier in the season, it is possible that spiderlings from late season egg sacs may slow down their development and stretch their life cycle over two additional growing seasons. By implementing a three year life cycle, synchrony of mating would be ensured. However, because only a small proportion of female *P. moesta* and *P. mackenziana* carry egg sacs in late August, it is unlikely that many individuals in the central Alberta populations of these species would exhibit three year life-cycles. Most egg sacs are carried in early or mid-season, suggesting the majority of individuals of *P. moesta* and *P. mackenziana* have biennial life cycles.

A two year life cycle for *P. moesta* and *P. mackenziana* is similar to that found for *P. lugubris* in central Scotland (Edgar, 1971b), and for several species living at high altitudes (Schmoller, 1970). Further south it is probable that *P. moesta* and *P. mackenziana* have annual life cycles. Schmoller (1970), for example, suggested that in high altitude regions of Colorado, *P. mackenziana* exhibits annual life cycles. *Pardosa lugubris* has an annual life-cycle on the European mainland (Vlijm *et al.*, 1963), and a biennial life-cycle in central Scotland (Edgar, 1971b). The difference in life-cycle is attributed to cooler conditions in Scotland. However, Edgar (1972) also showed that the life cycle of *P. lugubris* in the Netherlands may vary from annual to biennial depending on environmental conditions and the timing of spiderling dispersal. A mixed annual-biennial life cycle has also been suggested for *P. tesquorum* (Odenwall) in central Saskatchewan (D.J. Buckle, unpubl. data). Another variation in *Pardosa* life-cycles has been shown for *P. agrestis* (Westring) in central Europe. Here, Samu *et al.* (1998) reported a bimodal life-history pattern, with reproductive periods in May and August. Undoubtedly, *Pardosa* life-cycles are remarkably flexible, and this may aid in explaining their dominance in many terrestrial ecosystems.

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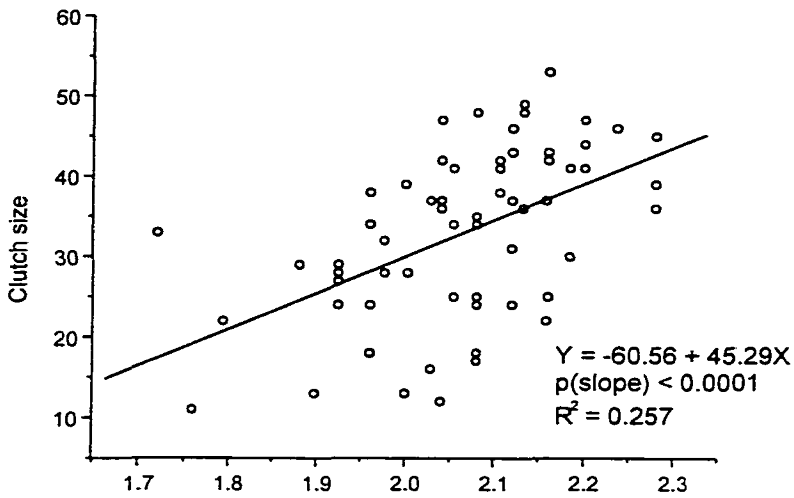
Table 4-1 Density (number m^{-2}) of immature (IM), sub-adult (SA), adult male, and adult female *Pardosa moesta* and *P. mackenziana* obtained from 241 samples (14.9 m^2 total sampling area) between 23 April – 15 June 1999.

		Pardosa moesta				*Pardosa mackenziana*			
Sample period	Area (m^2)	IM	SA	♂	♀	IM	SA	♂	♀
23 April - 10 May	4.4	2.73	0.68	0	0.23	2.04	1.13	0	0
11 May - 27 May	6.2	1.29	1.77	0.48	0.81	2.42	0.48	0	0.65
28 May - 15 June	4.3	1.61	0	0.92	1.61	2.99	0	0.46	1.15
Average		1.87	0.81	0.47	0.88	2.48	0.54	0.15	0.60

A) *Pardosa moesta*



B) *Pardosa mackenziana*

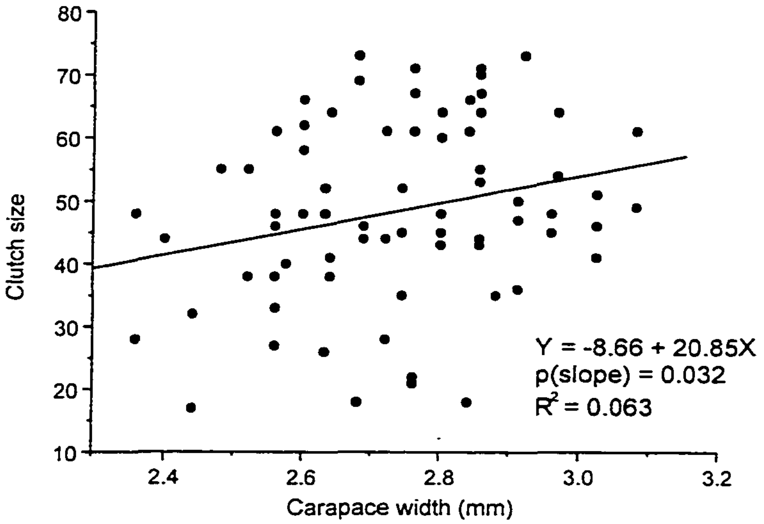


Figure 4-1 Linear regression of clutch size (number of spiderlings or eggs per egg sac) against carapace width (mm) for *Pardosa moesta* ($n = 66$) and *P. mackenziana* ($n = 73$).

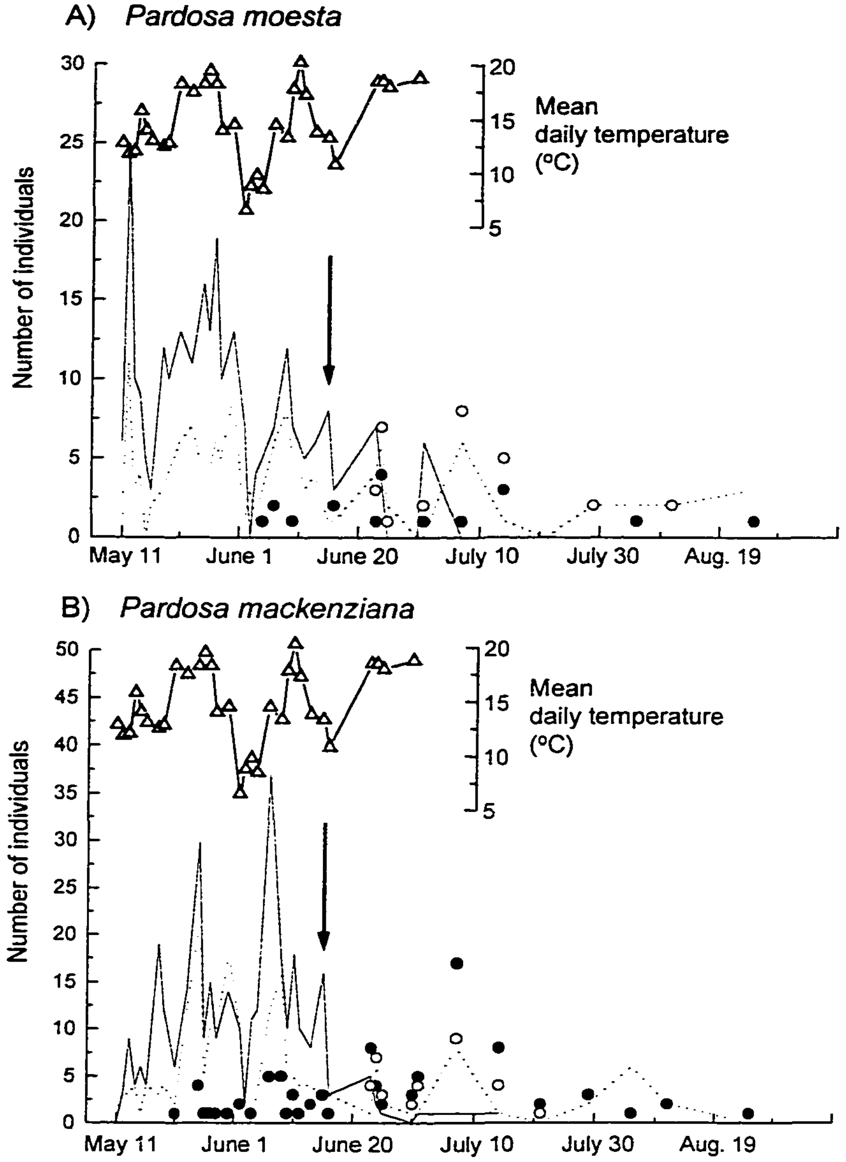


Figure 4-2 Number of *Pardosa moesta* and *P. mackenziana* collected by live trapping in enclosures between 11 May – 29 August 1998. Solid lines represent catches of males, dashed lines are females. Solid circles are females carrying egg sacs, open circles are re-captures for marked females (released June 16, solid arrow). Open triangles are mean daily temperatures (°C) for May and June.

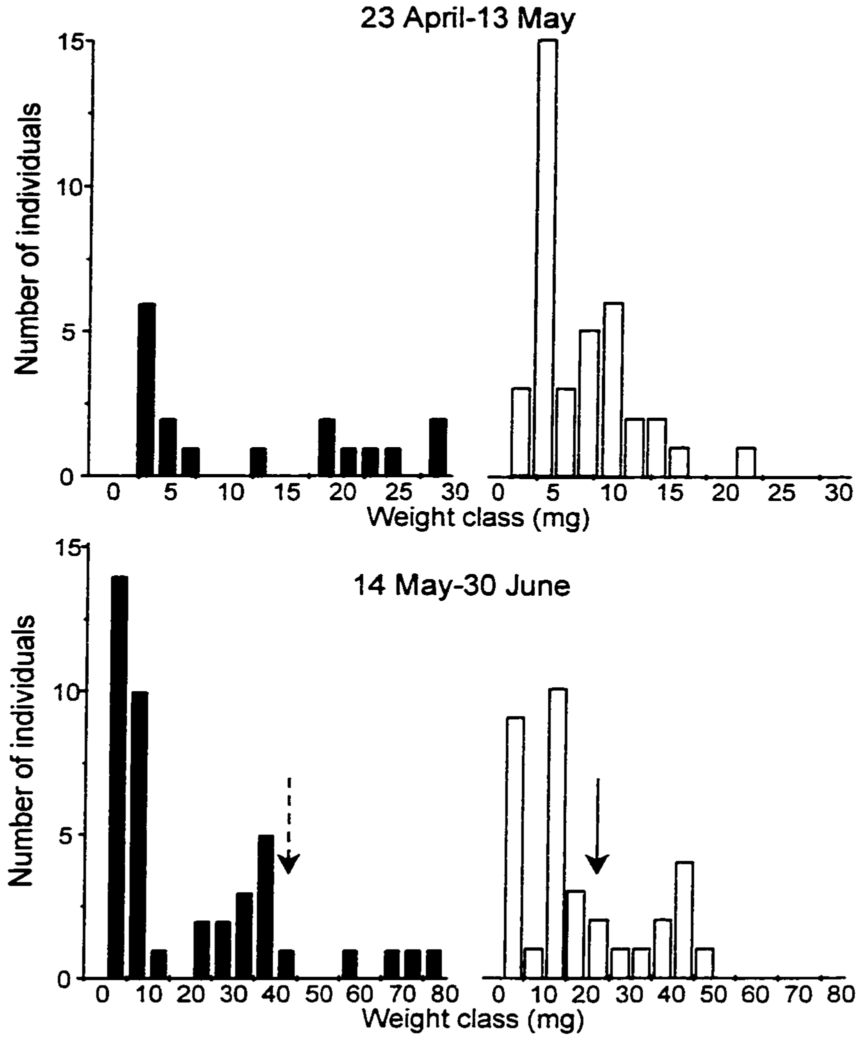


Figure 4-3 Frequency of *Pardosa moesta* (open bars) and *P. mackenziana* (solid bars) by weight class (mg) collected from 23 April – 30 June 1999. Period of spring emergence given as 23 April – 13 May, period of reproduction given as 14 May – 30 June. Solid arrow indicates average weight for adult *P. moesta*, dashed arrow indicates average weight for adult *P. mackenziana*.

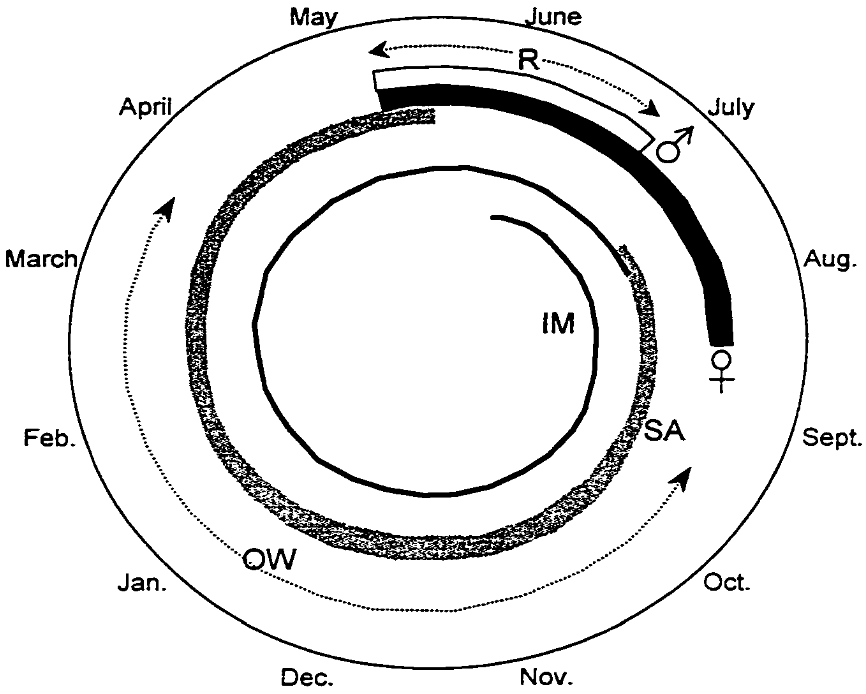


Figure 4-4 Generalized life cycle of *Pardosa moesta* and *P. mackenziana* in deciduous forests of central Alberta showing immatures (IM), sub-adults (SA), males, females, reproductive period (R), and overwintering period (OW).

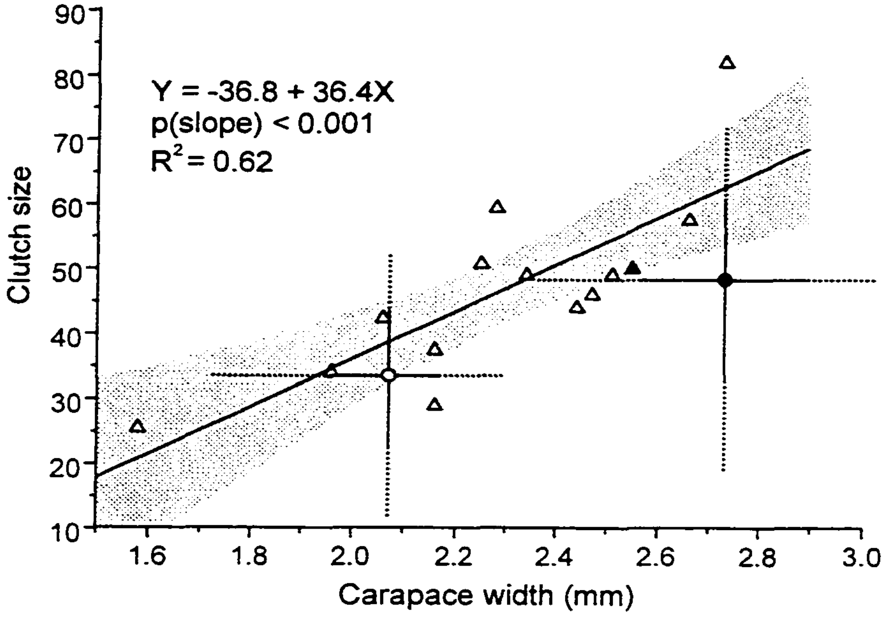


Figure 4-5 Linear regression of clutch size against carapace width (mm) for 14 species of *Pardosa* (triangles) using data from Schmoller (1970), Lowrie & Dondale (1981), Marshall & Gittleman (1994), and C.M. Buddle (unpubl.). Shaded area represents the 95% confidence limits for the regression line. Solid triangle represents a published estimate for *P. mackenziana* [from Lowrie & Dondale (1981)]. Estimates for *Pardosa moesta* (open circle) and *P. mackenziana* (solid circle) from George Lake are averages with 1 standard deviation (solid horizontal and vertical lines) and range (dashed horizontal and vertical lines) for both carapace width and clutch size.

5. Interactions among young stages of the wolf spiders *Pardosa moesta* and *P. mackenziana*

Introduction

Spiders (Araneae) are diverse, ubiquitous, and occupy virtually all habitats in terrestrial ecosystems (Turnbull, 1973; Coddington & Levi, 1991). They are also ecologically important, consuming large numbers of herbivores and detritivores (Moulder & Reichle, 1971; van Hook, 1971; Manley *et al.*, 1976). Predation by spiders can significantly influence processes such as plant-herbivore food webs (Riechert & Bishop, 1990) and litter decomposition (Lawrence & Wise, 2000). However, the role of spiders in many ecosystems is not fully understood (Wise, 1993), and unraveling the interactions between spiders and their prey and among spiders is an important step towards understanding the relative impact of spiders in various ecosystems.

It has been suggested that although spiders are frequently hungry [reviewed in Wise (1993)], exploitative competition is rare among spiders. However, most of the relevant studies have focused on web-building spider species (e.g., Horton & Wise, 1983; Riechert & Cady, 1983; Wise, 1983), and relatively little is known about the nature of the interactions between wandering or cursorial spiders (i.e., those not relying on webs to capture prey). Wise & Wagner (1992) argued that competition may be more common among ground-dwelling spiders than web-building spiders because 1) this guild may frequently experience prey shortages (Edgar, 1969; Anderson, 1974; Fritz & Morse, 1985), 2) cursorial spiders are abundant in the forest-floor community, and 3) predation pressure from spiders and other epigaeic invertebrates on the forest floor is high (Moulder & Reichle, 1972).

Some of the first evidence for exploitative competition among cursorial spiders comes from experiments with young stages of the wolf spider (Lycosidae) *Schizocosa ocreata* (Hentz). Increasing the density of *S. ocreata* spiderlings negatively affected spider growth rate and had a negative impact on Collembola numbers, together constituting evidence for intraspecific exploitative competition (Wise & Wagner, 1992). There was also a high rate of mortality and a strong convergence in spider densities; more recent work has established the role of cannibalism in regulating densities of *S. ocreata* (Wagner & Wise, 1996). However, with the exception of detailed work with *Schizocosa*, little is known of the relative strengths of cannibalism, inter- and intra-specific competition in governing other cursorial spider populations.

Wolf spiders in the genus *Pardosa* are dominant in most temperate ecosystems and there is frequently high overlap in the geographic range of many species (Vogel, 1972; Wolff, 1981; Dondale & Redner, 1990). Studies investigating the coexistence of species have largely portrayed small-scale habitat segregation as the method of avoiding direct contact and competition between congenerics (Hallander, 1967; Vlijm & Kessler-Geschiere, 1967; Lowrie, 1973; Greenstone, 1980). However, few manipulative experiments have directly assessed the relative strength of competition in *Pardosa* populations.

The wolf spiders *Pardosa moesta* Banks and *P. mackenziana* (Keyserling) are sympatric in deciduous forests in north-central Alberta (Buddle *et al.*, 2000), have nearly identical life cycles (Buddle, 2000), and young instars that are similar in size (Buddle, 2000); these factors suggest that juveniles of these species have the potential to interact on the forest floor. The present research investigates the role of inter- and intraspecific competition in governing survival, densities, and growth rates of young instars of *P. moesta* and *P. mackenziana*.

Methods

Field site and study species

This work was conducted at the George Lake Field Site located *ca.* 75 km northwest of Edmonton, Alberta (*ca.* 53°57'N, 114°06'W). The forest at the field site is dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.), interspersed with patches of birch [*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)], white spruce [*Picea glauca* (Moench) Voss], and black spruce [*P. mariana* (Mill.) BSP]. The study area for this research was approximately 0.2 ha of upland aspen forest as discussed by Niemelä *et al.* (1992).

Pardosa moesta and *P. mackenziana* are the most common wolf spiders found on the forest floor at George Lake. As adults, *P. moesta* are smaller in size and weight than *P. mackenziana* (Dondale & Redner, 1990; Buddle, 2000), but young stages of the two species are closer to the same size and weight early in the spring (Buddle, 2000). In the field, it is possible to distinguish adults and juveniles of both species based on body colouration and patterns (Buddle, 2000).

Pardosa moesta and *P. mackenziana* exhibit two-year life cycles in central Alberta (Buddle, 2000). Both species have similar phenologies with adults maturing and mating in May and June. At George Lake, mature female densities of *P. moesta* and *P. mackenziana* were previously established as 0.88 and 0.60 m^{-2}, respectively (Buddle, 2000). Females carry egg sacs into the summer months and spiderlings hatch, ride on the abdomens of their mothers, and disperse from late June to late July. The first overwintering period occurs when spiderlings are small (i.e., < 5 mg in weight) and the second overwintering period consists primarily of sub-adults (Buddle, 2000).

Experimental design

The basic experimental unit was a 0.25 m^2 circular arena delimited by a border of aluminum flashing, 15.2 cm in height and sunk 5 cm into the ground. The arena was covered with a fine mesh that was fastened to the flashing by a tight band of rubber tubing (pieces of bicycle inner tubes). The mesh served to prevent spider emigration and immigration and to prevent larger natural enemies (e.g., vertebrates) from preying upon the study species. Before the flashing was installed, the herbaceous plants were trimmed down to below the height of the arenas. Forty-two arenas were constructed with minimal disturbance to the leaf litter: six groups (separated by 15 – 20 m) of seven arenas (separated by 2 – 3 m) were built in mid to late June 1999.

Before experimental treatments were established, two pitfall traps (6.0 cm diameter, 7.0 cm depth, containing 1 - 2 cm of silicate-free ethylene glycol preservative) were placed in each arena on 29 June and removed 14 days later. This served to remove arthropods that may naturally prey upon spiders, thereby interfere with the experiment, and to homogenize the initial conditions in the arenas.

Collembola, a common prey of lycosids (Edgar, 1969, 1970; Hallander, 1970; Wise & Wagner, 1992), were also counted in the experimental arenas. On 12 July, collembolan densities were sampled in each arena using a plastic soil core that sampled 81.6 cm^3 of soil and leaf litter (a 4.0 cm diameter core was inserted to a depth of 6.5 cm). Collembola were extracted from each sample over a period of 7 days using a modified Kempson apparatus (Kempson *et al.*, 1963). Collembola were counted to establish pre-treatment levels of the main prey for the young wolf spiders. Additionally, the leaf litter within the arenas was searched for *Pardosa* and those found were removed prior to establishing the experimental treatments.

The experiment required 270 first instars of *P. moesta* and *P. mackenziana*. These were obtained by first collecting gravid females or females carrying egg sacs from late June until early July. Females were placed in clear plastic film canisters containing moistened plaster-of-paris to maintain humidity, and allowed to produce egg sacs in the laboratory. Spiders were held in an incubator at 25°C under long-day conditions (16 hr light: 8 hr dark). First instar spiderlings were allowed to hatch from their egg sacs and take up position on their mother's abdomen; when the progeny began to disperse they were gently brushed into vials in groups of 5 or 10.

Natural densities of first instar spiderlings of the two species were estimated by multiplying the natural densities of mature females by the average clutch size (i.e., number of spiderlings per egg sac) per female. Average (± SE) clutch size of *P. moesta* and *P. mackenziana* were 33.1 ± 1.29 and 48.4 ± 1.67, respectively (Buddle, 2000); these estimates were obtained from females collected within 100 - 200 m of the experimental arenas. Natural densities of first instar *P. moesta* and *P. mackenziana* were remarkably similar, at 29.1 and 29.0 m^{-2} respectively. Spiderlings were stocked within arenas at 10 spiderlings per arena, only slightly higher than 7.3 per arena, the estimated natural density. Higher densities were used because adult female densities may have been underestimated.

Each of the experimental treatments was randomly assigned to one arena in a clustered group of seven arenas, with these clusters replicated six times. Treatments were applied between 27 July and 4 August by removing the mesh from the arenas, and depositing spiderlings in the center of the arenas and replacing the mesh. Treatments were the following: 10 first instar *P. moesta* (single species, SS; natural density, ND), 20 *P. moesta* (SS; high density, HD), 10 *P. mackenziana* (SS; ND), 20 *P. mackenziana* (SS; HD), 5 *P. moesta* and 5 *P. mackenziana* (both species, BS; ND), 10 *P. moesta* and 10 *P. mackenziana* (BS; HD), and control (no spiderlings added) (Fig. 5-1). Spiderlings from two different mothers were used for each of the natural density treatments and spiderlings pooled from 3 - 4 mothers were used for high density treatments. Groups of spiderlings were weighed before being placed in the arenas and a weight (mg) per individual was calculated for each arena.

On 16 September 1999, Collembola were re-sampled in each of the arenas to determine post-treatment densities. Between 16 and 21 September, the leaf litter from each arena was sifted and searched for *Pardosa* spiderlings. Litter was sifted in the field using plastic tubs and a large wire mesh that acted as a coarse sieve. *Pardosa moesta* and *P. mackenziana* were collected, identified, counted, and weighed in the laboratory. Other predatory arthropods [e.g., ground and rove beetles (Coleoptera: Staphylinidae and Carabidae) and other spiders] were also counted and identified to family during the sifting and sorting process.

Statistical analyses

Planned comparisons of means were used for most statistical analyses (Sokal & Rohlf, 1995). To test for the effect of 'top-down' processes (i.e., predation pressure on *Pardosa* spiderlings), number of predatory arthropods at the beginning of the experiment (i.e., from pitfall trap samples) and at the end (i.e., from litter sifting) were compared for treatments with natural and high densities of spiderlings (ND vs. HD), and for the combination of *Pardosa* species in the arenas (SS vs. BS) (Table 5-1A). 'Bottom-up' processes were tested by evaluating how the spiderling's prey base (Collembola) was affected by experimental treatments. Collembola densities [pre-treatment (12 July sample) and post-treatment (16 September) and the change from pre- to post-treatment] were compared using the same contrasts used for predatory arthropods, with the addition of a comparison of control arenas to arenas containing *Pardosa* spiderlings (Table 5-1B). Planned comparisons for predatory arthropods and Collembola densities exhibited orthogonality (Table 5-1A,B), and were therefore analyzed using the method orthogonal comparisons (Sokal & Rohlf, 1995)

Tests on intra- and interspecific competition between and among the *Pardosa* species were done using measures of survival and mass gain (mg) of individuals on a per arena basis. Survival was calculated as number of spiderlings found and the end of the experiment divided by the number initially placed in arenas. Intraspecific competition can be inferred from lower survival or mass gain in single species treatments at high compared to natural density. Therefore, to assess intraspecific competition, variables were compared for treatments containing one species, at either natural or high density (*Pardosa moesta* or *P. mackenziana* at ND vs. HD) (Table 5-1C). Interspecific competition can be inferred from a change in survival or mass gain in treatments containing both species compared to treatments with a single species; thus, interspecific interactions were evaluated by comparing treatments with one species present vs. those with both species present at natural density and high density (Table 5-1C). Planned comparisons of spiderling variables were not orthogonal as they lack independence, and the comparisons involved more than 5 degrees of freedom (i.e., 6 comparisons and 6 treatments) (Sokal & Rohlf, 1995). Therefore, the value of α (Type I error) was adjusted using the Bonferroni method (Rice, 1989; Sokal & Rohlf, 1995) and the significance of the p-values resulting from the planned comparisons were compared to the adjusted experimentwise error rates.

Linear regression was used to test whether variation in the survival of *P. moesta* and *P. mackenziana* at the end of the experiment could be explained by the presence of other arthropod predators in the arenas. For these analyses, the *Pardosa* species were treated separately and their survival rates were regressed against the total number of other predators, the number of other spiders, and the number of beetles (Coleoptera) in the arenas at the end of the experiment.

Results

Arthropod predators in experimental arenas

A total of 251 arthropod predators was removed from arenas with pitfall traps. Sixty-two percent of these were ground beetles and 18% were spiders. Planned orthogonal comparisons showed that the arenas did not differ in the number of arthropod predators in the arenas at the beginning of the experiment by density treatments nor by the combination of *Pardosa* species in arenas at $p < 0.05$ (Table 5-2A). Although some predators in the arenas probably avoided the pitfall traps, trapping surely reduced the overall pool of potential natural enemies in the arenas.

Many potential spider predators remained in the arenas over the course of the experiment; 580 were found by sifting the arenas at the end of the experiment. Spiders and ground beetles accounted for 82% and 10% of the predatory individuals recovered. Seventy-three percent of the spiders recovered were from the family Linyphiidae, and 15% were from the family Amaurobiidae. These families build webs within the leaf-litter of deciduous forests. A total of 19 wolf spiders (4% of the spiders) were found at the end of the experiment; some of these were in the genus *Pardosa*, but were of a size class that was much larger than the spiderlings used in the experiment. Orthogonal comparisons revealed that the number of arthropod predators in the arenas at the experiment's end did not differ by the density treatments nor by the combination of *Pardosa* species in the arenas (Table 5-2A). Thus, *Pardosa* spiderlings were exposed to a similar number of arthropod predators during the course of the experiment.

Changes in Collembola densities

The density of Collembola in arenas at the beginning of the experiment did not differ for any of the planned contrasts (Table 5-2B). Similarly, the change in Collembola over the course of the experiment was not affected by any experimental treatment, and did not differ in control vs. treatment arenas (Table 5-2B). Although post-treatment Collembola densities were not affected by any experimental treatments containing spiderlings, there were significantly more Collembola in control arenas at the end of the experiment compared to all treatments containing *Pardosa* spiderlings (Table 5-2B, Fig. 5-2). Collembola increased in control arenas from July to September, but were significantly lower in the September samples from arenas containing spiderlings (Fig. 5-2).

Spiderling survival and mass gain

A total of 78 *P. moesta* and 51 *P. mackenziana* survived in the arenas to the end of the experiment; thus, overall average survival was 29.0 ± 4.10 % for *P. moesta* and 19.7 ± 1.90 % for *P. mackenziana*. No *Pardosa* spiderlings were found in the control treatments in September suggesting that arenas were effective barriers to immigration. Planned comparisons on intra- and interspecific interactions were not significant for survival measures for either species (Table 5-3A, Fig. 5-3) and there is little evidence that either intra- or interspecific interactions affected mass gain (Table 5-3B). However, mass gain observed for both species in natural density treatments was higher in treatments containing both *Pardosa* species (Fig. 5-4).

Arthropod predators and spiderling survival

Variation in survival rates of *P. moesta* and *P. mackenziana* could not be explained by the presence of arthropod predators in the arena. Linear regression of spiderling survival against number of spiders, beetles, and all predatory arthropod taxa revealed slopes that were not significantly different than zero, with p-values ranging from 0.06 to 0.79 (Table 5-4).

Discussion

The use of arenas or enclosures in competition experiments has been criticized (Underwood, 1989). Although field arenas will better approximate natural conditions than will laboratory environments, there are still numerous potential conflicting variables such as the effect of fencing, arena size, disturbance during arena construction, effect of mesh on micro-habitat conditions (i.e., exposure, temperature, humidity), and changes in rates of disease/parasitism in arenas. Underwood (1989) also pointed out that excluding certain natural enemies of the study organism, and thereby diminishing predation pressure, may inflate the occurrence of competition. However, enclosures of various sizes have been effectively employed for experiments with wolf spiders (Wise & Wagner, 1992; Wagner & Wise, 1996), and Collembola, the main prey of young wolf spiders, are not affected by fencing after several weeks of being enclosed (Wagner & Wise, 1996). Using enclosures may facilitate "teasing apart" relationships which can then be explored in more natural settings. To minimize the effects of fencing, the disturbance to the leaf-litter within the enclosures was low during arena construction, and spiderling densities were manipulated without disturbing the litter.

Pardosa spiderlings influence Collembola densities in a deciduous forest in central Alberta, as Collembola were depressed in experimental arenas containing spiderlings at the experiment's end (Fig. 5-2). This pattern is similar to that found for *S. ocreata* preying on Collembola in a deciduous forest in Maryland (Wise & Wagner, 1992). Collembola densities in control arenas were higher in September than in July, consistent with a seasonal peaks of Collembola in the autumn months (Wallwork, 1976; Edwards, 1991); the seasonal peak in autumn was not apparent in experimental treatments containing *Pardosa* spiderlings. Evidence of impact on prey numbers, however, is not sufficient to suggest that the resource was limited in the experimental treatments, and resource limitation is a necessary condition for exploitative competition (Underwood, 1989). Although *Pardosa* spiderlings certainly appeared to reduce Collembola populations, they did not deplete the resource enough to cause its scarcity, and Collembola numbers were not differentially affected by the experimental treatments.

In addition to some resource shortage, action of competition implies a change in survival and/or growth rate of a species. Spiderling survival and growth rates (i.e., inferred by measures of mass gain) were not affected by presence of a second *Pardosa* species in arenas, nor was there higher mortality in treatments with double the natural density of spiderlings. Thus, inter- and intraspecific competition do not appear to play a significant role in governing populations of young *P. moesta* and *P. mackenziana*. Wise & Wagner (1992) found density effects on the growth of *Schizocosa* in their competition experiment but these effects were most apparent in comparisons of 'normal' (natural density) and 'high' (4 x natural density) treatments to 'low' (0.25 x natural density) treatments. Few differences were noted between 'normal' and 'high' density treatments, a result consistent with my findings. Wise & Wagner (1992) suggested that lower growth rates under 'normal' and 'high' density conditions could have arisen from a higher degree of interference among spiderlings, resulting in decreased efficiency of prey capture. These effects would be less pronounced in 'low' density treatments where the evidence for exploitative competition is most striking for *S. ocreata* (Wise & Wagner, 1992). Thus, exploitative competition among wolf spiders may only prove important in low density conditions, a hypothesis that warrants further investigation with *P. moesta* and *P. mackenziana*.

Overall survival rates of 20% for *P. mackenziana* and 29% for *P. moesta* implicate action of other mortality factors on *Pardosa* spiderlings within the arenas. These survival rates are consistent with other estimates of lycosid spiderling survival; for example, Wagner & Wise (1996) report overall survival of *S. ocreata* spiderlings to be 19%. Although Wagner & Wise (1996) state that natural enemies, starvation, and disease/parasitism have some impact on the mortality of spiderlings, high rates of cannibalism (i.e., 43%) are the most probably cause of low spiderling survival (Wagner & Wise, 1996). Since conspecifics do form a substantial portion of the diet of many *Pardosa* species (Edgar, 1969; Hallander, 1970; Samu *et al.*, 1999), it is likely that *P. moesta* and *P. mackenziana* exhibit cannibalism during some stage of their life cycle. Cannibalism, along with predation by natural enemies and other factors such as disease/parasitism and unsuitable micro-habitat conditions within the experimental arenas likely account for much of the spiderling mortality.

Although the overall mass gain of *Pardosa* spiderlings was not significantly affected by the different treatment combinations, a higher mass gain was noted in natural density treatments containing both species of *Pardosa* (Fig. 5-4). This is suggestive of intraguild predation (IGP), here defined as one spider species preying upon another spider species. IGP has been well studied in a variety of spider species interacting with other predatory taxa, and in some cases removal of the intraguild predator results in an increase in the survival and/or density of spiders (Polis & McCormick, 1986; Wise & Chen, 1999). However, interactions between intraguild predators can be complex and difficult to tease apart from competitive interactions *sensu stricto* (Polis *et al.*, 1989; Hurd & Eisenberg, 1990; Spence & Cárcamo, 1991; Wise, 1993), and IGP can have the effect of reducing exploitative competition (Polis *et al.*, 1989). In the present experiment, since both species gained more weight in the presence of the second species, IGP may have an additive effect on *Pardosa* species growth rates under natural density conditions. Additionally, IGP, in concert with other mortality factors, may act to regulate the balance between food supply and spider population size. For example, if one species eats another, this could reduce predation pressure on resources which in turn could allow spiderling populations to persist.

Lack of evidence for competitive interactions and only indirect evidence of IGP point to alternate explanations for the apparent coexistence of young stages of *P. moesta* and *P. mackenziana*. It has been suggested that direct interactions between *Pardosa* are rare due to microhabitat preferences of congenerics (Vlijm & Kessler-Geschiere, 1967; Greenstone, 1980). Although adult *P. moesta* and *P. mackenziana* show some habitat segregation, with *P. moesta* tending to have higher populations in open areas (Dondale & Redner, 1990; Buddle *et al.*, 2000), mature females of both species do co-occur on the forest floor at George Lake (Buddle, 2000). However, some *Pardosa* females with egg sacs move to different habitats to deposit their young, and spiderlings may move from these locations to overwintering areas during their development (Edgar, 1971). Therefore, the initial assumption that *P. moesta* and *P. mackenziana* spiderlings live together in the leaf-litter may be flawed. Young stages of these species may move to different habitats throughout the season, and interactions between the two species at this life-stage may be minimal. If they do meet, the arena experiment suggests that competition plays, at most, a small role in determining spiderling survival at natural and 2 x natural density conditions. Factors such as cannibalism and IGP may have a larger relative impact on populations of *P. moesta* and *P. mackenziana* under these experimental conditions.

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Table 5-1 Planned comparisons for tests on predators, Collembola densities, and *Pardosa* survival and mass gain. Treatments: ND, natural density; HD, high density; *Pmo*, *Pardosa moesta*; *Pma*, *Pardosa mackenziana*; BS, both species.

A) Predatory arthropods (pre- and post-treatment)

	ND, *Pmo*	HD, *Pmo*	ND, *Pma*	HD, *Pma*	ND, BS	HD, BS
Density	-1	+1	-1	+1	-1	+1
Species combination	-1	-1	-1	-1	+2	+2

B) Collembola densities (pre-, post-treatment and change)

	Control	ND, *Pmo*	HD, *Pmo*	ND, *Pma*	HD, *Pma*	ND, BS	HD, BS
Pardosa vs. Control	+6	-1	-1	-1	-1	-1	-1
Density	0	-1	+1	-1	+1	-1	+1
Species combination	0	-1	-1	-1	-1	+2	+2

C) *Pardosa* survival and mass gain

	ND, *Pmo*	HD, *Pmo*	ND, *Pma*	HD, *Pma*	ND, BS	HD, BS
Pmo, intraspecific	-1	+1	0	0	0	0
Pma, intraspecific	0	0	-1	+1	0	0
Pmo interspecific, ND	-1	0	0	0	+1	0
Pmo, interspecific, HD	0	-1	0	0	0	+1
Pma, interspecific, ND	0	0	-1	0	+1	0
Pma interspecific, HD	0	0	0	-1	0	+1

Table 5-2 F and p-values from planned orthogonal comparisons for predatory arthropods and Collembola sampled in arenas. Pre-treatment arthropod predators were sampled using pitfall traps and post-treatment arthropod predators were sampled by sifting litter. Treatments: ND, natural density; HD, high density; *Pmo*, *Pardosa moesta*; *Pma*, *Pardosa mackenziana*.

A) Arthropod predators

	Density (ND vs. HD)		Species combination	
	$F_{1,30}$	p	$F_{1,30}$	p
Pre-treatment	0.048	0.83	3.26	0.08
Post-treatment	0.457	0.50	0.175	0.68

B) Collembola densities

	Pardosa vs. Control		Density (ND vs. HD)		Species combination	
	$F_{1,35}$	p	$F_{1,35}$	p	$F_{1,35}$	p
Pre-treatment	0.441	0.51	0.123	0.73	0.393	0.53
Post-treatment	4.355	**0.04**	0.775	0.38	0.053	0.82
Change	1.57	0.22	0.005	0.94	0.427	0.52

Table 5-3 F and p-values from planned comparisons on spiderling survival and mass gain for tests on *Pardosa moesta* and *P. mackenziana*. Survival df 1,20; Mass gain df 1,15 (*Pardosa moesta*, 5 missing values when no spiderlings were present in arena and mass gain data were not available) and df 1,19 (*P. mackenziana*, 1 missing value).

	Survival			Mass gain		
	F	p	α_c*	F	p	α_c*
Pmo, intraspecific	0.891	0.36	0.010	0.015	0.90	0.025
Pma, intraspecific	0.084	0.77	0.017	0.238	0.63	0.013
Pmo interspecific, ND	1.277	0.27	0.008	2.458	0.14	0.010
Pmo, interspecific, HD	0.002	0.96	0.050	0.105	0.75	0.017
Pma, interspecific, ND	0.375	0.55	0.013	3.514	0.08	0.008
Pma interspecific, HD	0.083	0.78	0.025	0.004	0.95	0.050

* critical α calculated from the Bonferroni method with $k = 6$.

Table 5-4 Linear regression (r and p values) of spiderling survival against number of spiders (Araneae), beetles (Coleoptera), and total arthropod predators (all taxa), $n = 24$.

	r	p
Pardosa moesta		
Spiders	-0.12	0.58
Beetles	0.22	0.28
Total	-0.06	0.79
P. mackenziana		
Spiders	0.39	0.06
Beetles	-0.12	0.59
Total	0.31	0.14

		Number of *Pardosa moesta*			
		0	5	10	20
Number of *Pardosa mackenziana*	0	Control		ND, SS	HD, SS
	5		ND, BS		
	10	ND, SS		HD, BS	
	20	HD, SS			

Figure 5-1 Experimental design for competition experiment. Treatments are represented by shaded blocks: ND, natural density (10 spiderlings per arena); HD, high density (20 spiderlings per arena); SS, single species (*Pardosa moesta* or *P. mackenziana*); BS, both species (*P. moesta* and *P. mackenziana*).

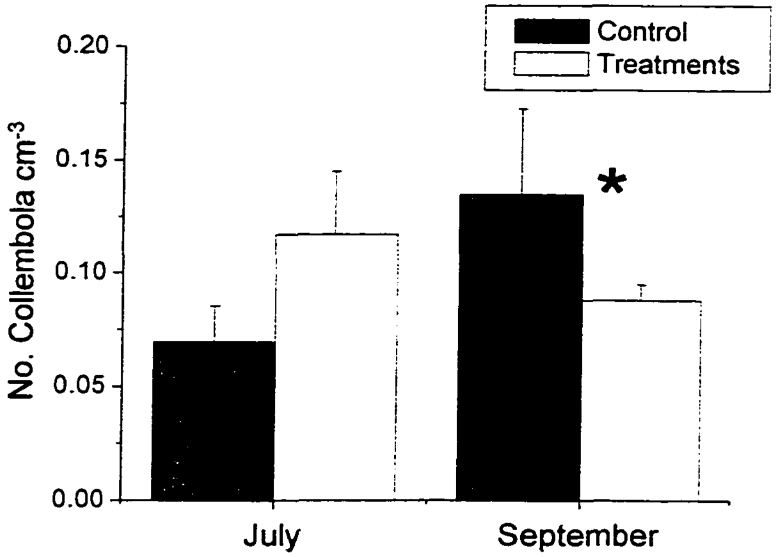
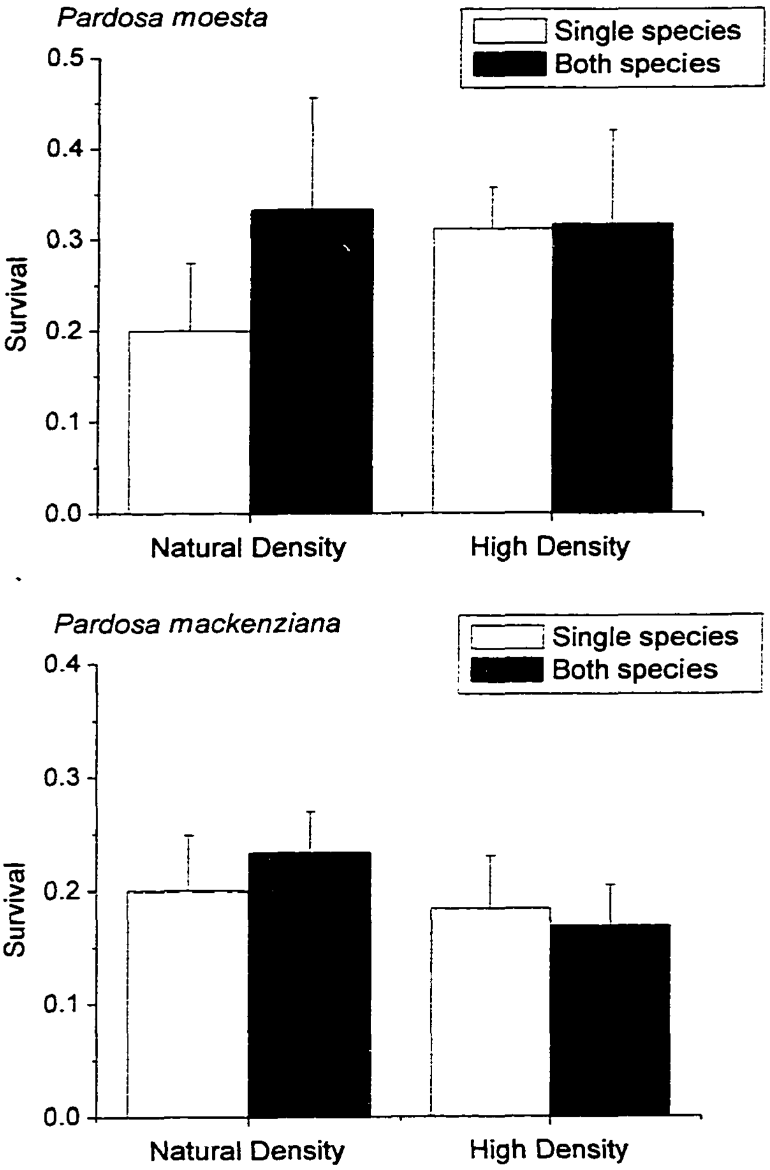


Figure 5-2 Average (± SE) number of Collembola in control (*n* = 6) and treatment arenas (*n* = 36) in July (pre-treatment) and September (post-treatment) soil samples. Treatments are the addition of *Pardosa* spiderlings (see text). * indicate significance at $p < 0.05$ on tests between control and treatment arenas.



Pardosa moesta

Pardosa mackenziana

Figure 5-3 Average (± SE, $n = 6$) survival of *Pardosa* spiderlings by experimental treatment.

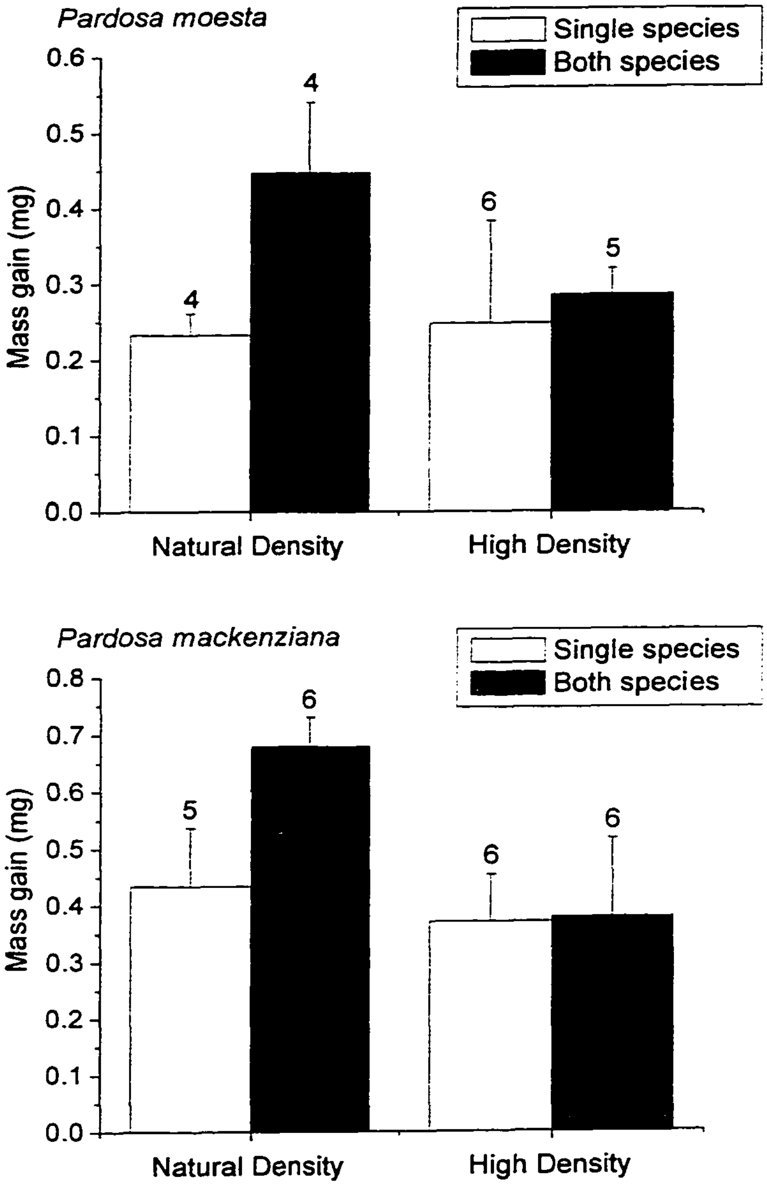


Figure 5-4 Average (± SE, *n* given above bars) mass gain (mg) of *Pardosa* spiderlings by experimental treatment.

6. Spiders associated with downed woody material in a deciduous forest in central Alberta*

Introduction

Coarse woody debris (CWD), in the form of standing dead trees (snags) and fallen logs (downed woody material, DWM), is an essential element in forest ecosystems. CWD plays important roles in nutrient recycling (Harmon *et al.*, 1986; Franklin *et al.*, 1987; Harmon & Hua, 1991) and provides habitat for a variety of organisms including cryptogams (Kruys & Jonsson, 1999), hypogeous fungi (Amaranthus *et al.*, 1994), herbaceous plants (McCullough, 1948; Falinski, 1978), vertebrates (Bowman *et al.*, 2000; Butts & McComb, 2000), and numerous invertebrate taxa (e.g., Harmon *et al.*, 1986; Speight, 1989; Hammond, 1996, 1997; Hendrix, 1996; Marra & Edmonds, 1998; Martikainen *et al.*, 1999). Thus, it has been argued that CWD management must become an important aspect of modern forestry (Franklin *et al.*, 1997; Lee *et al.*, 1997; Hagan & Grove, 1999).

After one logging rotation CWD volume is reduced to as little as 20% (Angelstam, 1997), and managed forests often have less CWD than their unmanaged counterparts (Duvall & Grigal, 1999; Siitonen *et al.*, 2000). This has been cited as a major factor leading to the decrease in the diversity and abundance of certain invertebrate groups (Siitonen & Martikainen, 1994; Martikainen *et al.*, 1999). For example, Siitonen & Martikainen (1994) have shown that many red-listed dead wood dependent beetle species were more prevalent in Russian Karelia where decaying aspen trees were more abundant than in Finland where dead wood

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is uncommon; differences in the amount of CWD is attributed to the different management history of the two regions.

Many arthropods are known to be CWD-dependent; such 'saproxylic' species require dead wood during some stage of their life-cycle (Speight, 1989; Hammond, 1996, 1997). However, little is known about how many forest dwelling arthropods utilize CWD or the extent to which particular taxa are dependent on fallen logs or snags. Generalist predators such as spiders (Araneae) may utilize CWD for shelter, as a foraging or mating substrate, as an overwintering site, or as a location for laying egg sacs. Spiders are one of the most diverse arthropod taxa, the Order ranking seventh in global diversity (Coddington & Levi, 1991). Given the importance of spiders in forest ecosystems (Moulder & Reichle, 1972; Turnbull, 1973; Petersen & Luxton, 1982; Wise, 1993), and their diversity and abundance in temperate and northern forests (e.g., Huhta, 1971; McIver *et al.*, 1992; Pajunen *et al.*, 1995; Buddle *et al.*, 2000), it is of interest to establish how spiders interact with CWD.

Surprisingly, with the exception of anecdotal evidence provided by Lowrie (1948), there have been few quantitative studies investigating whether spider species use CWD, and what characteristics of CWD may be important for spiders. Lowrie (1948) suggested that although many spider species may live on DWM or under the bark of decaying logs, few of these are obligate log dwellers. Scattered notes in various identification guides and faunistic surveys also suggest many spiders species are frequently found on or under the bark of DWM (e.g., Kaston, 1948; Dondale & Redner, 1978, 1982; Platnick & Dondale, 1992), but seldom are the species found exclusively on dead wood. The presence of bark is also cited as one of the criteria for site selection by a variety of web-building spider species (Riechert & Gillespie, 1986).

The present research investigates whether ground-dwelling spider assemblages actively use DWM in a *Populus*-dominated forest in central Alberta. I trapped spiders directly on the surface of fallen logs with and without bark, and compared these collections to spiders found on the immediately adjacent forest floor. I also compared catches of spiders on elevated DWM, ground-level DWM, and on old, wooden telephone poles to assess what features of DWM are important to spiders.

Methods

Site description

This work was conducted at the George Lake Field Site, located 75 km north-west of Edmonton, Alberta (*ca.* 53°57'N, 114°06'W). The *ca.* 180 ha of continuous forest at the site is dominated by trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.), interspersed with birches [*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)] and patches of white spruce [*Picea glauca* (Moench) Voss] and black spruce (*P. mariana* (Mill.) BSP) [see Niemelä *et al.* (1992) for further site description]. The 2.5 ha area chosen for this research was a homogeneous region of *Populus*-dominated forest on the western edge of the field site.

Experimental design and sampling

Sixteen logs and 8 telephone poles were sampled for spiders from 21 April - 22 September 1999. *Populus* logs of decay stage 3 were selected for study during August and September 1998. Decay stage 3 logs are classified as having < 60% coverage by bark (or no bark), > 30% coverage by mosses and lichens, and > 60% of the cross-sectional area showing decay (Hammond, 1996). Telephone poles were used to mimic the coarse structure of *Populus* logs, without offering the same habitat complexity as found on decay stage 3 logs. Telephone poles were made of softwood (primarily *Thuja* species) and were untreated; they were brought into the forest in September 1998. Logs and telephone poles were approximately 6 m in length and had an average (± SE) diameter of 20.9 ± 0.41 cm. Logs were selected so they were at least 30 - 40 m apart from each other. Telephone poles had to be dragged into the forest by four people, and thus were placed as far apart as physically possible (i.e., at least 10 - 15 m).

To test whether particular spiders actively use DWM, pitfall traps were placed on the surface of logs and telephone poles (BOLT traps), directly adjacent to or under logs and telephone poles (ADJ traps), and on the forest floor 2 m from the wood (FOR traps). This design was treated as a 1-factor analysis of variance (ANOVA) with three levels of the main factor 'trap placement' (BOLT, ADJ, and FOR traps); for these analyses, all wood types were grouped together (i.e., logs with bark, logs without bark, and telephone poles), giving 24 replicates for each treatment level.

Pitfall traps were 6.0 cm in diameter with a permanent outer cup (7.0 cm height) and an inner sampling cup (5.0 cm height) containing a preservative (silicate-free ethylene glycol) to a depth of 1-2 cm. A circular plastic roof (12.0 cm in diameter) was elevated over each trap by two nails to provide protection from rain. Traps were emptied about every 19 days throughout the study. BOLT traps were established by drilling a 6.4 cm diameter hole into the upper surface of the wood; pitfall traps were set into the hole so the trap lip was flush with the wood surface. Three traps were placed at least 2 m apart on each log and telephone pole: one near each end (*ca.* 20 cm from the end) and one in the middle. ADJ traps were placed in the ground so that the trap lip was flush with the forest floor; these traps were placed directly adjacent to or directly beneath logs and telephone poles, and were aligned with BOLT traps. FOR traps were placed in the ground on the forest floor (not adjacent to any DWM) at a distance of 2 m from the ADJ traps. For most analyses, catches for each set of three traps were pooled as the statistical sampling unit of interest is not the individual traps, but rather the log or telephone pole and their associated ADJ and FOR traps.

The 24 logs and telephone poles were further subdivided into two additional factors to test for the importance of elevated versus ground-level wood, and to test for the effect of bark and telephone poles on spider assemblages. For these comparisons, the statistical design is a 2-factor ANOVA with 'wood substrate' being the first factor (three levels: logs with bark, logs without bark, and telephone poles) and 'elevation' as the second factor (two levels: elevated wood and ground-level wood). For these comparisons, only data from traps inserted in wood (BOLT traps) were used as the focus was on spiders using wood surfaces. There were 4 replicates of each treatment combination. Logs and telephone poles were elevated to an average height of 40.9 ± 3.7 cm by propping up each end using small sections of DWM from the adjacent forest; these were positioned under each end of the log or telephone pole.

Spider identifications and statistical analyses

All spiders were identified to species using The Insects and Arachnids of Canada publications (e.g., Dondale & Redner, 1978, 1982, 1990; Platnick & Dondale, 1992), and miscellaneous literature for the more difficult spider families (e.g., Linyphiidae, Theridiidae). Some of the more difficult taxa were sorted to morphospecies and accurate species identifications were not possible for immature spiders or some damaged specimens. Classification of spider species and families followed Platnick (1993, 1997). Voucher specimens are deposited in the Strickland Entomological Museum (University of Alberta) and at the Northern Forestry Centre, both in Edmonton, Alberta.

Responses of several dependent variables were studied, including total number of spiders collected, ratio of male to female spiders, proportion of immature specimens collected, number of hunting spiders, number of web-building spiders, number of common spiders collected (i.e., those representing > 3% of the total number collected), and number of female wolf spiders (Lycosidae) carrying egg sacs. Web building spiders were defined as those relying on silk to capture prey whereas hunting spiders adopt alternative strategies for capturing prey. In most cases, the data did not meet the assumptions of normality for parametric statistics and log(x+1) transformations were required on the raw data. Tukey's post-hoc test was used for comparisons of means. Additionally, the statistical significance of p-values was adjusted to account for multiple statistical tests using the sequential Bonferroni method (Sokal & Rohlf, 1995), with an experimentwise error rate of $\alpha = 0.05$. The SAS statistical package (SAS Institute Inc., Cary, NC) was used for all ANOVA tests.

Rarefaction analysis was used to estimate the expected number of species collected in BOLT compared to ADJ and FOR traps, and for comparisons between wood substrate and elevation for collections of spiders caught exclusively in BOLT traps. Rarefaction estimates can be interpreted as diversity measures as these estimates account for both species richness and relative abundance (Simberloff, 1978). Internet-based software by Brzustowski (2000) was used for rarefaction analyses. Additionally, the Shannon and Simpson's indices of diversity (Magurran, 1988) were calculated and comparisons were made between the different levels of trap placement, wood substrate, and elevation.

The number of species shared between BOLT, ADJ, and FOR traps and between different levels of wood substrate and elevation was evaluated to assess what proportion of the total species pool used dead wood. To assess DWM dependence, species that were more frequently collected (i.e., > 50% of the total number of that species collected) in BOLT traps compared to ADJ and FOR traps were considered to be favoring the wood surface as a habitat. For these comparisons, species represented by 1 or 2 individuals were excluded as this number is too few to make statements about habitat affinities.

Ordination, using Detrended Correspondence Analysis (DCA) (Hill & Gauch,1980; ter Braak, 1995), was used to better understand the sources of variation in the data, and to portray the community-level response to trap placement, wood substrate, and elevation. Individual trap data were used for the DCA, and rare species (i.e., species that were rarer than F/5, where F represents the frequency of the most common species collected) were downweighted in proportion to their frequency (McCune & Mefford, 1999). The computer program PC-Ord was used for ordination analysis (McCune & Mefford, 1999).

Results

Catch rates

Over 10 000 spiders were collected during the study (Table 6-1). Immature specimens accounted for 7.1% of the total number collected (Table 6-1), and 220 individuals were too damaged for identification. Significantly more individuals were collected on the forest floor than on wood, and more web-building spiders, hunting spiders, and eight of the nine most common species were caught less frequently in BOLT traps (Table 6-2). Only the wolf spider species *Pardosa mackenziana* (Keyserling) was more frequently collected in BOLT traps (Table 6-2). Similarly, immature spiders represented a higher proportion of the overall catch in BOLT compared to ADJ and FOR traps (Table 6-2). The ratio of male to female spiders did not differ by trap placement (Table 6-2).

The 2-factor ANOVA revealed a significant effect of 'wood substrate' on the total catch, with more spiders collected on logs without bark compared to telephone poles (Table 6-2). Web-building spiders were also significantly more abundant on logs (with and without bark) compared with telephone poles. There were significant effects of 'elevation' on the total catch, hunting spiders, web-building spiders, number of *Bathyphantes pallidus* (Banks), *Amaurobius borealis* Emerton, and *Pardosa xerampelina* (Keyserling); these were more frequently collected on ground-level compared to elevated wood (Table 6-2). A significant interaction between substrate and elevation was noted for *Trochosa terricola* Thorell and *Lepthyphantes intricatus* (Emerton) (Table 6-2). The wolf spider *T. terricola* was infrequently collected in all BOLT traps with the exception of logs without bark that were located on the ground. *Lepthyphantes intricatus* was collected on the surface of logs with and without bark located on the ground and were seldom collected in BOLT traps from other treatment combinations. The adult sex ratio, and the proportion of immature specimens did not differ by wood substrate or elevation (Table 6-2).

Species richness and diversity

A total of 100 species from 16 spider families was identified (Table 6-1, Appendix 2); four of these species, all in the family Linyphiidae, are currently undescribed. Species richness was similar for BOLT, ADJ, and FOR traps for data pooled across replicates (Table 6-1). Forty-six species of the total species pool were shared among all three trap locations, 52 were shared between ADJ and FOR traps, 49 were shared between BOLT and ADJ traps, and 51 species were shared between BOLT and FOR traps. More unique species were collected adjacent to wood and on wood compared to traps further from DWM (Table 6-1).

Estimates of the expected number of species based on rarefaction curves show that spider diversity was significantly higher on the wood surface than on the forest floor (i.e., at a sub-sample of 800 individuals, Fig. 6-1). Furthermore, the accumulation of species from BOLT traps had not leveled off at a sub-sample size of 800 individuals, suggesting that more sampling would result in a higher expected species richness. At a sub-sample size of 3700 individuals, diversity was significantly higher in ADJ compared to FOR traps (Fig. 6-1). Both the Shannon and Simpson's diversity indices also indicated that collections from BOLT traps were the most diverse, followed respectively by collections from ADJ traps and FOR traps (Table 6-3).

Wood substrate affected some aspects of species richness and diversity. BOLT traps on logs without bark had the highest raw species richness compared to BOLT traps in logs with bark and those in telephone poles (Table 6-1). The Shannon and Simpson's diversity indices revealed that logs without bark harbored the most diverse spider assemblages (Table 6-3). These results, however, may be a function of sample size, as rarefaction estimates of spider diversity in BOLT traps show that there was little difference in the expected number of spider species by wood substrate (Fig. 6-2).

Of the species collected from BOLT traps, 12 were collected only on logs without bark, 7 were found exclusively on telephone poles, and 5 were unique to logs with bark. Fewer species from the total species pool were unique to logs with bark compared to logs without bark and telephone poles (Table 6-1). Twenty-six species collected in BOLT traps were shared between logs with bark, logs without bark, and telephone poles. A total of 37 species was shared between logs with bark and logs without bark; fewer species were shared between logs with bark and telephone poles (29 species) and between logs without bark and telephone poles (30 species).

Elevation was also an important factor for species richness and diversity. BOLT traps in elevated wood contained fewer species than ground-level wood (Table 6-1). Rarefaction estimates and the Shannon and Simpson's diversity indices revealed that spider diversity was higher on ground-level compared to elevated wood (Fig. 6-3, Table 6-3). BOLT traps located on ground-level wood shared 33 species with BOLT traps on elevated wood.

Species-specific patterns

Eleven spider species from 8 families were collected more frequently in BOLT traps compared to ADJ and FOR traps (Appendix 2). Some of these species have previously been noted as being commonly collected on or under bark, or on tree trunks [e.g., *Clubiona moesta* Banks, *Coriarachne utahensis* Gertsch, and *Drapestica alteranda* Chamberlin (Kaston, 1948; Dondale & Redner, 1978, 1982)], but little detailed habitat information is available for many of these species.

Sixteen female wolf spiders carrying egg sacs were collected in this study; these represented four different species of *Pardosa*. Only *P. mackenziana* were common enough to establish affinities with trap placement, with 9 of the 11 females collected in BOLT compared to ADJ and FOR traps.

Community patterns

Results from the DCA ordination show that spider assemblages from traps located further from logs and telephone poles were indistinguishable from assemblages of spiders found directly adjacent to wood (Fig. 6-4). Traps located on the wood surface accounted for most of the variation in the ordination. The first ordination axis separates spider assemblages based on elevation; traps located directly on the ground (FOR and ADJ traps) occupy a different space in the ordination than BOLT traps on ground-level wood compared to BOLT traps from elevated wood (Fig. 6-4). No clear patterns were evident based on wood substrate, although some of the elevated telephone pole traps have extreme positions in the ordinations, and one trap from an elevated log with bark shows a high value along the second ordination axis (Fig. 6-4). The second axis in this ordination, however, had little explanatory power given its low eigenvalue of 0.151.

Discussion

Spiders of downed woody material

A large and diverse assemblage of spiders actively use DWM in a *Populus* forest; 69 species and 1102 individuals were collected on the surface of wood and 15 species were caught only on logs or telephone poles. Although fewer spiders use wood than use the forest floor, most species found on the forest floor were also found directly on the wood surface. The most common species in this study, *Agroeca ornata* Banks, *Allomengea dentisetis* (Grube), *B. pallidus*, and *Ozyptila sincera canadensis* Dondale & Redner, are known to be forest floor species common in a variety of *Populus*-dominated forests throughout north-central Alberta (Buddle *et al.*, 2000); all of these species use wood only infrequently (Appendix 2). Spider species found on DWM are therefore largely a sub-set of the species that are regularly collected from the forest floor.

Eleven species were most frequently collected in BOLT traps and at least two of these could be considered as having adaptations (i.e., colouration and habitus) for life on logs: *Coriarachne utahensis* (Thomisidae, crab spider) and *D.*

alteranda (Linyphiidae, sheet-web spider) (Kaston, 1948; Dondale & Redner, 1978). Both of these species were collected only in BOLT traps.

A number of other species found most frequently on the wood surface cannot be classed as log specialists as they were also collected on the forest floor, or they are known from various other habitats. The wolf spider *P. mackenziana* was significantly more abundant on logs. This species is widely distributed in North America, and is well known as a forest floor species in both coniferous and deciduous forests (Dondale & Redner, 1990; Buddle *et al.*, 2000). *Pardosa mackenziana* may therefore have very general habitat requirements; it uses various elements of its environment located on or near the forest floor. Female *P. mackenziana* carrying egg sacs were also more common on the wood surface, possibly to sun themselves and speed the development of their eggs. Such behaviour has been noted with other *Pardosa* species; Vlijm *et al.* (1963) showed that *P. amentata* (Clerck) females expose their egg sacs to the sun while they hide in crevices in the soil, and Edgar (1971) found that *P. lugubris* (Walckenaer) females sun their egg sacs on logs or other elevated surfaces. In a forest with a thick understorey, fallen logs may be one of the few habitats that allow ground-dwelling spiders to move above the herbaceous layer.

Two species of sac spiders (Clubionidae, *Clubiona moesta* and *C. canadensis* Emerton) were collected on the wood surface more frequently than on the forest floor. Although these species have been previously collected on or under bark (Dondale & Redner, 1982), they are known from a variety of other habitats including on trees and shrubs, under stones, and in leaf-litter. Many clubionids hide in retreats during the daytime (Dondale & Redner, 1982); crevasses and bark on fallen logs likely provide ideal sites for this behavior.

Little is known about the habitat affinities of many of the other species frequently collected in BOLT traps [e.g., *Lepthyphantes turbatrix* (O.P.-Cambridge), *Dictyna annulipes* Blackwall, *Sergiolus montanus* (Emerton) and *Eridantes utibilis* Crosby & Bishop], even though these species are widespread in North America. *Eridantes utibilis* is now known from only three localities in

North America: New York, Wisconsin, and Alberta (Buckle *et al.*, 1995). In this study, 6 of the 7 *E. utibilis* were found on logs and the seventh was found adjacent to a log, and males and females were both collected on logs. This species may specialize on fallen logs and its rarity may reflect poor collection records for spiders on DWM.

Spider diversity was substantially higher on the surface of wood than on the forest floor. Additionally, rarefaction curves suggest the possibility for even higher diversity if sampling on logs were to continue. High diversity in BOLT traps is explained by the four types of spiders collected on the surface of wood: accidental captures, occasional captures of forest floor species, collections of species more frequently found on the wood surface, and the presence of species specializing in the DWM habitat. Accidental captures include the infrequent collections of species that are not typically ground-dwelling spiders such as the three orb-web species (Araneidae) collected in BOLT traps: *Araneus iviei* (Archer), *Larinioides cornutus* (Clerck), and *L. patagiatus* (Clerck). These species typically build vertical webs higher in the vegetation (Kaston, 1948; Levi, 1971). Additionally, juvenile and adult spiders (especially in the family Linyphiidae) are known to disperse long distances by aerial ballooning (Greenstone *et al.*, 1987), and many may accidentally land on the exposed surface of DWM.

The ratio of male to female spiders remained unchanged across the different trap locations indicating that spiders do not select logs specifically for reproductive sites. However, the proportion of immature spiders was significantly higher on the wood surface than on the forest floor. Immature spiders may select the surface of logs as a foraging substrate, as a place to sun themselves and speed their development, or as a 'launch pad' for dispersal via aeronautic ballooning. Different life stages of spiders may use different habitat types (Edgar, 1971), and in a mature deciduous forest, fallen logs likely act as one of the alternatives.

Habitat complexity and wood elevation

Wood substrate was an important factor for some aspects of the spider fauna collected in BOLT traps. The total number of spiders collected, number of web-building spiders, and the Shannon and Simpson's diversity indices were lower on telephone poles compared to logs; there were also fewer species shared between logs and telephone poles than between logs with and without bark. These differences may be explained by three features of telephone poles: permanence, prey availability, and wood species. Telephone poles were a new addition to the forest and it is unlikely they were immediately suitable for many spider species. Additionally, telephone poles made from cedar are meant to be resistant to wood rot. Therefore, without fungi and the associated fungivores and scavengers, there are likely fewer prey items for spiders. In contrast, decay class 3 *Populus* logs have a large and diverse assemblage of fungi and fungivores (Hammond, 1996), and would offer spiders a larger pool of prey items.

Some spider species may be sensitive to the tree species of the DWM. *Thuja* species do not naturally occur at George Lake and some aspect of cedar DWM may actually deter arthropod colonization. However, a variety of other variables suggest that spiders did not distinguish between telephone poles and logs. Rarefaction estimates of diversity, the number of hunting spiders collected, and the abundance of common species did not show any significant differences by wood substrate. The overall community response, as illustrated with the DCA ordination, was also insensitive to wood substrate. Although telephone poles were hard, smooth, and without numerous cracks and openings on their surface, many spider species, and the community at large, were not deterred by the lack of variety of habitat or by the temporary nature of the telephone poles.

Some elements of the spider fauna may avoid telephone poles because they do not provide suitable habitat complexity for foraging or shelter, whereas others appear indifferent which suggests telephone poles adequately capture the essential coarse structure of fallen logs. Web-building spiders often rely on complex architecture for placing webs (Robinson, 1981; Riechert & Gillespie,

1986) and thus may avoid telephone poles because of this lack of physical complexity. Many web-building species were common in BOLT traps, but were poorly represented on telephone poles [e.g., only 5 of the 36 *Agelenopsis utahana* (Chamberlin & Ivie), 2 of the 37 *L. intricatus* and 0 of the 23 *L. turbatrix* collected from BOLT traps were found on telephone poles]. The latter two species, both from the family Linyphiidae, typically construct small sheet-webs in the complex microhabitats on the forest floor (Huhta, 1971). The infrequent capture of certain linyphiids on telephone poles may simply reflect lack of suitable web-building habitat.

Although hunting spiders also depend on habitat complexity (Uetz, 1991), they may be less dependent on complexity than web-building species given their mode of prey capture. Lycosids, for example, tend to increase in their relative abundance in more simple habitats [e.g., along a gradient towards decreasing litter depth and structure (Uetz, 1991)]. The wolf spider *P. mackenziana* was captured as frequently on telephone poles (101 individuals) as on logs with and without bark (90 and 97 individuals respectively). Many hunting spiders use DWM for its coarse structure, rather than for the fine-scale habitat complexity it may provide.

Spider assemblages on elevated wood differed in some important ways from those found on ground-level wood; fewer spiders, fewer species, and a less diverse spider fauna was found on elevated wood. Less than half of the spider species collected on elevated wood were shared with those collected from ground-level wood. The overall community of spiders also differed on elevated wood as evident from the DCA ordination (Fig. 6-4). Several species, including *Clubiona canadensis* and *C. moesta*, were collected more frequently on elevated wood than on ground-level wood. Both of these species use the vertical structure in forests as they are known as tree inhabitants and as forest-floor dwellers (Dondale & Redner, 1982). Many of the true forest-floor species, such as the wolf spider *T. terricola* and the linyphiid *L. intricatus* were seldom found on elevated wood.

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Table 6-1 Number of spiders (total number and number of immature specimens), number of spider species, and number of unique spider species collected on the forest floor (FOR traps), adjacent to wood (ADJ traps), and on wood (BOLT traps); BOLT traps are broken down by those collected on logs without bark, logs with bark, telephone poles, ground-level wood, and elevated wood.

	Number of traps	Total number collected	Number of immature spiders	Number of species	Number of unique species
FOR traps	72	4861	259	67	10
ADJ traps	72	4143	268	70	15
BOLT traps	72	1102	186	69	15
Logs without bark	24	467	54	53	4
Logs with bark	24	367	68	46	2
Telephone poles	24	268	64	41	4
Ground-level wood	36	752	105	64	6
Elevated wood	36	350	81	38	5
Total (all traps)	216	10 106	713	100	

Table 6-2 ANOVA of spider catches, sex ratio, proportion of immature specimens, and number of common species by trap placement (FOR, forest trap; ADJ, trap adjacent to wood; BOLT, trap on wood), wood substrate (L, log without bark; LB, log with bark; T, telephone pole) and elevation (ground-level and elevated wood). Post-hoc differences at $p < 0.05$ (Tukey's test). NS at $p > 0.0021$ after Bonferroni correction.

	1-factor ANOVA	2-factor ANOVA	
	Trap placement (d.f. 2,69)	Wood substrate (d.f. 2,18)	Elevation (d.f. 1,18)
Total number collected	(FOR=ADJ) > BOLT	(L=LB) > (T=LB)	ground > elevated
Male : female ratio	NS	NS	NS
Proportion (immature)	BOLT > (ADJ=FOR)	NS	NS
Number of hunting spiders	(FOR=ADJ) > BOLT	NS	ground > elevated
Number of web spiders*	(FOR=ADJ) > BOLT	(L=LB) > T	ground > elevated
Agroeca ornata	(FOR=ADJ) > BOLT	NS	NS
Allemengea dentisetis	(FOR=ADJ) > BOLT	ND	
Bathyphantes pallidus	(FOR=ADJ) > BOLT	NS	ground > elevated
Ozyptila sincera canadensis	(FOR=ADJ) > BOLT	ND	
Trochosa terricola[†]	(FOR=ADJ) > BOLT	Significant interaction	
Pardosa mackenziana	BOLT > (ADJ=FOR)	NS	NS
Cybaeopsis euopla	(FOR=ADJ) > BOLT	ND	
Lepthyphantes intricatus[†]	ADJ > FOR > BOLT	Significant interaction	
Amaurobius borealis	(FOR=ADJ) > BOLT	NS	ground > elevated
Pardosa xerampelina[†]	ND	NS	ground > elevated
Agelenopsis utahana	ND	NS	NS

* (1-factor ANOVA) and [†] (2-factor ANOVA) indicate data that were not transformed prior to analysis.

Table 6-3 Shannon and Simpson's diversity indices of spiders collected on the forest floor (FOR traps), adjacent to wood (ADJ traps), and on wood (BOLT traps); BOLT traps are broken down by those collected on logs without bark, logs with bark, telephone poles, ground-level wood, and elevated wood.

Trap	Number of traps	Shannon index	Simpson's index
FOR traps	72	2.26	5.39
ADJ traps	72	2.49	7.6
BOLT traps	72	2.99	8.1
Logs without bark	24	3.07	11.78
Logs with bark	24	2.87	8.3
Telephone poles	24	2.37	3.84
Ground-level wood	36	3.15	12.43
Elevated wood	36	2.06	3.11

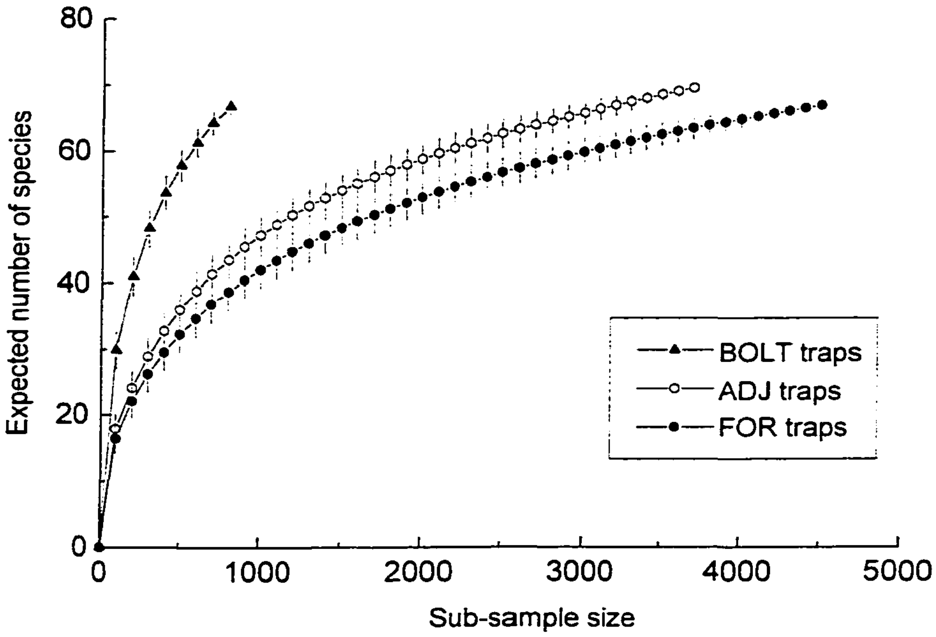

Figure 6-1 Rarefaction estimates of spider diversity in traps placed on wood (BOLT traps), adjacent to wood (ADJ traps) and on the forest floor (FOR traps). Error bars are 1 standard deviation.

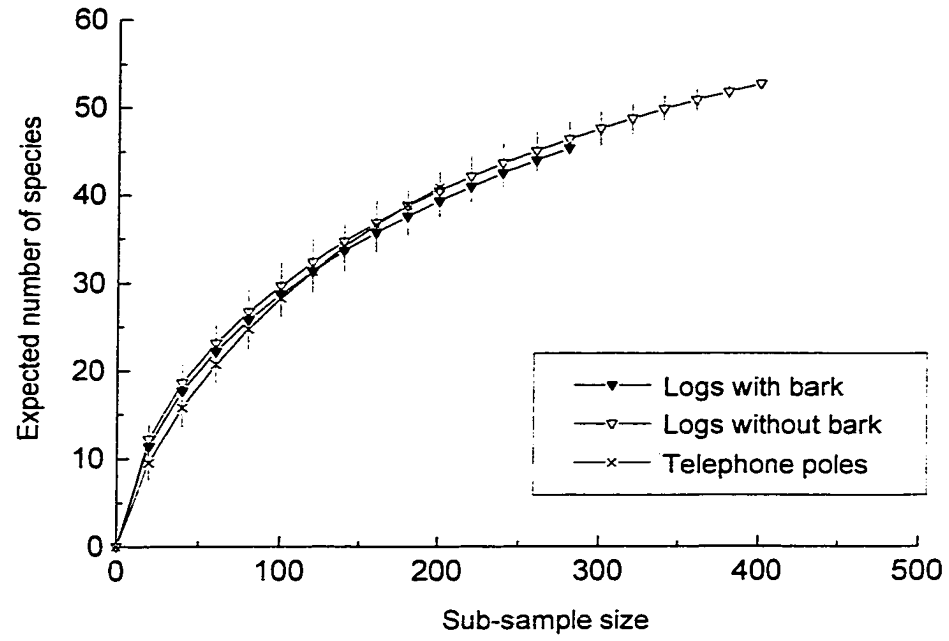

Figure 6-2 Rarefaction estimates of spider diversity on logs with bark, logs without bark, and telephone poles. Error bars are 1 standard deviation.

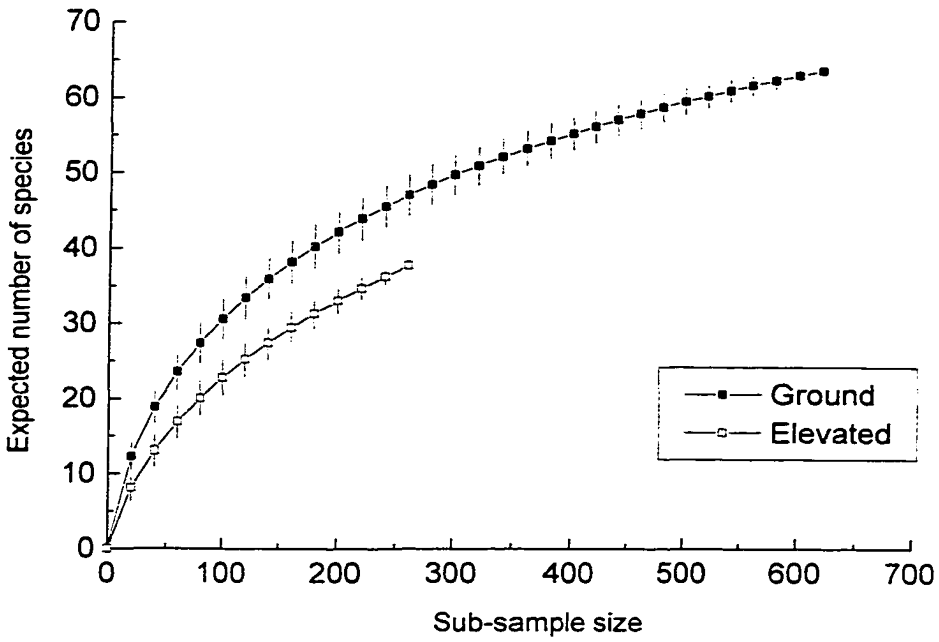

Figure 6-3 Rarefaction estimates of spider diversity on wood located on the ground or elevated. Error bars are 1 standard deviation.

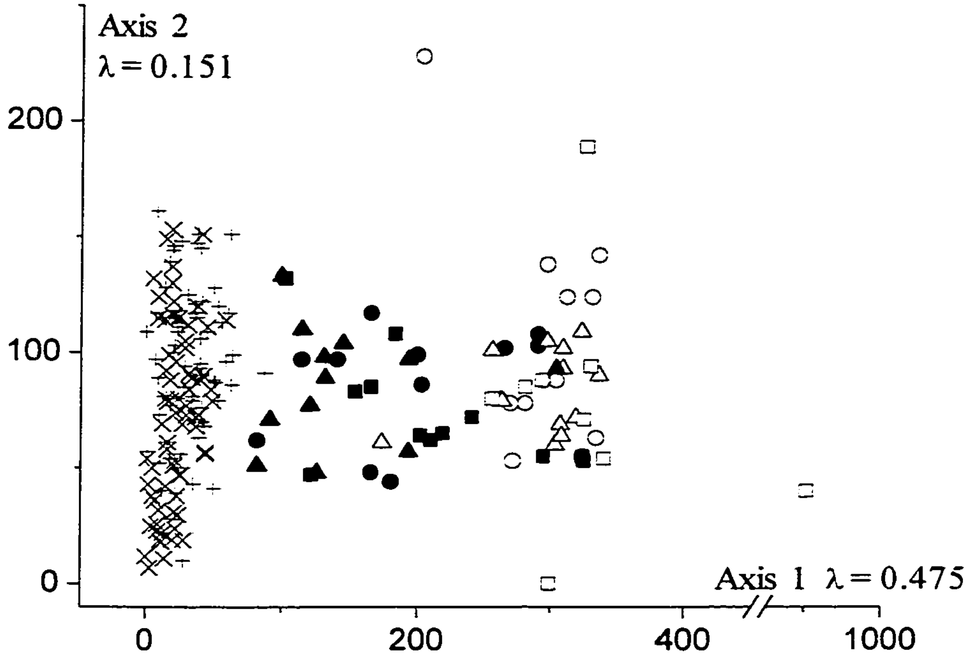

Figure 6-4 DCA ordination (axis 1 and 2) of sample scores (216 pitfall traps) for 100 spider species collected on the forest floor (x), adjacent to wood (+), on logs with bark (circles), logs without bark (triangles), and telephone poles (squares). Open symbols are traps in elevated wood, solid symbols are traps in ground-level wood.

7. Downed woody material and ground-dwelling spider assemblages: an experiment in a *Populus* forest

Introduction

A large body of research has illustrated the importance of coarse woody debris (CWD) in the form of snags (standing dead trees) and fallen logs (downed woody material, DWM), in forest ecosystems. CWD plays important roles in nutrient cycling (Harmon *et al.*, 1986; Harmon & Hua, 1991) and provides habitat for a variety of organisms including vertebrates (Haapanen,1965; Mannan *et al.*, 1980; Bowman *et al.*, 2000; Butts & McComb, 2000), plants (McCullough, 1948; Falinski, 1978), fungi (Amaranthus *et al.*, 1994), and invertebrates (Harmon *et al.*, 1986; Hammond, 1996, 1997; Hendrix, 1996; Marra & Edmonds, 1998; Martikainen *et al.*, 1999). In many cases, increases in the volume of CWD in a forest are correlated with increases in the abundance or diversity of various taxa (Haapanen, 1965; Martikainen *et al.*, 1999; Bowman *et al.*, 2000; Butts & McComb, 2000). Given the high diversity of many arthropods collected from CWD (Speight, 1989; Hammond, 1996, 1997; Martikainen *et al.*, 1999), and the role of CWD in maintaining rare species (e.g., Speight, 1989; Siitonen & Martikainen, 1994), it is clear that CWD in forests is critical for conservation of the large number of species that depend on it.

Current forestry practices now aim to incorporate biodiversity considerations into management goals (Probst & Crow, 1991; Burton *et al.*, 1992), and CWD management has been highlighted as one way to balance harvesting demands on the landscape with maintenance of biodiversity (Lee *et al.*, 1997; Hagan & Grove, 1999; Siitonen *et al.*, 2000). Some stand management models are even using CWD as a direct surrogate for biodiversity considerations (Wikström & Eriksson, 2000). However, there have been few studies on CWD that provide the information required to assess this approach, as illustrated by a recent paper in the *Journal of Forestry*: "Because ecologists have not figured out how much coarse woody debris is required to support all coarse woody debris-dependent species for an area...most best management practices (BMP) assume that some [CWD] is better than none, and that more is almost always better" (Hagan & Grove, 1999). However, few studies have even illustrated, using clear manipulative experiments, that changes in CWD volume directly relate to changes in species diversity or abundance. Although there is little doubt that strict CWD-dependent species will be affected by losses of their primary habitat (e.g., Siitonen & Martinkainen, 1994; Martikainen *et al.*, 1999), there is a need for direct cause-and-effect studies with a variety of taxa to support or disprove the hypothesis that more CWD is always better, and reductions in CWD is detrimental from a biodiversity perspective.

The present research addresses these issues by directly manipulating one aspect of CWD, DWM volume, and then following the changes in ground-dwelling spider (Araneae) assemblages before and after their habitat has been modified. Globally, spiders are one of the most diverse arthropod Orders (Coddington & Levi, 1991) and are among the dominant arthropod predators found on the forest floor in most forest ecosystems (Turnbull, 1973; Wise, 1993). Spiders contribute significantly to the nutrient dynamics of the forest floor (Moulder & Reichle, 1972), have a large impact on detritus- and soil-based food webs (Petersen & Luxton, 1982; Lawrence & Wise, 2000), and show high diversity and abundance in many northern forests in Canada and Europe (Huhta, 1971; Koponen, 1994; Pajunen *et al.*, 1995; Buddle *et al.*, 2000). Research has also shown that spiders exhibit a clear and definable response to modifications of their habitat [e.g., following clear-cutting and wildfire (Huhta, 1971; Coyle, 1981; McIver *et al.*, 1992; Buddle *et al.*, 2000)].

Although spiders are not a strict DWM-dependent taxon, recent research has shown that the ground-dwelling spiders in a deciduous forest in central Alberta frequently use the surface of fallen logs (Chapter 6). Spider diversity was substantially higher on log surfaces compared to the forest floor, and most species collected on the forest floor were also collected on the log surface. The proportion of immature spiders was also higher on the surface of DWM, suggesting this habitat may be important in maintaining viable populations of some species. In a study of wildfire and clear-cut forest stands in north-central Alberta, Buddle *et al.* (2000) suggested that the high variation in spider assemblages in certain forest stands may be partially explained by high volumes of CWD. Clearly there is evidence to suggest that CWD may be important for spider assemblages. To further elucidate spider dependence on CWD, two experiments, operating at different scales, were devised to assess how changes in the volume of DWM in a *Populus*-dominated forest in central Alberta may affect ground-dwelling spider assemblages.

Methods

Study site and experimental plots

This research was completed at the George Lake Field Site, located 75 km north-west of Edmonton, Alberta (53°57'N, 114°06'W). There is approximately 180 ha of continuous forest at the research site. The George Lake forest is an old-growth mixed-wood stand that has remained undisturbed by fire or harvest over the past century. It is surrounded by a primarily agricultural landscape to the west and south, George Lake to the east, and continuous *Populus*-dominated forest of a younger age-class to the north. Dominant tree species at the field site include trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*P. balsamifera* L), interspersed with birches [*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)], patches of white spruce [*Picea glauca* (Moench), Voss] and black spruce [*Picea mariana* (Mill.) BSP] in wet areas. Common shrubs include wild rose

(*Rosa acicularis* Lindl.), green alder [*Alnus crispa* (Ait.) Pursh], bracted honeysuckle [*Lonicera involucrata* (Richards.) Banks], mooseberry or low-bush cranberry [*Viburnum edule* (Michx.) Raf.], and raspberry (*Rubus idaeus* L.).

A series of 20 plots, each measuring 40 x 40 m were selected for the experiments; plots were delimited such that edges ran in cardinal directions. Plots were *ca.* 50 m apart, dominated by *Populus* trees, and were selected to be as homogeneous as possible with respect to a variety of characteristics (e.g., moisture, topography, plant cover, etc.).

The volume of DWM (> 10 cm diameter) was estimated for each plot in 1998 since the experiments outlined below were dependent on knowledge of the variation in DWM volume per plot. DWM estimates were obtained by placing two temporary sub-plots, each 2 x 40 m, with the long axes oriented north-south in each plot. Transects were 10 m from the east and west edges respectively. For each piece of DWM present in the sub-plots, the length, diameter (at mid-length), decay class, and tree species was recorded and estimates of DWM m^3 ha^{-1} was obtained for each plot. Decay class was determined according to criteria used by Hammond (1996). Volume of DWM ranged from 27.4 to 159.4 m^3 ha^{-1} and averaged (± SE) 74.8 ± 8.17 m^3 ha^{-1} per plot. All dead wood was *Populus*, and the decay class was stage 3 for virtually all dead wood on the ground [i.e., < 60% coverage by bark, > 30% coverage by mosses and lichens, and > 60% of the cross sectional area showing decay (Hammond, 1996)].

Spider sampling and identification

Ground-dwelling spider assemblages were sampled using continuous pitfall trapping throughout the snow free seasons of 1998, 1999 and 2000. Data from 2000, however, are not yet available and are not included in the remainder of this chapter. Pitfall traps were white 1 L plastic containers containing an inner sampling cup filled with 2 - 3 cm of silicate-free ethylene glycol as a preservative (Spence & Niemelä, 1994). Traps were covered with a 15 x 15 cm elevated plywood roof to reduce flooding and to reduce the amount of debris entering the sampling cup. Sampling occurred from 4 May – 10 September in 1998 and 20 April – 24 September in 1999. Traps were emptied approximately every 16 days in 1998 and every 20 days in 1999. Few traps were disturbed throughout the sampling period; only 4.1% of the traps experienced disturbance in 1998 and 3.3% were disturbed in 1999.

All adult spider species were identified to species using available literature (e.g., Leech, 1972; Dondale & Redner, 1978, 1982, 1990; Platnick & Dondale, 1992). Immature specimens were identified to only generic level. Some poorly known taxa, especially in the family Linyphiidae, were assigned to morphospecies as further taxonomic research is required to properly determine species. Classification of spider species and families followed Platnick (1993, 1997). Voucher specimens from this research are deposited in the Canadian Forest Service arthropod collection at the Northern Forestry Centre and at the Strickland Entomological Museum (University of Alberta), both in Edmonton, Alberta.

Experiment 1: large-scale DWM removal

To test the effect of relatively large-scale removal of DWM on spider assemblages, 8 of the 20 experimental plots were selected based on having a similar volume of DWM that was as close as possible to the average DWM volume across all plots. The volume of DWM for the selected 8 plots ranged from 54.3 – 74.3 m^3 ha^{-1}, and averaged 64.1 ± 2.54 m^3 ha^{-1}.

Five pitfall traps were placed in each plot; one trap in the center and one in each corner, 10 m from the edges. Spiders sampled in 1998 represent the pre-treatment data. During the last two weeks in September 1998, all DWM > 10 cm in diameter was removed from 4 randomly selected plots. Removal entailed cutting and dragging DWM at least 10 m beyond the plot boundary. The remaining 4 plots were left as undisturbed controls. Spiders were sampled again in 1999, representing the post-treatment data. The overall design is a "before-after with control-impact" experiment [BACI, Underwood (1991)].

The statistical sampling unit for this experiment was individual plots. Collections from the five pitfall traps per plot were therefore pooled, giving four replicates each of the control and DWM removal treatments. As there was uneven sampling effort among plots (i.e., the sampling period was longer in 1999 than in 1998 and some traps were disturbed), the data was standardized to the mean number of trapping-days (number of traps x number of active trap-days) per plot averaged over the two collection years (693.3 trap-days).

Experiment 2: small-scale DWM manipulation

The remaining 12 plots were used in a separate BACI experiment to assess the effect of changes in the volume of DWM on spider assemblages at a smaller scale than Experiment 1. These plots had a larger range of initial DWM volume (27.4 – 159.4 m^3 ha^{-1}) and average (82.0 ± 13.56 m^3 ha^{-1}) than in Experiment 1. Spider assemblages were sampled in a similar manner to Experiment 1 (i.e., 5 pitfall traps per plot). After one year of collecting in 1998 (pre-treatment data), the plots were subdivided into four sections or quadrats each measuring 20 x 20 m.

In the final two weeks of September 1998 the following four treatments were applied randomly within each of the 12 plots: 1) quadrat 1 had all DWM > 10 cm diameter disturbed by cutting and rolling or moving DWM a short distance within the quadrat (disturb treatment); 2) all of the DWM > 10 cm diameter was removed from quadrat 2 (remove treatment); 3) DWM removed from quadrat 2 was placed in quadrat 3 and dispersed evenly over the quadrat (addition treatment); 4) quadrat 4 was left untouched (control). The disturb treatment was included to test for the potential effect of trampling and dragging DWM on spider assemblages independently of the removal or addition treatments. Spiders sampled in 1999 represent the post-treatment collection data.

In this experiment the statistical sampling unit is the quadrat, each sampled by one pitfall trap located in the middle of the quadrat. Therefore, there were 12 replicates for each of the treatments and a total of 48 pitfall traps or quadrats. The pre-treatment data from the center trap were not used in the analyses as this trap was not operated in the post-treatment collection year. Data were standardized to mean number of trapping days per quadrat averaged over the two collection years (136.4 trap-days).

Abiotic parameters

Several abiotic parameters were measured at each pitfall trap location between 14 June – 8 July 1999. These included litter depth (cm) (i.e., of "litter layers", LFH), shade, and moisture content of soil. Shade was estimated as the % coverage at a height of 0.5 m; this was estimated for a circular area (1.5 m radius) centered over each pitfall trap. Moisture content was estimated by taking a soil core of approximately 150 cm^3 (using PVC piping 5 cm diameter and 8 cm height) on 14 June. Soil was weighed, dried in an oven at 30 - 35 °C for two weeks, and weighed again to allow calculation of % moisture content. Additionally, the volume of DWM was calculated for each quadrat (pre- and post-treatment) for Experiment 2 by splitting the original 2 x 40 m DWM sub-plots into two 2 x 20 m DWM sub-plots.

Analyses

To test whether the plots (Experiment 1) and quadrats (Experiment 2) were homogeneous with respect to moisture content, litter depth, and shade coverage, these parameters were tested using a 1-factor analysis of variance (ANOVA) with treatments as the main effect for both experiments. Variables were averaged over all 5 trap locations within each plot for Experiment 1 prior to analysis. Additionally, the volume of DWM was tested with ANOVA to asses the homogeneity of the plots and quadrats prior to the treatments being applied. In Experiment 2 the post-treatment DWM volume was tested to see if the treatments resulted in the desired outcome in terms of re-distribution of DWM. Some data were transformed prior to analysis [ln(x+1) or square-root transformations], and the non-parametric Mann-Whitney *U*-test was used to compare the control and removal treatment in Experiment 1 when transformations did not produce normalized data.

To investigate whether variation in spider catches could be related to natural variation in DWM volume on the forest floor before experimental treatments were applied, correlation analysis was used on pre-treatment spider variables and pre-treatment DWM estimates. These correlations were done at the plot level, with the spider variables averaged per plot ($n = 20$) [i.e., averaged over 5 (Experiment 1) or 4 (Experiment 2) pitfall traps].

To test treatment effects, differences in spider assemblages were examined by analyzing the post-treatment spider data with a one-factor analysis of covariance (ANCOVA), using the pre-treatment data as the covariate in the analysis. With this approach it was possible to separate year-to-year changes in spider assemblages from the treatment effects, as ANCOVA tests treatment effects on post-treatment data using means adjusted for the effect of the covariate (pre-treatment data). The factor in the ANCOVA had either two levels in Experiment 1 (removal treatment and control) or four levels in Experiment 2 (disturb, remove, addition treatments, and control).

The following spider variables were used in the analyses: species richness, species diversity [Simpson's and Shannon diversity indices (Magurran, 1988)], total catch, catch of immature specimens, number of the dominant spider families collected, and the number of the most commonly collected species (i.e., those representing > 5% of the total catch). With the exception of the two diversity indices, standardized data were used in the analyses and data were $\ln(x+1)$ transformed prior to analysis to meet the assumptions of normality for parametric statistical tests. P-values from each set of analyses were corrected for multiple statistical tests using the sequential Bonferroni method with an experimentwise error rate of $\alpha = 0.05$ (Sokal & Rohlf, 1995). SPSS for windows (SPSS Inc. 1999, Chicago, IL) was used for ANOVA, ANCOVA tests, and correlation analyses.

Treatment effects on spider diversity were also evaluated through rarefaction analysis (Simberloff, 1978). Rarefaction estimates can be interpreted as diversity indices as both the species richness and abundance are included in the algorithm. Rarefaction is preferable to many traditional diversity indices as it corrects for varying sample sizes and the resulting rarefaction curves allow for unbiased comparisons of diversity. Raw data was used for rarefaction analyses, and calculations were done using the Internet software provided by Brzustowski (2000a).

Cluster analysis was used to better understand the community-wide response to the different treatments. Log-transformed standardized data were used to group the pre- and post-treatment plots and treatments (Experiment 1) and treatments (Experiment 2) based on the similarity of spider assemblages. Pair-wise similarities were calculated using the Bray-Curtis Index of percent similarity (Bray & Curtis, 1957) and dendrograms were produced using unweighted arithmetic averaging. Internet software by Brzustowski (2000b) was used for cluster analyses.

To further assess potential factors that may influence spider variables, stepwise multiple regression was used on spider data and abiotic parameters for Experiment 2. This was only done for Experiment 2 as data about DWM volume were not available for each trap location in Experiment 1. Post-treatment data were used for this analysis as the abiotic parameters were measured in 1999. Abiotic parameters included DWM volume, litter depth, shade, and moisture content of soil. Spider variables were the same as those used in the previous ANCOVA analyses. Best fit models were assessed on the R^2 values and the regression ANOVAs, and correlation coefficients of dependent variables were evaluated to check for multicollinearity.

Results

Pre-treatment correlation analysis

Spider variables (species richness, Simpson's and Shannon diversity indices, total catch, number of immatures, dominant spider families, and common species) were not correlated to DWM volume (m^3 ha^{-1}) at the plot level ($n = 20$) (p-values ranging from 0.09 to 0.92) before the treatments were applied. The dominant spider families included the Linyphiidae (micro-sheet web spiders), Lycosidae (wolf spiders, 20%), and the Liocranidae (represented by one species, *Agroeca ornata* Banks). Other common species, representing > 5% of the total catch or > 200 individuals, included *Allomengea dentisetis* (Grube), *Pardosa mackenziana* (Keyserling), *Cybaeopsis euopla* (Bishop & Crosby), *Ozyptila sincera canadensis* Dondale & Redner, *Bathyphantes pallidus* (Banks), and *Trochosa terricola* Thorell (Appendix 3).

Experiment 1: large-scale DWM removal

Plots were homogeneous with respect to the abiotic parameters as ANOVA or Mann-Whitney *U*-tests revealed no significant differences among control and removal plots for moisture content ($F_{1,6} = 0.421$, $p = 0.541$), litter depth ($U = 7.5$, ns), and shade coverage ($F_{1,6} = 0.143$, $p = 0.791$). Additionally, the volume of DWM did not differ between removal and control plots before treatment application ($F_{1,6} = 2.78$, $p = 0.148$).

A total of 5246 individual spiders was collected, 2123 in pre- and 3123 in post-treatment years; about 6% were immature specimens. More spiders were collected in post- compared to pre-treatment years (Table 7-1). Overall, the post-treatment control plots had the most spiders and the pre-treatment removal plots the fewest (Table 7-1).

Sixty-five species were collected (Appendix 3). Average standardized species richness was higher in control than removal plots and there were few apparent differences in average species richness between years (Table 7-1).

The Linyphiidae accounted for 29% of the total catch, the Lycosidae accounted for 20% of total catch, and the Liocranidae, 20% of the total catch (Fig. 7-1). The 7 common species (outlined above) accounted for 72% of the total catch. Many species collected were rare or uncommon; twenty species were represented by only one or two individuals.

The dominant spider families varied more by collection year than by treatment (Fig. 7-1). The lycosids and liocranids increased and linyphiids decreased in post-treatment catches. Results of the ANCOVA on species richness, species diversity (Simpson's and Shannon indices), total catch, catch of immature specimens, number of linyphiids and lycosids, and the number of the 7 commonly collected species did not differ by treatment (p-values ranging from 0.09 – 0.965). After the Bonferroni correction, the effects of all covariates (pre-treatment data) were also non-significant. However, a low p-value ($p = 0.005$) for the pre-treatment total catch of spiders suggests temporal constancy among the plots [i.e., high catches of spiders in a plot in the pre-treatment year gnerally corresponded to high catch in the same plot in the post-treatment collection year (Fig. 7-2A)]. The most common species collected, *A. ornata*, showed some degree of temporal constancy, but was much less abundant in the pre- versus post-treatment collection year (Fig. 7-2B); catches of *A. ornata* were not affected by removal of DWM. Similarly, spider species richness was not affected by the removal of DWM, and species-rich plots in the pre-treatment year did not closely correspond to species-rich plots following the treatment application (Fig. 7-2C).

Estimates of spider diversity, using rarefaction, show that in both pre- and post-treatment collection years, spider diversity was significantly lower in removal compared to control plots (Fig. 7-3A,B). The change in rarefaction estimates from the pre- to post-treatment year, however, showed that spider diversity actually decreased in control plots at higher sub-sample sizes and increased in removal plots at similar sub-sample sizes (Fig. 7-3C).

If treatment effects were important to community structure, one would expect the overall spider community in post-treatment removal plots to be distinct from the control plots; this pattern was not evident from the cluster analysis as the general pattern was that pre- and post-treatment years were most dissimilar regardless of treatment (Fig. 7-4). In only one case did post-treatment removal plots cluster together (plots 1 and 2). As expected, there were no clear patterns in the pre-treatment data, although the control plots 1 and 4 were the most dissimilar to all other plots (Fig. 7-4).

Experiment 2: small-scale DWM manipulation

Measures of abiotic parameters did not differ significantly by treatment (control, disturb, add, and remove DWM) (moisture: $F_{3,44} = 0.124$, $p = 0.945$; litter depth: $F_{3,44} = 0.322$, $p = 0.810$; shade coverage: $F_{3,44} = 0.411$, $p = 0.746$). Pre-treatment data on the volume of DWM was also non-significant by treatment ($F_{3,44} = 0.272$, $p = 0.846$), and post-treatment DWM volume was highly significant ($F_{3,44} = 36.766$, $p < 0.001$). As expected, the volume of DWM remained unchanged for control and disturb quadrats following DWM manipulations (80.4 ± 15.09 and 74.3 ± 20.40 $m^3 ha^{-1}$ respectively), was significantly higher in addition quadrats with an average DWM volume of 144.5 ± 22.04 $m^3 ha^{-1}$ (Tukey's test, $p < 0.05$), and one year after manipulations there was no DWM in post-treatment removal quadrats.

A total of 5663 individual spiders was collected, 2491 in pre- and 3172 in post-treatment years; about 7% were immature specimens. Comparisons of average standardized catch showed higher collections in pre- and post-treatment removal quadrats and post-treatment addition quadrats, and the lowest average catch occurred in pre-treatment disturb quadrats (Table 7-2).

Seventy three spider species were collected (Appendix 3). Average standardized species richness was lowest in post-treatment control quadrats and was highest in pre-treatment removal quadrats (Table 7-2). As in the larger-scale manipulation (Experiment 1), linyphiids and lycosids were the dominant families collected (28% and 26% of the total catch respectively) (Fig. 7-5). The families Amaurobiidae and Liocranidae (*A. ornata*) represented 17% and 16%, respectively, of the total catch. The 7 common species represented 77% of the total catch, and twenty-three species were represented by one or two individuals.

The dominant spider families also varied more by collection year than by treatment (Fig. 7-5), with the same patterns observed in Experiment 1 (i.e., lycosids and liocranids increased and linyphiids decreased in their relative abundance in the post-treatment year). Treatment effects were non-significant for all spider variables analyzed using ANCOVA, with p-values ranging from 0.138 – 0.858. Thus, after adjustment for year-to-year effects, adding, removing, or disturbing DWM had no effect on spider assemblages. After Bonferroni correction, the covariate (pre-treatment data) was significant for species richness ($p = 0.002$), Shannon diversity index ($p < 0.001$), number of lycosids ($p < 0.001$), *P. mackenziana* ($p = 0.001$), and *O. sincera canadensis* ($p < 0.001$). Unlike the results from Experiment 1, high pre-treatment catches did not correspond to high post-treatment catches (Fig. 7-6A). Although treatments had no significant effect on catches of *P. mackenziana*, high pitfall trap collections of this species in the pre-treatment year generally corresponded to high catches in the same traps in the post-treatment collection year (Fig. 7-6B). High species richness per trap in the pre-treatment collections generally corresponded to low species richness per trap in the following year (Fig. 7-6C).

The Shannon and Simpson's diversity indices were clearly non-significant by treatment ($p = 0.419$ and $p = 0.802$ respectively). However, the post-treatment averages of these diversity indices were highest in addition quadrats (2.1 ± 0.09 and 6.3 ± 0.68 respectively) and were lowest in the control quadrats (1.9 ± 0.08 and 5.4 ± 0.55). Rarefaction estimates of spider diversity in the pre-treatment year revealed a significantly higher diversity in control and disturb compared to removal and addition quadrats (Fig. 7-7A). Post-treatment estimates of diversity using rarefaction suggest a significantly higher diversity in addition quadrats compared to the other treatments (Fig. 7-7B).

The change in spider diversity from pre- to post-treatment collections revealed a clear decrease in the expected number of species in control and disturb quadrats, a slight increase in removal plots, and an increase of over 5 species in addition plots (i.e., compared at sub-sample size of 450 individuals, Fig. 7-7C). Additionally, the number of locally rare species (represented by 1 or 2 individuals) increased from 16 to 21 species in addition quadrats; the change in rare species was less pronounced in removal quadrats (14 to 17 species) and decreased in disturb quadrats from 23 to 18 species and decreased from 25 to 19 species in control quadrats. The increase in the diversity in addition and removal quadrats from pre- to post-treatment collections is partially explained by the increase in rare species collected in these quadrats.

The overall spider community was again separated on the basis of collection year as illustrated with the dendrogram produced from the cluster analysis (Fig. 7-8). In the post-treatment year, the most dramatic treatments (addition and remove quadrats) were most similar with respect to spider communities, with control plots being the most dissimilar compared to the other treatments (Fig. 7-8).

Results from the stepwise multiple regression indicated the measured abiotic parameters and DWM volume were relatively poor predictors of the different spider response variables tested (Table 7-3). The highest R^2 value was able to explain only 29% of the variation in the catch of *Allomengea dentisetis*. Among significant regression models, DWM volume and shade coverage predicted the total catch of spiders. Shade coverage was important in explaining the variation in catches of linyphiids, lycosids, *A. ornata*, *Allomengea dentisetis*, and *T. terricola*. Litter depth was included in the significant model for *Allomengea dentisetis*. Variation in the Simpson's diversity index was partially explained by both litter depth and moisture content of the soil.

Discussion

Pre-treatment DWM variation and spider variables

The natural volume of DWM at George Lake varied dramatically, ranging from 27.4 to 159.4 $m^3 ha^{-1}$. The average DWM volume at George Lake (74.8 ± 8.17 $m^3 ha^{-1}$) was less than other estimates from mature and old aspen-dominated forests in north-central Alberta (109.1 ± 7.6 and 124.3 ± 7.1 $m^3 ha^{-1}$ respectively) (Lee *et al.* 1997); however, the variation in DWM at George Lake was similar to that reported by Lee *et al.* (1997). Although Buddle *et al.* (2000) suggested variation in some aspects of spider assemblages may be explained by the presence of CWD, and several spider variables were correlated to CWD estimates, no spider variables were correlated with pre-treatment DWM estimates at George Lake. However, the wolf spider *T. terricola* had been noted as being positively correlated to DWM volume throughout north-central Alberta ($r = 0.58$) (Buddle *et al.*, 2000), and at George Lake the correlation coefficient between catches of *T. terricola* and DWM volume was 0.392 ($p = 0.088$). Although the latter coefficient is non-significant, the trend supports the results of Buddle *et al.* (2000), and this wolf spider may show general affinities towards areas with high DWM volumes.

Species richness and diversity

Spider species richness showed little change in the first year after the DWM manipulations were applied. However, there are several trends that suggest that diversity, which takes into account both species richness and the relative abundance of species (Magurran, 1988), was higher in treatments that drastically altered the habitat. In both experiments, the change in rarefaction estimates showed an increase from the pre- to post-treatment collections in the removal treatments. Furthermore, in Experiment 2 the rarefaction estimates were highest in the addition quadrats, showing an increase of over 5 species following DWM augmentation. Although not statistically different, the Shannon and Simpson's diversity indices were also highest in the DWM addition quadrats. Thus, weak effects of the manipulations are suggested.

Other studies have demonstrated that spider diversity increases following severe modifications of the habitat such as clear-cutting (Coyle, 1981) and wildfire (Johnson, 1995; Collins *et al.*, 1996). Increased diversity in these instances is often explained by the rapid appearance of pioneer species (Duffey, 1993), and colonization of the disturbed habitats by open-habitat specialists (e.g., lycosids) (Huhta, 1971; Coyle, 1981; Pajunen *et al.*, 1995; Buddle *et al.*, 2000). Together with species that are insensitive to disturbance [i.e. generalists, Duffy (1993)], these elements of the fauna cause elevated diversity following disturbance. Although addition or removal of DWM in relatively small-scale experiments is not directly comparable to landscape-level disturbance, the effects on spider diversity may be comparable. Pioneer species and those specializing in open habitats (e.g., a forest floor void of DWM) or species that frequently use DWM (Chapter 6), may colonize plots or quadrats affected by removal or addition treatments, thus increasing the diversity. Furthermore, given that fallen logs harbour high spider diversity and diversity tends to be higher adjacent to dead wood compared to further from DWM (Chapter 6), it is possible that diversity in DWM addition quadrats is elevated due to the close proximity of pitfall traps to fallen logs.

Relative abundance and species specific patterns

Overall, the total catches of spiders, and the number of the most common families and species collected, were unaffected by DWM manipulations. Background year-to-year variation was also more notable than treatment effects. Changes in the relative abundance of families and species is known to vary from year to year (Huhta, 1971), implying that factors above and beyond the experimental treatments drive some aspects of the spider fauna. In the present experiment, given the homogenous nature of the forest at George Lake, it is probable that yearly variations in temperature, rainfall, and other climatic processes caused the yearly variations in spider assemblages.

The total catch of spiders varied little between years in 40 x 40 m plots, with data from 5 pitfall traps pooled across each plot (Experiment 1). High catches in individual traps in the pre-treatment year (Experiment 2), however, did not correspond to higher catches in the same traps in the second sampling year in 20 x 20 m quadrats. This is likely a feature of higher trap-to-trap variation compared to plot-to-plot variation; plots with high numbers of spiders continue to have high numbers of spiders after one year of sampling, even though individual traps catches varied substantially.

Abiotic parameters such as shade, litter depth, and moisture were overall more important than DWM volume in explaining catch rates of spiders. Although the total catch of spiders was negatively associated with DWM volume, this effect was coupled with changes in the shade coverage at each pitfall trap location. Number of lycosids was negatively associated with increased litter depth, a pattern consistent with research showing that lycosids increase along gradients of decreasing litter depth and complexity (Uetz, 1991). Web-building spiders, however, tend to show affinities towards complex litter structure (Bultman & Uetz, 1982), and litter structure is positively associated with litter depth. The linyphiid *Allomengea dentisetis* showed an opposite pattern; this species had higher catches in regions with shallow litter but with higher shade coverage. Ground-dwelling linyphiids occupy the complex leaf-litter matrix of the forest floor (Huhta, 1971) and since shade influences this microhabitat, it is expected that shade coverage will affect linyphiid spiders (McIver *et al.*, 1992; Pajunen *et al.*, 1995; Muzika & Twery, 1997). Thus, in a forestry context, spiders may be more sensitive to changes in microhabitats on the forest floor than to changes in the volume of DWM resulting from forest harvesting.

The step-wise regression suggested shade was the best predictor for catches of the wolf spider *T. terricola*. However, since a positive relationship between this species and pre-treatment DWM volume was previously established, correlation analyses on the post-treatment catches of *T. terricola* (Experiment 2) to post-treatment DWM volume was done. The resulting correlation coefficient (r = 0.336) was significant (p = 0.045), supporting the results from the pre-treatment year. Although treatment effects were non-significant for catches of *T. terricola* (Experiment 1, p = 0.234; Experiment 2, p = 0.582), it is of interest that in Experiment 2 this wolf spider had the highest catches in DWM addition quadrats and the lowest catches in DWM removal quadrates (Appendix 3). In Experiment 1, *T. terricola* was more commonly collected in control compared to removal plots (Appendix 3). In concert with the positive relationships between this species and DWM estimates and the results from Buddle *et al.* (2000), the generality of *T. terricola* showing strong affinities towards DWM holds. Furthermore, Dondale & Redner (1990) suggest that *T. terricola* is commonly collected under logs; *Trochosa terricola* may depend on the habitat associated with fallen logs, and losses of DWM may have detrimental effects of the long-term viability of populations of *T. terricola.*

With the exception of *T. terricola*, none of the remaining species collected showed definable responses to any of the DWM treatments at either scale (Appendix 3), even though several species have previously been identified as showing strong affinities towards DWM (Chapter 6). These included *P. mackenziana* (1260 individuals), *Agelenopsis utahana* (Chamberlin & Ivie) (88), *Clubiona canadensis* Emerton (7), *C. moesta* Banks (5), *Steatoda borelis* (Hentz) (2), *Drapetisca alteranda* Chamberlin (1), and *Lepthyphantes turbatrix* (O.P.-Cambridge) (1). The rarity of the latter 3 species, all of which are web-builders, may reflect that these species seldom move far from fallen logs. If indeed these species are dependent on fallen logs, DWM removal may have a detrimental effect on their local populations. However, such statements are difficult to prove given the rarity of these species. The clubionid species are known from a variety of habitat types, ranging from the forest floor, under bark and stones, to occupation of trees and shrubs (Dondale & Redner, 1982). These habitat affinities suggest *C. canadensis* and *C. moesta* are able to easily adapt to their environment, and removal of DWM may have little influence on their populations. Although the funnel-web spider *Agelenopsis utahana* may have some preference towards the surface of fallen logs, ground-dwelling populations of these species were not affected by the removal, disturbance, or addition of DWM. Thus, *Agelenopsis utahana* may use the DWM habitat on an opportunistic basis.

Pardosa mackenziana is a ubiquitous species known from a variety of forest types throughout its range (Dondale & Redner, 1990; Buddle *et al.*, 2000). Although this wolf spider frequently uses the surface of fallen logs, activity of this species appears indifferent to the short-term loss or addition of DWM on the forest floor. However, it has been argued that *P. mackenziana* females select the surface of DWM to sun their egg sacs and speed development of their young (Chapter 6). Since this species is known to take two years to reach maturity in the George Lake forest (Buddle, 2000), any effects of DWM manipulations on *P. mackenziana* populations may not be apparent one year after the treatments were applied. If fewer young are produced in regions lacking DWM, there may be negative population effects on *P. mackenziana* over the course of several years.

There are potentially many other lag effects of DWM manipulations on spider species. Spiders that use DWM for a foraging substrate, as shelter, or as an overwintering site may show long-term population changes in experimental units with modified DWM. Additionally, other arthropod taxa that may act as competitors or potential prey may show different responses to DWM manipulations, and these responses may occur over longer time scales. Collembola, a common prey for many spider species (Huhta, 1971; Wise & Wagner, 1992), are known to be affected by DWM, as Bengtsson *et al.* (1997) showed decreased Collembola in plots without logging residues compared to plots with twice the normal amount of residues. If a main prey resource of spiders, such as Collembola, is affected by DWM manipulations, there may be long-term effects on populations of many spider species.

Data from the 2000 collection year will certainly aid in interpreting some of these temporal effects. Furthermore, it would be worthwhile revisiting this experiment several years post-treatment to better understand the long-term (i.e., 5 – 10 years) effects of DWM manipulations on spider assemblages.

Community patterns

As evident from the cluster analyses, the overall community structure of spiders was not affected by DWM manipulations. In both experiments, background temporal variation was much greater than any treatment effects. The similarity measures were also high for all pair-wise comparisons of plots or quadrats (i.e., > 65 % in Experiment 1 and > 70 % in Experiment 1); the overall spider community sampled was relatively homogeneous within a single sampling year.

Niemelä *et al.* (1996) and Buddle *et al.* (2000) have shown that spider catches vary more between traps placed in young compared to older successional forest stages. The environment may be more heterogeneous in younger forests and canopy closure has been cited as a major feature structuring older-forest spider assemblages (Huhta, 1971; McIver *et al.*, 1992; Niemela *et al.*, 1996). Older forest spider assemblages are typically defined by a higher proportion of web-building spider species (especially linyphiids), whereas younger forest age-classes are usually dominated by large-bodied wolf spiders (McIver *et al.*, 1992; Pajunen *et al.*, 1995; Buddle *et al.*, 2000). The ground-dwelling spider fauna at George Lake is representative of an old-growth forest; linyphiids were the dominant spider family collected and the common wolf spiders (e.g. *P. mackenziana* and *T. terricola*) are typically known from closed-canopy forests (Dondale & Redner, 1990; Buddle *et al.*, 2000)

The lack of treatment effects may relate directly to both the homogeneous nature of the ground-dwelling spider fauna at George Lake and to the scales at which the experiments were designed. Plots sizes of 40 x 40 m or 20 x 20 m were chosen for practical reasons (i.e., given the labor-intensive nature of the experiments) and they were chosen to be large enough to capture the population boundaries of many species in the system. However, wolf spiders in the genus

Pardosa can move distances upwards of 10 m in a single day (Hallander, 1967): scales of these experiments may have been too small to capture any population effects on such long-ranging species. Although the experimental treatments produced significant deviations from the typical volume of DWM on the forest floor, all pitfall traps were in close proximity to potential source populations of many species (i.e., 10 or 20 m from the plot boundary). The mobility and dispersal ability of these spiders may have overridden any treatment effects. In contrast, many small-bodied linyphiids (e.g., *Allomengea dentisetis*) build sheet-webs within the leaf-litter matrix (van Helsdingen, 1974) and their range in movement is much less. The plot sizes may have been too large to see treatment responses for linyphiids.

Lack of treatment effects may also be partially explained by the sampling technique. Pitfall trapping spiders provides reliable data on ground-dwelling spider assemblages, but fails to capture the spider fauna living higher in the vegetation. Many web-building spiders use the vertical structure of a forest and the spatial structure or architecture of the vegetation layer is known to directly effect the diversity and abundance of many web-building species (Hatley & MacMahon, 1980; Robinson, 1981; Greenstone, 1984). Fallen logs provide such web-building species numerous sites for the attachment of webs, and web-building species appear to use DWM partially because of the complexity of the habitat (Chapter 6). Modifications of DWM may therefore have a larger impact on the spider fauna living above the forest floor and future research should be directed at sampling this element of the spider fauna.

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Table 7-1 Average (± SE) total standardized catch and average standardized species richness per plot (*n* = 4 for control and removal treatment, *n* = 8 for total) in pre- and post-treatment collections in control and DWM removal plots (Experiment 1). Data were standardized to 693.3 trap-days.

Pre-treatment:	Control	Removal	Total
Total catch	336.2 ± 64.73	255.8 ± 15.97	296.0 ± 32.87
Species richness	32.5 ± 2.95	22.0 ± 1.36	27.3 ± 2.53
Post-treatment:	**Control**	**Removal**	**Total**
Total catch	359.1 ± 41.30	346.6 ± 25.97	352.9 ± 21.06
Species richness	29.1 ± 0.92	25.2 ± 1.73	26.7 ± 1.03

Table 7-2 Average (± SE) total standardized catch and average standardized species richness per quadrat (*n* = 12 for treatments, *n* = 48 for total) in pre- and post-treatment collections in control, disturb, add, and remove DWM quadrats (Experiment 2). Data were standardized to 136.4 trap-days.

Pre-treatment:	Control	Disturb	Add	Remove	Total
Total catch	62.8 ± 8.05	52.7 ± 8.47	46.1 ± 5.83	70.6 ± 11.12	58.1 ± 5.19
Species richness	15.2 ± 1.30	13.8 ± 1.54	11.6 ± 0.87	14.2 ± 1.78	13.7 ± 0.69
Post-treatment:	**Control**	**Disturb**	**Add**	**Remove**	**Total**
Total catch	44.4 ± 7.04	59.5 ± 11.05	65.5 ± 9.53	70.0 ± 7.96	59.9 ± 5.39
Species richness	10.5 ± 1.14	11.9 ± 1.36	12.9 ± 0.84	13.6 ± 1.46	12.2 ± 0.60

Table 7-3 Best fit models for stepwise multiple regression of post-treatment spider variables against volume of DWM (m^3 ha^{-1}), litter depth (cm), shade coverage (% at 0.5 m height), and moisture content of soil (%). Regressions were NS ($p > 0.05$) for species richness, Shannon diversity index, no. immature specimens, and number of *Pardosa mackenziana*, *Cybaeopsis euopla*, *Bathyphantes pallidus*, and *Oxyptila sincera canadensis*. Abiotic variables were square root transformed and spider variables (except for Shannon and Simpson's diversity indices) were ln(x+1) transformed prior to analysis.

	R^2	Predictor(s)	β[†]	Regression ANOVA	
Simpson's diversity	0.154	Litter depth	0.493	$F_{2,45} = 4.099$	$p = 0.023$
		Moisture	0.312		
Total catch	0.125	DWM volume	-0.312	$F_{2,45} = 3.226$	$p = 0.049$
		Shade	-0.264		
No. of Linyphiidae	0.107	Shade	-0.328	$F_{1,46} = 5.529$	$p = 0.023$
No. of Lycosidae	0.134	Shade	-0.286	$F_{2,45} = 3.496$	$p = 0.039$
		Litter depth	-0.250		
Agroeca ornata	0.083	Shade	-0.287	$F_{1,46} = 4.141$	$p = 0.048$
Allomengea dentisetis	0.290	Litter depth	-0.533	$F_{2,45} = 9.171$	$p < 0.001$
		Shade	0.225		
Trochosa terricola	0.132	Shade	-0.363	$F_{1,46} = 6.970$	$p = 0.011$

[†] standardized coefficient

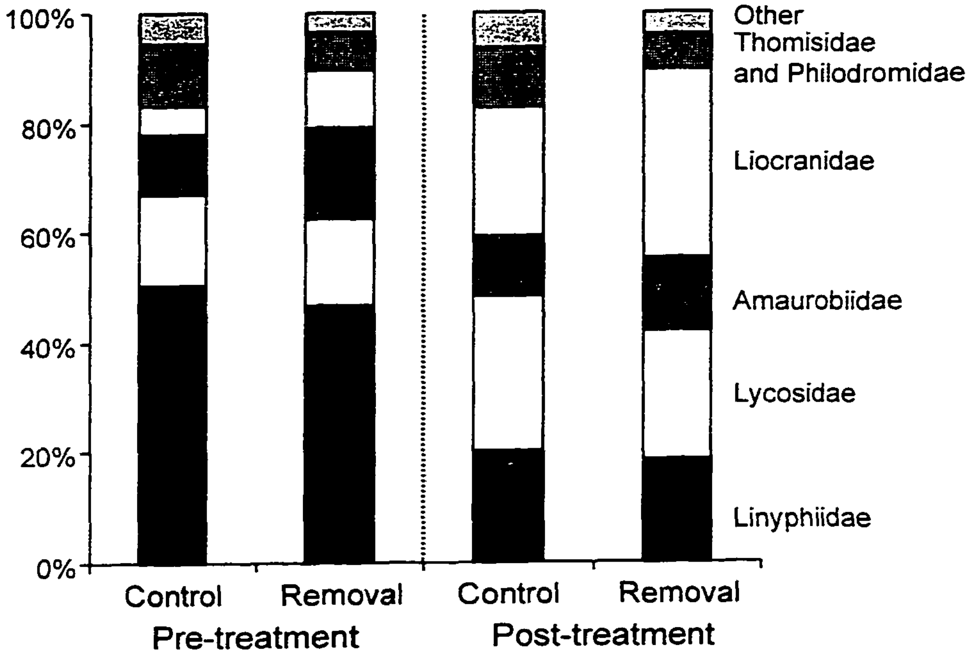

Figure 7-1 Relative frequency of dominant families (standardized data) in pre- and post-treatment control and DWM removal plots (Experiment 1).

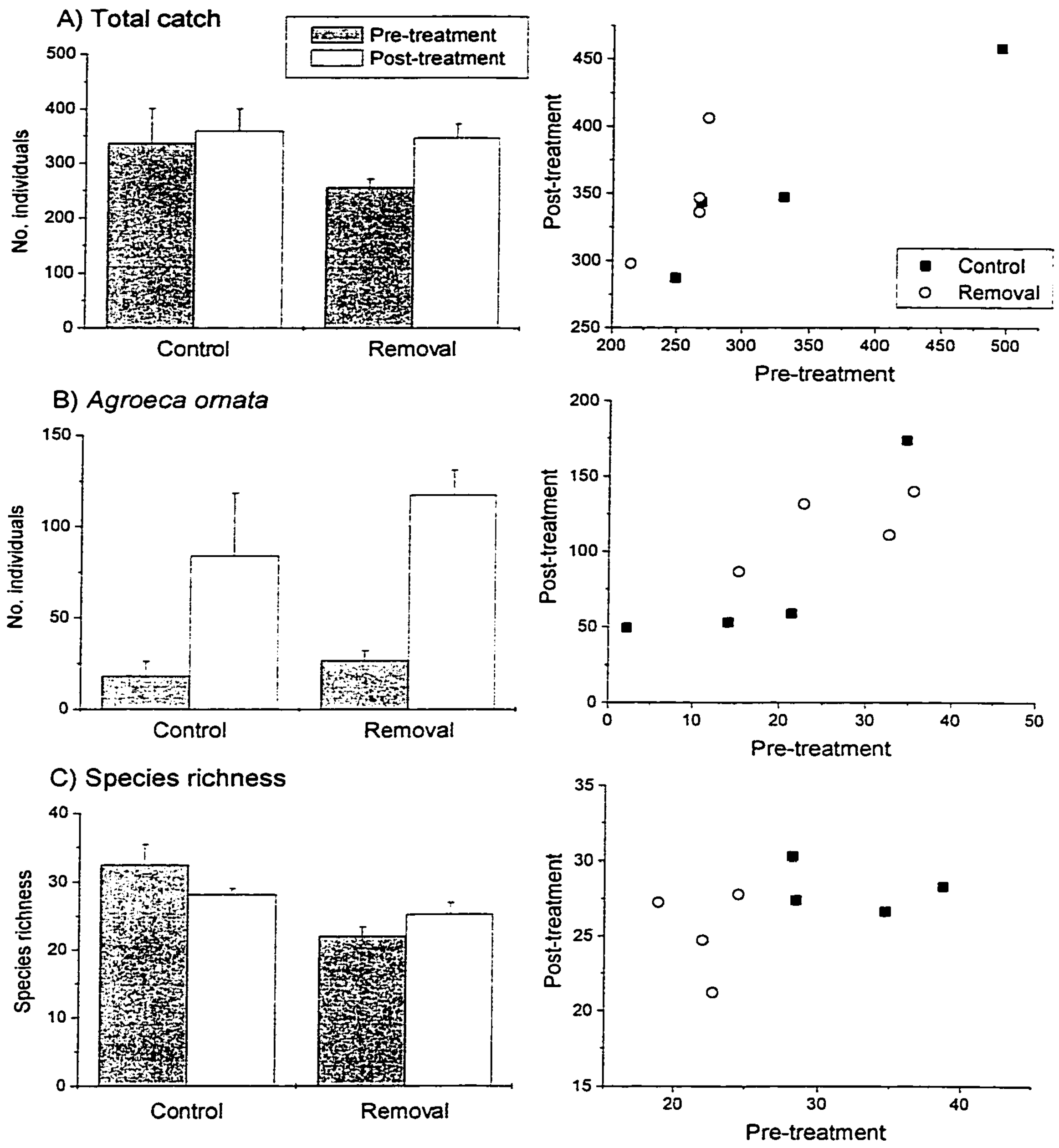

Figure 7-2 Pre- and post-treatment averages (left) (± SE, *n* = 4), and post-treatment catches plotted against pre-treatment catches (right) per control and treatment plot for Experiment 1.

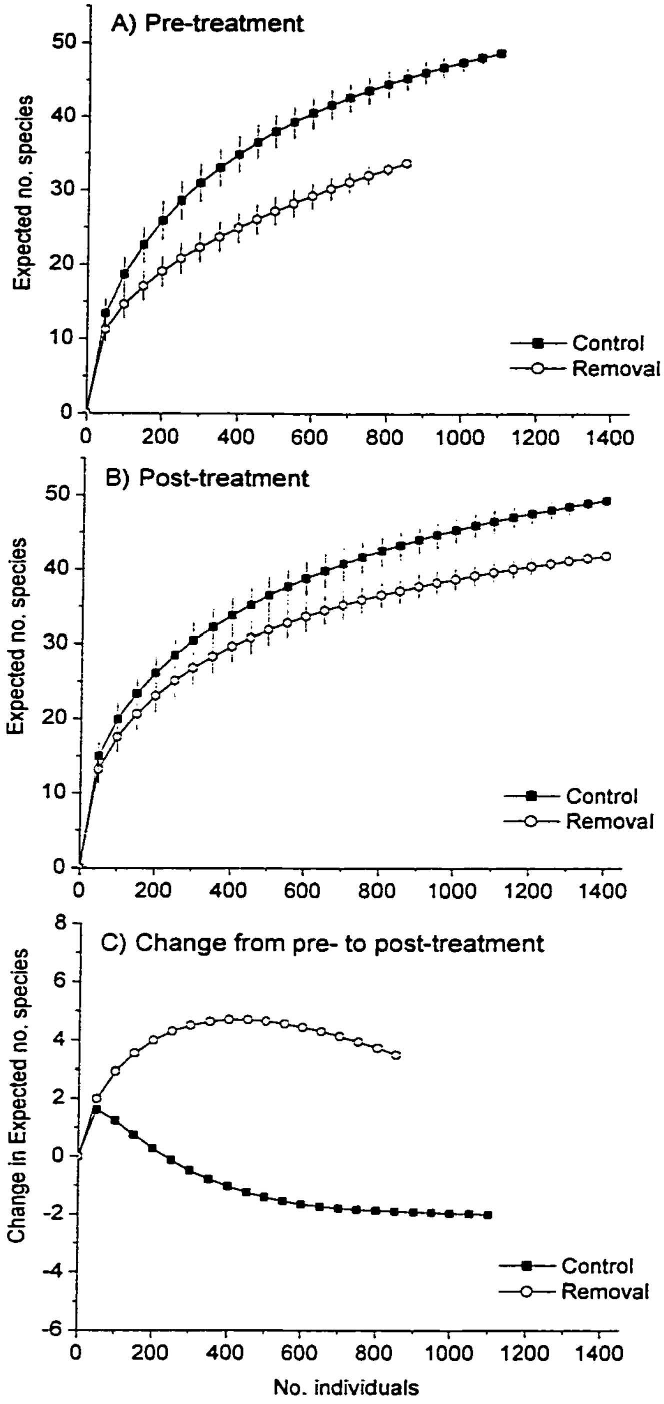

Figure 7-3 Rarefaction estimates of spider diversity by sub-sample size for spiders collected in control and DWM removal plots (Experiment 1). The change in number of species expected calculated from subtracting post-treatment estimates from pre-treatment estimates. Error bars are 1 standard deviation.

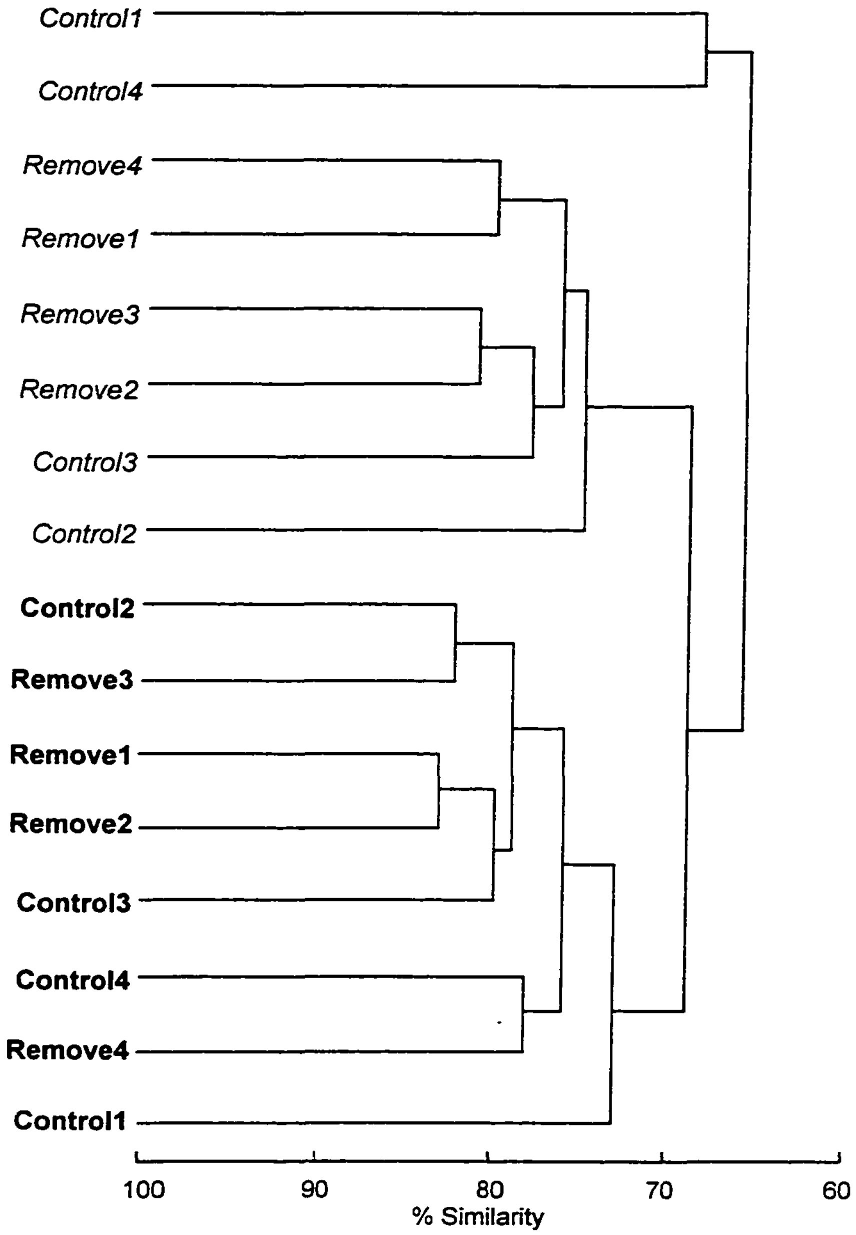

Figure 7-4 Cluster analysis of Bray-Curtis measures of percent similarity for spider assemblages collected in pre- (*italics*) and post-treatment (**bold**) control and DWM removal plots 1 - 4 (Experiment 1).

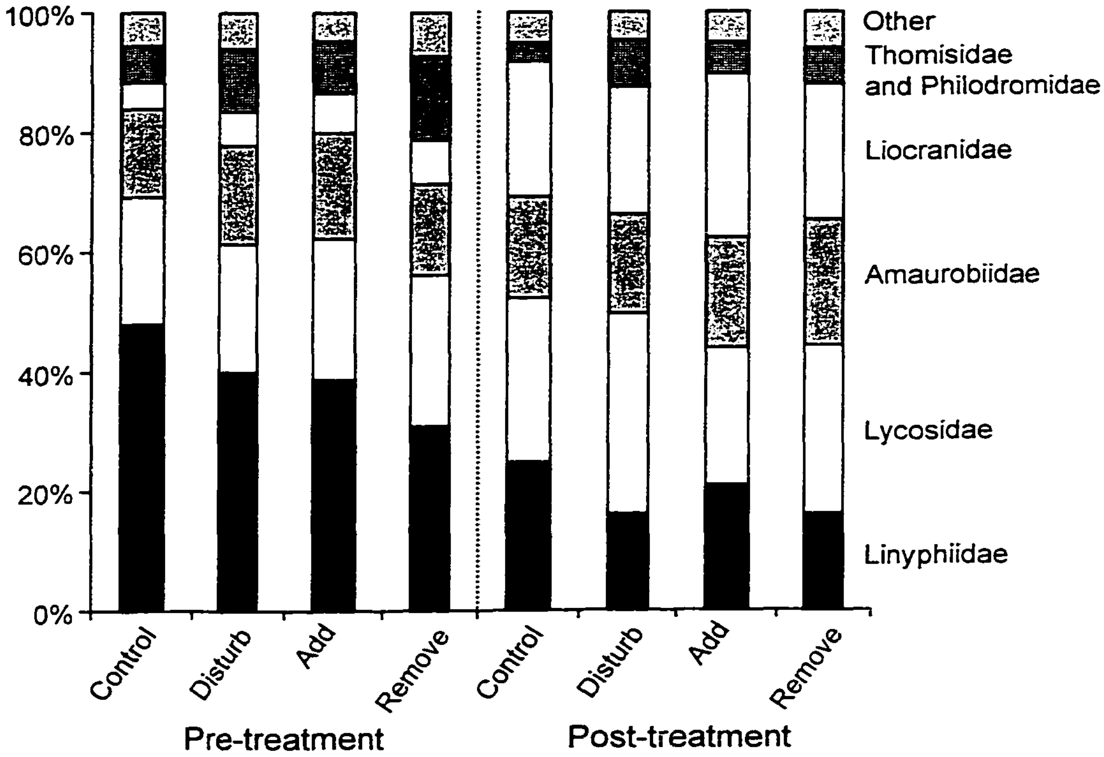

Figure 7-5 Relative frequency of dominant families (standardized data) in pre- and post-treatment control, disturb, addition, and DWM removal plots (Experiment 2).

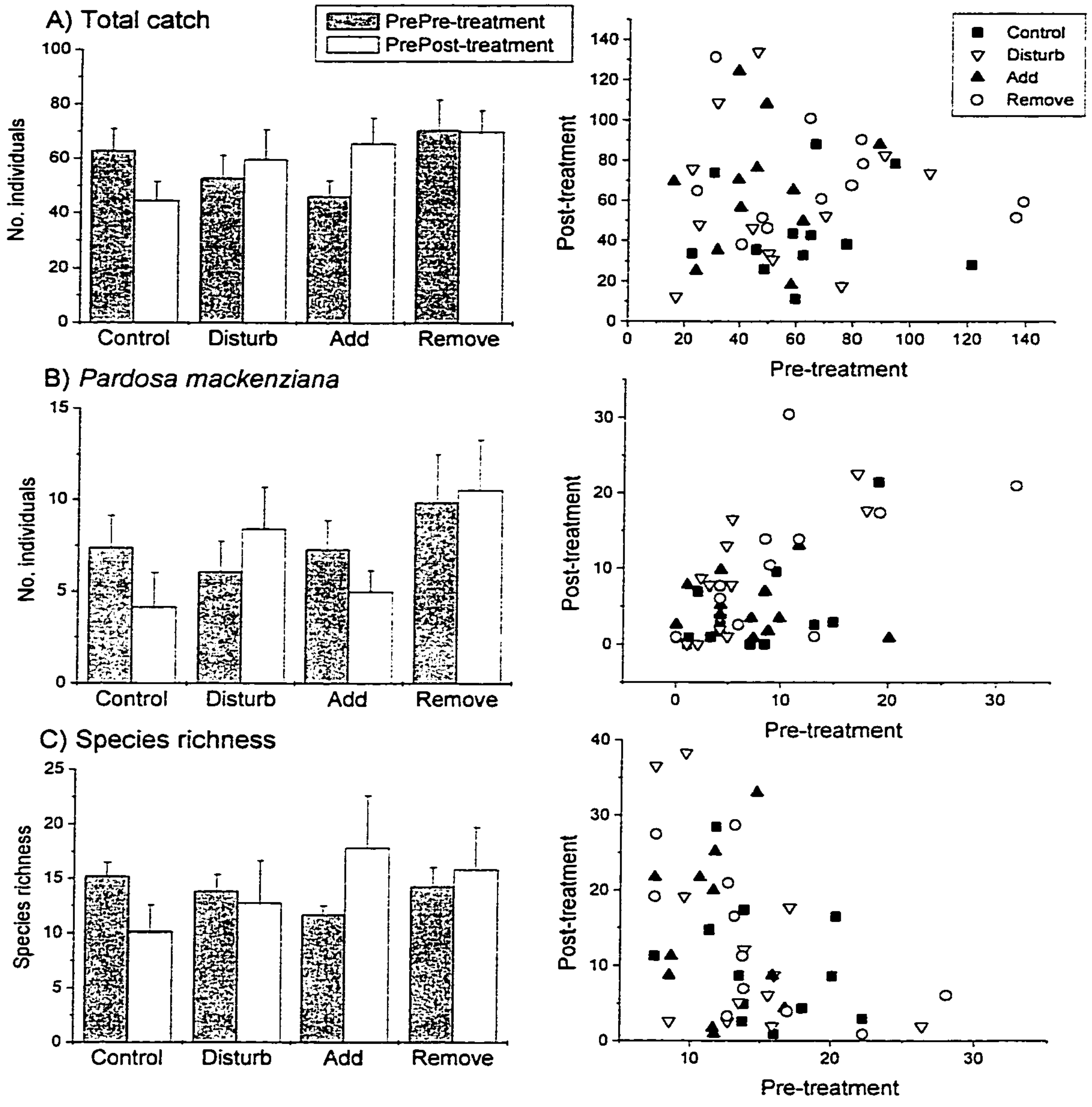

Figure 7-6 Pre- and post-treatment averages (left) (± SE, $n = 12$), and post-treatment catches plotted against pre-treatment catches (right) per pitfall trap for control, disturb, add, and remove DWM treatments (Experiment 2).

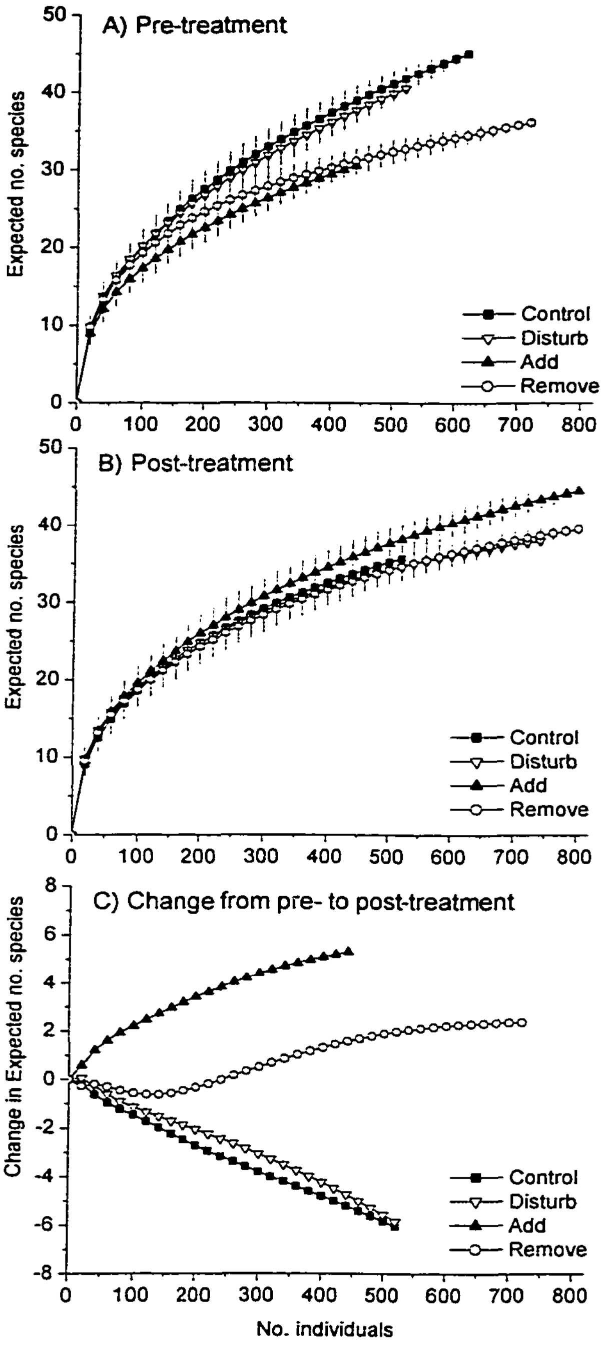

Figure 7-7 Rarefaction estimates of spider diversity by sub-sample size for spiders collected by control, disturb, add, and remove DWM treatments (Experiment 2). The change in number of species expected calculated from subtracting post-treatment estimates from pre-treatment estimates. Error bars are 1 standard deviation.

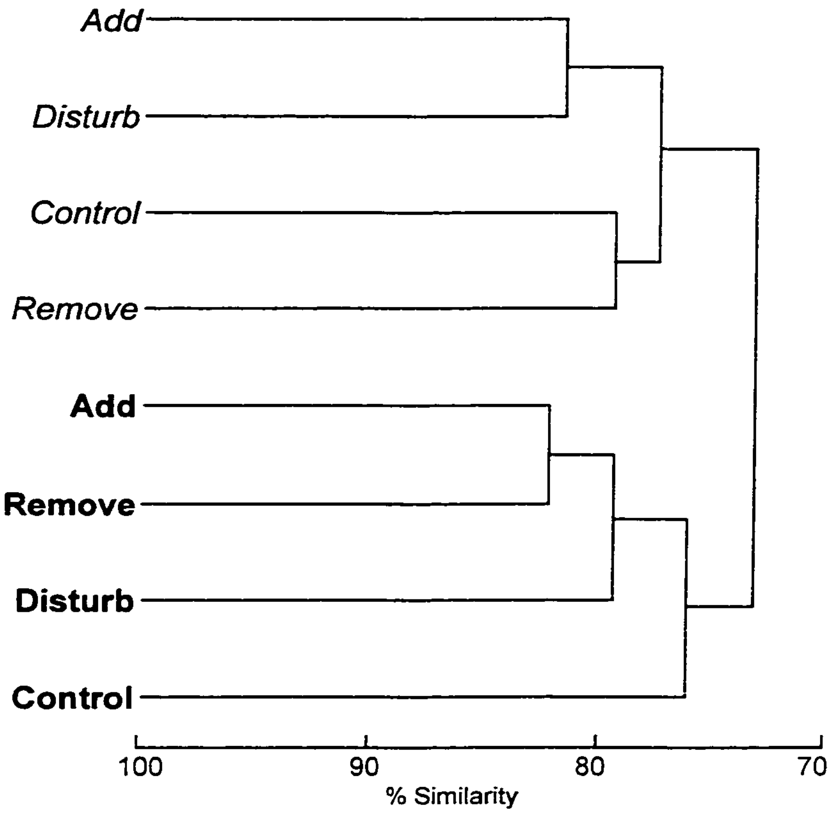

Figure 7-8 Cluster analysis of Bray-Curtis measures of percent similarity for spider assemblages collected in pre- (*italics*) and post-treatment (**bold**) years for Experiment 2: control, disturb, add, and remove DWM treatments.

8. General Discussion and Conclusions

Synthesis

My doctoral dissertation encompasses a series of natural and manipulative experiments that contribute to knowledge about spiders (Araneae) in boreal mixed-wood forests of Alberta. I have shown that spiders, as one element of biodiversity, can provide insights into ecological theory and provide a better understanding of how forestry may influence the forest biota. The "natural experiments" from Chapters 2 and 3 suggested intriguing patterns and provided insights into some of the processes important to spider assemblages in the boreal forest. I generated testable hypotheses from some of these patterns and established ecological field experiments aimed to test hypotheses about community structure (Chapters 4 and 5) and the importance of downed woody material (DWM) to spiders (Chapters 6 and 7).

Although there are many faunal surveys and checklists of spiders in Canada (e.g., West *et al.*, 1984; Aitchison-Benell & Dondale, 1990; Dondale & Redner, 1994; Koponen, 1994), my research represents one of the few quantitative studies of spider assemblages in the boreal forests of Canada. Chapters 2, 3, 6 and 7 were demanding studies with a foundation in alpha-level taxonomy; over 31 000 individual spiders representing 170 species were identified. Several species represent new records for the province of Alberta [e.g., *Eridantes utibilis* Crosby & Bishop, *Micrargus longitarsus* (Emerton), *Cnephalocotes obscurus* (Blackwall)] (Buckle *et al.*, 1995), and many species in the family Linyphiidae may be new to science (see Appendices). The long-term value of this work should not be underestimated: my studies provide base-line data for future projects on spiders in the boreal forests of Canada, and the spider data contributes to our knowledge of the biodiversity of forest ecosystems.

Chapters 2, 3, 6 and 7 have the most direct implications for the forest industry. Overall, spiders show a rapid recovery from disturbances such as wildfire and clear-cutting, and by *ca.* 30 years post-disturbance, the fauna is similar to the fauna of old and mature forest stands (Chapters 2 and 3). These results do support the basis of the natural disturbance paradigm because harvesting and wildfire give rise to similar spider assemblages after 30 years. However, there were also some important differences between the fauna of wildfire- and harvest-origin stands, as spider diversity was higher in wildfire stands and young stands initiated by wildfire showed high variation in the spider fauna. This likely reflects a greater diversity of habitats, especially moist micro-sites, following wildfire. Several species [e.g., *Gnaphosa borea* Kulczyński and *Arctosa alpigena* (Doleschall)] may be dependent on these conditions and may be at risk with increased forest harvesting and further fire suppression on the landscape. It was hypothesized that the presence of coarse woody debris (CWD) in wildfire stands contributes to the overall habitat complexity in certain stands, and this was quantitatively tested with the experiments outlined in Chapters 6 and 7.

My experiments with DWM were original and represent one of the first attempts to assess quantitatively how DWM may influence generalist predators that may not directly depend on dead wood for their survival. Although many species, and a diverse spider fauna, use the surface of DWM (Chapter 6), manipulating the volume of DWM on the forest floor had few short-term effects on spider assemblages (Chapter 7). One exception was that the wolf spider *Trochosa terricola* Thorell was positively associated with DWM volume, and this result was consistent with finding from Chapter 2. This species may depend on the habitat associated with fallen logs. Overall, however, it appears that DWM does not lead to the higher habitat complexity predicted for ground-dwelling spiders and there may be other features of young wildfire stands that result in variable spider assemblages. However, subsequent analysis of the second year of post-treatment spider data following DWM manipulations may provide other insights.

A common theme throughout Chapters 2, 6, and 7 was that high spider diversity is in part explained by the presence of DWM. If consideration of biodiversity is a priority for forest management (e.g., Probst & Crow, 1991), DWM should certainly be left following forest harvesting. Although I was unable to provide forest managers with data on quantity and quality of wood to be left behind (Hagan & Grove, 1999), the generality of more DWM being better than no DWM holds with respect to spider diversity.

In boreal mixed-wood forests, closed-canopy forests support a remarkably homogeneous spider fauna, as evident from the multivariate ordinations from Chapters 2, 3 and 6 and the cluster analyses from Chapter 7. Spider diversity was also low in old and mature mixed-wood stands (Chapter 3). No spider species were established to be true "old-growth" species; the fauna of older forests tended to have a high proportion of web-building species that typically live in the leaf-litter of closed-canopy forests (e.g., linyphiids) (Huhta, 1971; Pajunen *et al.*, 1995). From a forest management perspective, simply targeting species richness as a goal for biodiversity considerations is flawed. Such logic would suggest harvesting in a manner to promote the establishment of young stand age-classes. In a successional context, such "pre-climax" stands harbour a fauna in transition (Odum, 1969) and this fauna has a high species richness (e.g., stands originating in 1982 and 1968, Chapter 2). Forests should be managed instead with information on specific species that may be differentially affected by certain forestry practices, and on how the overall communities change in relation to management practices.

Chapter 2 established that along with linyphiid spiders, wolf spiders in the genus *Pardosa* are dominant in the boreal mixed-wood forests of Alberta; a pattern consistent with other studies in northern forests (e.g., Pajunen *et al.*, 1995). Two species [*P. moesta* Banks and *P. mackenziana* (Keyserling)] accounted for 25% of all spiders collected. Although *P. moesta* tended to show affinities with open-canopy stands and *P. mackenziana* was most commonly collected in closed-canopy forests, both species could be found together in all of the study sites. This leads to questions about potential interactions between these wolf spiders and whether such an understanding can help explain the patterns observed at a large-scale. Since little is known of these species, the logical starting point was to seek a better understanding of their natural history.

The detailed work on the life-history of *P. moesta* and *P. mackenziana* (Chapter 4) contributes to our understanding of northern spiders. Two-year life-cycles are not typical for most temperate spiders (Gertsch, 1979), and my research suggests *Pardosa* species have flexible life-history strategies; they may exhibit annual life-cycles farther south in their distribution. This work has implications for other parts of my thesis research. For example, knowing that *P. mackenziana* has a two year life cycle may help explain why this species was unaffected by changes in the DWM on the forest floor (Chapter 7). I showed that *P. mackenziana* frequently uses the surface of DWM (Chapter 6), and females of this species appeared to selectively use wood surfaces, possibly to sun their egg sacs. Changes in DWM should, therefore, affect populations of this species, but this will not be apparent within a single year of collection. A second year of post-treatment data in the DWM manipulation experiment could confirm or refute this hypothesis.

Chapter 4 established that *P. moesta* and *P. mackenziana* are not temporally nor spatially segregated. Immature, sub-adult, and adults coexist on the forest floor and their life-cycles are virtually identical. All of these conditions suggest the potential for competition to drive populations of these species. Following the general experimental design utilized by Wise & Wagner (1992), my competition experiment was one of the first to ask questions about intra- and interspecific exploitative competition in ground-dwelling spiders.

Although *Pardosa* spiderlings did affect their prey resources, intra- and interspecific exploitative competition was not apparent (Chapter 5). However, it was established that intraguild predation (IGP) and cannibalism may play a role in spiderling mortality, and it is known that these effects may make it difficult to observe direct resource-mediated competition (e.g., Polis *et al.*, 1989). Alternatively, since female wolf spiders may selectively search for specific micro-habitats to deposit their young (Edgar, 1971), it was hypothesized that *P. moesta* and *P. mackenziana* may spatially segregate their young in this manner, making direct interactions rare between these species. Perhaps *P. mackenziana* uses the surface of DWM for such behaviour, since females of this species are frequently on the surface of DWM and the proportion of immature spiders is higher on the surface of fallen logs than on the forest floor (Chapter 6).

I surmise that the results from the competition experiment (Chapter 5) can help explain patterns in the occurrence of *P. moesta* and *P.mackenziana* across a variety of forest stands at a landscape scale (i.e., Chapter 2). In general terms, habitat segregation by adults largely keeps the two species from meeting, a pattern typical for the genus (Greenstone, 1980); open areas tend to be dominated by *P. moesta* and closed-canopy forests harbour large populations of *P. mackenziana*. When these species occur together in a forest stand, exploitative competition does not affect the survival or growth of one species over another. Small-scale spatial segregation of spiderlings may operate to keep interactions between the species low, allowing for coexistence at a larger scale.

Outlook

Not surprisingly, my dissertation has raised as many questions as it has answered. Aside from a desire for more replicates and additional time to follow experiments, there are other areas of my thesis research that could be improved upon, and that lead to other interesting and important avenues of research.

All of my work has utilized spiders as a model study taxon. However, it is essential that other elements of the biota be studied, especially given the importance of the issues surrounding forest management. In collaboration with other researchers, I have analyzed other arthropod data from the studies outlined in Chapters 2 and 3. Including ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in the analyses still shows a faunal convergence between wildfire and clear-cutting, but a faunal recovery to a pre-disturbance state was not apparent (C.M. Buddle, J.R. Spence, D.W. Langor, & G.R. Pohl, unpubl.). Such beetles may take longer to recover following disturbance than do spiders.

Following the same logic, manipulating DWM on the forest floor may have a larger impact on other taxa than on spiders. Some staphylinid beetles, for example, are fungivores (Klimaszewski, 2000), and the loss of fungi associated with dead wood may have detrimental effects on rove beetle populations. In short, care must be taken when drawing conclusions from single-taxon studies and it is critical to extend the results of this thesis to other epigaeic taxa.

Natural experiments, such as those outlined in Chapter 2 and 3, provide countless opportunities for future research. For example, virtually nothing is known about the factors governing the distribution, abundance, and diversity of the majority of species and families of spiders that were collected. Linyphiids represent most of the diversity of spiders in boreal forests, and are known to inhabit the complex micro-habitat of the forest floor and they may segregate spatially within this habitat (Huhta, 1971). However, we know embarrassingly little about these spiders: What role do linyphiids play in the food web of the forest floor? Why are they so diverse? Why are so many linyphiid species represented by so few individuals?

Work with CWD can also be extended in various ways. It would be worthwhile performing manipulative DWM experiments in other forest types and at different scales. One approach would be to experimentally add DWM to clear-cut stands and see whether this may alter faunal re-colonization. There is a good basis in understanding the role of CWD in coniferous forests (e.g., Harmon *et al.*, 1986) and the trapping technique used in Chapter 6 could be implemented in other forests and could target other invertebrate taxa. Future work could also establish a biologically-relevant classification system for CWD. I used a simple 3-class system for dead wood and the majority of the DWM studied was of decay stage 3. However, there is high variation within this decay stage, and quantifying differences in reference to invertebrate habitat, for example, would be useful for ecologists and foresters; the quality and quantity of CWD is relevant.

My research on the life-history of *P. moesta* and *P. mackenziana* has offered several avenues for future research. I found that female size alone was a poor predictor of fecundity in these species, and future work establishing the factors governing the reproductive potential in northern wolf spiders would provide a more complete picture of invertebrate life-history adaptations to northern environments. It is feasible to perform a series of experiments such as those done by Spence *et al.* (1996) and Zimmermann & Spence (1998) on the pisaurid *Dolomedes triton* Walckaener. One factor of interest may be the role of habitat in determining the maximum reproductive output. For example, females of populations of *P. moesta* in open habitats may have higher clutch sizes compared to populations in closed-canopy forests.

Work on competition between *Pardosa* illustrated the potential for IGP and cannibalism to influence wolf spider populations in northern forests. Detailed laboratory experiments could investigate direct measures of these factors. My research established that *Pardosa* spiderlings affect Collembola on the forest floor in central Alberta. Lawrence & Wise (2000) have shown that spider predation on Collembola has the potential to influence leaf-litter decomposition in a deciduous forest in Kentucky. Such experiments could be done in northern forests to establish if this is a general ecological pattern; this has implications on nutrient cycling and other essential ecosystem services.

My dissertation research used a variety of approaches to better understand how spiders are affected by forest harvesting and has identified some of the factors and processes that govern spider assemblages in the boreal mixed-wood forests of Alberta. My thesis has also provided a basis for future studies on applied problems of balancing pressures on our land-base with consideration of biodiversity and provided important insights into spider ecology. I have shown how biodiversity studies can generate testable hypotheses and how, through careful experimentation and analyses, it is possible to break down and understand some of the complexity of ecological systems.

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Appendix 1 Summary of spider families and species collected in *Populus* stands initiated by wildfire or harvest (stand origin in 1995, 1982, and 1968) and old and mature stands (O/M). * indicates species collected only by sweep-net; † indicates species collected by pitfall traps and sweep-net.

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Agelenidae										
Agelenopsis	*utahana*	(Chamberlin & Ivie)	6	8	2	1	9	10	7	43
Amaurobiidae										
Amaurobius	*borealis*	Emerton	6	9	84	23	173	102	56	453
Arctobius	*agelenoides*	(Emerton)	1							1
Cybaeopsis	*euopla*	(Bishop & Crosby)	78	19	184	87	125	174	265	932
Araneidae										
Araneus	*marmoreus**	Clerck	2	1		2	1	1		7
Cyclosa	*conica**	(Pallas)	1							1
Hyposinga	*rubens*†	(Hentz)		3						3
Larinioides	*patagiatus*†	(Clerck)	2	1						3
Neoscona	*arabesca**	(Walckenaer)	3	1		1				5

				Fire			Harvest			
			1995	1982	1968	1995	1982	1968	O/M	Total
Clubionidae										
Clubiona	*moesta*	Banks		1				1		2
Clubiona	*opeongo*	Edwards					2			2
Clubiona	*canadensis*†	Emerton	1	2	4			7	7	21
Clubiona	*furcata*	Emerton	1							1
Clubiona	*kulczynskii*	Lessert	1	5	2	4	10	10	9	41
Gnaphosidae										
Drassodes	*neglectus*	(Keyserling)	2			1				3
Drassyllus	*niger*	(Banks)						1		1
Gnaphosa	*muscorum*	(L. Koch)	2	6			1	1		10
Gnaphosa	*parvula*	Banks	1	8		14	1	1	5	30
Gnaphosa	*microps*	Holm	8	26	1	4	5		2	46
Gnaphosa	*borea*	Kulczyński	2	14	4					20
Gnaphosa	*brumalis*	Thorell	6	3		1	1			11
Haplodrassus	*signifer*	(C.L. Koch)		1						1
Haplodrassus	*hiemalis*	(Emerton)		16	2	6	4	5	8	41

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Micaria	*pulicaria*	(Sundevall)			1	2	1	4		8
Micaria	*tripunctata*	Holm		1						1
Micaria	*aenea*	Thorell		3		2		2	2	9
Orodrassus	*canadensis*	Platnick & Shadab		1						1
Zelotes	*fratris*	Chamberlin		13	2	7	12	6	6	46
Hahniidae										
Cryphoeca	*exlinae*	Roth			1			1		2
Hahnia	*cinerea*	Emerton					1			1
Linyphiidae										
Agyneta	*olivacea*	(Emerton)		2	1	1	2	3		9
Allomengea	*dentisetis*	(Grube)	8	64	105	235	184	201	609	1406
Bathyphantes	*pallidus*	(Banks)	8	16	67	29	144	82	50	396
Ceraticelus	*fissiceps*	(O.P.-Cambridge)		2		1	5	1	1	10
Ceraticelus	*laetabilis*	(O.P.-Cambridge)		1		2				3
Ceratinella	*alaskae*	Chamberlin & Ivie			1					1
Ceratinella	*brunnea*	Emerton		1						1

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Ceratinopsis	*stativa*	(Simon)		1			2			3
Cnephalocotes	*obscurus*	(Blackwall)				1				1
Collinsia	*clypiella*	(Chamberlin)					1			1
Diplocentria	*bidentata*	(Emerton)	7	8	10	11	32	10	6	84
Diplocephalus	*subrostratus*	(O.P.-Cambridge)		1		1		1	2	5
Eperigone	*trilobata*	(Emerton)	1			5	1			7
Erigoninae	sp. A					1				1
Erigoninae	sp. B							1		1
Erigoninae	sp. C						1			1
Erigoninae	sp. D		1							1
Estrandia	*grandaeva**	(Keyserling)			1			1		2
Frontinella	*pyramitela**	(Walckenaer)	7	3	1	2		1		14
Gnathonarium	*suppositum**	(Kulczyński)						1		1
Gonatium	*crassipalpum*	Bryant				1	1	2	2	6
Grammonata	*gigas*	(Banks)		1			3			4
Helophora	*insignis*†	(Blackwall)	5	13	31	4	27	42	63	185

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Hybauchenidium	*gibbosum*	(Soerenson)	1	8	8		32	7		56
Hypselistes	*florens*†	(O.P.-Cambridge)	4	14	8	4	8	2	3	43
Lepthyphantes	*alpinus*	(Emerton)	1		1	1	1	1		5
Lepthyphantes	*complicatus*	(Emerton)		1	5		3	1		10
Lepthyphantes	*intricatus*	(Emerton)	2	2	100	61	135	144	158	602
Maro	sp. A		1		1	1		1		4
Microlinyphia	*mandibulata*	(Emerton)							4	4
Microneta	*viaria*	(Blackwall)		3	6	1	4	13	7	34
Neriene	*clathrata*	(Sundevall)					2	1	2	5
Neriene	*radiata**	(Walckenaer)			1					1
Oedothorax	*trilobatus*	(Banks)			1					1
Oreonetides	*rectangulatus*	(Emerton)				1				1
Oreonetides	*recurvatus*	(Emerton)			3	1	3	4	4	15
Oreonetides	*vaginatus*	(Thorell)	10	7	10	5	6	6	1	45
Pityohyphantes	*costatus*	(Hentz)		1					2	3
Pityohyphantes	*subarcticus**	Chamberlin & Ivie		1	1			1		3

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Pocodicnemis	*americana*	Millidge						1		1
Sciastes	*truncatus*	(Emerton)	1	4	3		9	2	4	23
Scironis	*tarsalis*	Emerton						2		2
Sisicottus	*nesides*	(Chamberlin)						1		1
Sisicottus	*montanus*	(Emerton)	3		1	1	1	1		7
Tunagyna	*debilis*	(Banks)	1			1	14			16
Walckenaeria	*castanea*	(Emerton)	7	3	15	2	12	17	3	59
Walckenaeria	*directa*	(O.P.-Cambridge)	1	10	8	2	7	14	1	43
Walckenaeria	*karpinskii*	(O.P.-Cambridge)			1					1
Walckenaeria	*exigua*	Millidge		1						1
Walckenaeria	*atrotibialis*	O.P.-Cambridge			1				2	3
Zornella	*cultrigera*	(L.Koch)	2	2	43	12	15	53	4	131
Liocranidae										
Agroeca	*ornata*	Banks	17	42	91	25	63	78	152	468
Lycosidae										
Alopecosa	*aculeata*	(Clerck)	14	68	17	13	1	1	2	116

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Arctosa	*alpigena*	(Doleschall)	15			1				16
Arctosa	*raptor*	(Kulczyński)		1				1		2
Arctosa	*emertoni*	Gertsch	1		2					3
Pardosa	*mackenziana*	(Keyserling)	95	193	67	129	106	116	229	935
Pardosa	*xerampelina*	(Keyserling)	321	76	9	234	30	8	2	680
Pardosa	*tesquorum*	(Odenwall)	1			4				5
Pardosa	*furcifer*	(Thorell)				3				3
Pardosa	*fuscula*	(Thorell)	8	4	1	81	9	1		104
Pardosa	*hyperborea*	(Thorell)	83	2		20	2	1	1	109
Pardosa	*moesta*	Banks	89	101	17	644	242	31	12	1136
Pardosa	*uintana*	Gertsch	110	13		1				124
Pirata	*bryantae*	Kurata	31	1		2	1			35
Trochosa	*terricola*	Thorell	8	61	29	5	52	55	18	228
Mimetidae										
Ero	*canionis*	Chamberlin & Ivie					1		3	4
Philodromidae										

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Philodromus	*rufus quartus*†	(Dondale & Redner)	3						1	4
Thanatus	*formicinus*	(Clerck)	1							1
Thanatus	*striatus*	C.L. Koch				3				3
Tibellus	*maritimus**	(Menge)						1		1
Tibellus	*oblongus*†	(Walckenaer)	1	1						2
Salticidae										
Bianor	*aemulus*	(Gertsch)			4		1	1		6
Eris	*militaris**	(Hentz)	2	3		4	1	1		11
Evarcha	*hoyi*	(Peckham & Peckham)				1				1
Neon	*nelli*	(Peckham & Peckham)							2	2
Pelegrina	*montana**	(Emerton)	1	1	1		2			5
Pelegrina	*flavipedes**	(Peckham & Peckham)	1							1
Tetragnathidae										
Tetragnatha	*extensa**	(L.)	3							3
Tetragnatha	*straminea**	Emerton			1					1
Tetragnatha	*laboriosa**	Hentz			1					1

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Tetragnatha	*versicolor**	Walckenaer	1							1
Theridiidae										
Euryopis	*argentia*	Emerton			2		1			3
Robertus	*fuscus*	(Emerton)		1	2		1	1	1	6
Theridion	*aurantium*†	Emerton			1		9	6	1	17
Theridion	*differens**	Emerton					1			1
Theridion	*sexpunctatum*	Emerton					1	1		2
Theridion	*impressum**	L. Koch				3				3
Theridula	*emertoni**	Levi	1	1		1	1	3		7
Thomisidae										
Misumena	*vatia**	(Clerck)	7	3	1	4		1		16
Ozyptila	*sincera canadensis*	Dondale & Redner		2	21	16	7	3	10	59
Xysticus	*luctuosus*	(Blackwall)	13	10	17	8	22	38	76	184
Xysticus	*ferox*	(Hentz)	1			1				2
Xysticus	*durus*	(Soerenson)	3							3

			Fire			Harvest				
			1995	1982	1968	1995	1982	1968	O/M	Total
Xysticus	*obscurus*	Collett							18	18
Xysticus	*britcheri*	Gertsch				1				1
Xysticus	*canadensis*	Gertsch						1		1
Xysticus	*elegans*	Keyserling	1		1		4	1	6	13
Xysticus	*emertoni*†	Keyserling	22	1	4	29	4	22	4	86
Xysticus	*ellipticus*	Turnbull *et al.*				1				1

Appendix 2 Summary of spider families and species collected on or near downed woody material: FOR, traps on the forest floor; ADJ, traps adjacent to wood; BOLT, traps on wood surface. Immature and damaged specimens not included. * indicate species represented by > 2 specimens that are found more frequently in BOLT compared to ADJ and FOR traps.

			FOR	ADJ	BOLT	Total	
Agelenidae							
Agelenopsis	*utahana*	(Chamberlin & Ivie)	6	7	36	49	*
Amaurobiidae							
Amaurobius	*borealis*	Emerton	195	158	42	395	
Cybaeopsis	*euopla*	(Bishop & Crosby)	174	246	6	426	
Araneidae							
Araneus	*iviei*	(Archer)			1	1	
Larinioides	*cornutus*	(Clerck)			2	2	
Larinioides	*patagiatus*	(Clerck)			1	1	
Clubionidae							
Clubiona	*canadensis*	Emerton	2	4	13	19	*
Clubiona	*kastoni*	Gertsch	6	4	7	17	
Clubiona	*kulczynskii*	Lessert	5	2	6	13	
Clubiona	*moesta*	Banks	1	1	6	8	*
Dictynidae							
Dictyna	*annulipes*	Blackwall	1	1	5	7	*
Dictyna	*minuta*	Emerton	2	1	1	4	
Gnaphosidae							
Gnaphosa	*parvula*	Banks	5	7	2	14	
Haplodrassus	*hiemalis*	(Emerton)	16	8	11	35	
Micaria	*aenea*	Thorell	1	1	1	3	
Micaria	*pulicaria*	(Sundevall)	3	2		5	
Sergiolus	*montanus*	(Emerton)	1		2	3	*
Zelotes	*fratris*	Chamberlin	13	10	3	26	
Zelotes	*puritanus*	Chamberlin		1		1	
Hahniidae							
Hahnia	*cinerea*	Emerton	26	8	3	37	
Linyphiidae							
Agyneta	sp. A			2		2	

			FOR	ADJ	BOLT	Total	
Allomengea	*dentisetis*	(Grube)	513	536	21	1070	
Bathyphantes	*pallidus*	(Banks)	546	479	38	1063	
Ceratinella	*brunnea*	Emerton	2	5	5	12	
Ceraticelus	*fissiceps*	(O.P.-Cambridge)	2			2	
Ceratinopsis	*stativa*	(Simon)	4	1	3	8	
Centromerus	*sylvaticus*	(Blackwall)	11	11	1	23	
Dismodicus	*alticeps*	Chamberlin & Ivie			1	1	
Diplocentria	*bidentata*	(Emerton)	7	7	1	15	
Diplocephalus	*subrostratus*	(O.P.-Cambridge)		4		4	
Drapetisca	*alteranda*	Chamberlin			5	5	*
Erigone	*blaesa*	Crosby & Bishop		1		1	
Erigone	*dentrigera*	O.P.-Cambridge			1	1	
Eridantes	*utibilis*	Crosby & Bishop		1	6	7	*
Gnathonaroides	*pedalis*	(Emerton)		1		1	
Gonatium	*crassipalpum*	Bryant	1	1		2	
Grammonota	*gigas*	(Banks)		2		2	
Helophora	*insignis*	(Blackwall)	26	9	26	61	
Lepthyphantes	*alpinus*	(Emerton)		2		2	
Lepthyphantes	*intricatus*	(Emerton)	149	237	37	423	
Lepthyphantes	sp. A		2	2		4	
Lepthyphantes	*turbatrix*	(O.P.-Cambridge)		5	23	28	*
Lepthyphantes	*zebra*	(Emerton)	6	11	2	19	
Maro	sp. A			1		1	
Microlinyphia	*mandibulata*	(Emerton)	4	1		5	
Microneta	*viaria*	(Blackwall)	30	48	8	86	
Neriene	*clathrata*	(Sundevall)	3	5	4	12	
Oedothorax	*trilobatus*	(Banks)	1			1	
Oreonetides	*recurvatus*	(Emerton)		1	1	2	
Oreonetides	*rotundus*	(Emerton)			1	1	
Oreonetides	*vaginatus*	(Thorell)	12	20	3	35	
Phlattothrata	*minuta*	(Emerton)	1			1	
Pityohyphantes	*costatus*	(Hentz)	5	8	12	25	
Pocadicnemis	*americana*	Millidge	3	4	1	8	
Porrhomma	*terrestre*	(Emerton)		1		1	
Sciastes	*truncatus*	(Emerton)	9	12	5	26	
Sisicottus	*montanus*	(Emerton)	1	6	1	8	

			FOR	ADJ	BOLT	Total	
Souessa	*spinifera*	(O.P.-Cambridge)			2	2	
Tapinocyba	*simplex*	(Emerton)		1		1	
Tunagyna	*debilis*	(Banks)	1			1	
Walckenaeria	*atrotibialis*	O.P.-Cambridge	3	4	2	9	
Walckenaeria	nr. *breviaria*		1		1	2	
Walckenaeria	*castanea*	(Emerton)	4	7	3	14	
Walckenaeria	*directa*	(O.P.-Cambridge)	11	15	5	31	
Walckenaeria	*prominens*	Millidge	18	8	14	40	
Zornella	*cultrigera*	(L.Koch)		2		2	
Erigoninae	sp. A		1			1	
Liocranidae							
Agroeca	*ornata*	Banks	1658	990	58	2706	
Lycosidae							
Alopecosa	*aculeata*	(Clerck)	4	4	2	10	
Pardosa	*fuscula*	(Thorell)	3		3	6	
Pardosa	*hyperborea*	(Thorell)			1	1	
Pardosa	*mackenziana*	(Keyserling)	56	90	288	434	*
Pardosa	*moesta*	Banks	28	23	7	58	
Pardosa	*ontariensis*	Gertsch	1	1	1	3	
Pardosa	*xerampelina*	(Keyserling)	44	51	58	153	
Pirata	*insularis*	Emerton	1			1	
Pirata	*piraticus*	(Clerck)	1			1	
Trochosa	*terricola*	Thorell	244	181	28	453	
Mimetidae							
Ero	*canionis*	Chamberlin & Ivie	2	6	2	10	
Philodromidae							
Philodromus	*oneida*	Levi			2	2	
Philodromus	*rufus quartus*	Dondale & Redner	1			1	
Philodromus	*rufus vibrans*	Dondale			2	2	
Thanatus	*formicinus*	(Clerck)		1		1	
Thanatus	*striatus*	C. L. Koch			1	1	
Salticidae							
Bianor	*aemulus*	(Gertsch)	2		1	3	
Eris	*militaris*	(Hentz)	1			1	
Tetragnathidae							
Pachygnatha	*clercki*	Sundevall		1		1	

			FOR	ADJ	BOLT	Total	
Tetragnatha	*versicolor*	Walckenaer	1			1	
Theridiidae							
Enoplognatha	*intrepida*	(Sorensen)			1	1	
Euryopis	*argentea*	Emerton	14	24	11	49	
Robertus	*fuscus*	(Emerton)	1	3		4	
Steatoda	*borealis*	(Hentz)			3	3	*
Theridion	*aurantium*	Emerton	2	5		7	
Theridion	*sexpunctatum*	Emerton		4		4	
Thomisidae							
Coriarachne	*utahensis*	(Gertsch)			8	8	*
Ozyptila	*sincera canadensis*	Dondale & Redner	541	434	26	1001	
Xysticus	*elegans*	Keyserling	9	3	5	17	
Xysticus	*emertoni*	Keyserling		1		1	
Xysticus	*luctuosus*	(Blackwall)	48	29	7	84	
Xysticus	*obscurus*	Collett	7		1	8	

Appendix 3 Summary of spider families and species collected in downed woody material (DWM) experiments 1 (40 x 40 m plots, 5 traps per plot) and experiment 2 (20 x 20 m quadrats, 1 trap per quadrat): Pre, pre-treatment data; Con, control; Rem, remove DWM treatment; Add, add DWM treatment; Dis, disturb DWM treatment. Immature and damaged specimens not included.

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
Agelenidae											
Agelenopsis	*utahana*	(Chamberlin & Ivie)	23	13	11	25	6	2	6	2	88
Amaurobiidae											
Amaurobius	*borealis*	Emerton	28	41	48	45	10	50	38	28	288
Cybaeopsis	*euopla*	(Bishop & Crosby)	243	130	152	322	83	123	109	94	1256
Araneidae											
Araneus	*iviei*	(Archer)	1								1
Clubionidae											
Clubiona	*canadensis*	Emerton	3			3				1	7
Clubiona	*kastoni*	Gertsch	5	3		8	1	3	3	2	25
Clubiona	*kulczynskii*	Lessert	11	4	1	7	2	1	4	2	32

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
Clubiona	*moesta*	Banks	2			1	1			1	5
Dictynidae											
Dictyna	*minuta*	Emerton				1					1
Gnaphosidae											
Gnaphosa	*parvula*	Banks	4	2	3	9	1	2		2	23
Haplodrassum	*hiemalis*	(Emerton)	7	17	9	14	2	5	7	5	66
Micaria	*aenea*	Thorell	3	1	3	4			1		12
Micaria	*pulicaria*	(Sundevall)		1		4	2	6			13
Zelotes	*fratris*	Chamberlin	6	8	5	13	2	7	5	4	50
Zelotes	*puritanus*	Chamberlin				1					1
Hahniidae											
Hahnia	*cinerea*	Emerton	1		1					1	3
Neoantistea	*magna*	(Keyserling)	1	2		2					5
Linyphiidae											
Allomengea	*dentisetis*	(Grube)	720	118	125	559	70	43	55	48	1738
Bathyphantes	*pallidus*	(Banks)	145	101	71	211	35	47	72	37	719

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
Centromerus	*sylvaticus*	(Blackwall)	1	1	3	1	2	1	1	5	15
Ceratinella	*brunnea*	Emerton			1	2			2		5
Ceratinopsis	sp. A			2							2
Ceratinopsis	sp. B		1								1
Ceratinopsis	*stativa*	(Simon)	3	1	1	2	1	2		1	11
Diplocentria	*bidentata*	(Emerton)	6	3	3	9		1	3		25
Diplocephalus	*subrostratus*	(O.P.-Cambridge)				1					1
Drapetisca	*alteranda*	Chamberlin						1			1
Grammonota	*gigas*	(Banks)	1	1		3			1		6
Helophora	*insignis*	(Blackwall)	6	10	5	3	3	4	2	3	36
Lepthyphantes	*intricatus*	(Emerton)	57	28	28	79	10	26	25	17	270
Lepthyphantes	sp. A			2	4			3	3		12
Lepthyphantes	*turbatrix*	(O.P.-Cambridge)				1					1
Lepthyphantes	*zebra*	(Emerton)		6	3		1		1	2	13
Micrargus	*longitarsus*	(Emerton)	1			1					2
Microlinyphia	*mandibulata*	(Emerton)	2			2	1	1	1		7

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
Microneta	*viaria*	(Blackwall)	12	13	7	22	4	3	1	2	64
Neriene	*clathrata*	(Sundevall)	1	6	5	1		3	2	2	20
Oreonetides	*recurvatus*	(Emerton)				2					2
Oreonetides	*vaginatus*	(Thorell)	8	8	6	5	2	3	6	3	41
Phlattothrata	*minuta*	(Emerton)			1						1
Pityohyphantes	*costatus*	(Hentz)	5	1	2	3	1		1	1	14
Pocadicnemis	*americana*	Millidge	3	2	2	6			1		14
Sciastes	*truncatus*	(Emerton)	4	1		3	2				10
Scirites	*pectinatus*	(Emerton)						1			1
Tunagyna	*debilis*	(Banks)	2			3			1		6
Walckenaeria	*atrotibialis*	O.P.-Cambridge	3	2	1	7			1	2	16
Walckenaeria	*castanea*	(Emerton)	5	2		3	1	1	3		15
Walckenaeria	*directa*	(O.P.-Cambridge)	1	4			1	2	1		9
Walckenaeria	*prominens*	Millidge	2	3	9	4	3	1	3	2	27
Zornella	*cultrigera*	(L.Koch)								1	1
Agroeca	*ornata*	Banks	160	369	516	147	133	202	245	172	1944

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
Lycosidae											
Alopecosa	*aculeata*	(Clerck)	7	1	2	21	5		3	1	40
Pardosa	*fuscula*	(Thorell)	5	4	2	4			1	6	22
Pardosa	*mackenziana*	(Keyserling)	245	170	153	330	52	133	67	110	1260
Pardosa	*moesta*	Banks	16	27	16	72	11	21	15	30	208
Pardosa	*ontariensis*	Gertsch						2			2
Pardosa	*xerampelina*	(Keyserling)	10	58	21	28	13	26	22	38	216
Pirata	*bryantae*	Kurata			1						1
Pirata	*insularis*	Emerton					1				1
Pirata	*piraticus*	(Clerck)	1	3		2					6
Trochosa	*terricola*	Thorell	40	132	105	72	52	48	67	56	572
Mimetidae											
Ero	*canionis*	Chamberlin & Ivie	1	2		1	4	1	2		11
Philodromidae											
Philodromus	*praelustris*	Keyserling	1								1
Philodromus	*rufus quartus*	Dondale & Redner				1					1

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
Thanatus	*formicinus*	(Clerck)		1				1	1		3
Salticidae											
Bianor	*aemulus*	(Gertsch)				1					1
Eris	*militaris*	(Hentz)	1								1
Neon	*nelli*	Peckham & Peckham	2			1		1			4
Tetragnathidae											
Pachygnatha	*clercki*	Sundevall	1	1							2
Theridiidae											
Euryopis	*argentea*	Emerton	2	10	2	15		4	1	2	36
Robertus	*fuscus*	(Emerton)	2	3	1	1				1	8
Steatoda	*borealis*	(Hentz)		1			1				2
Theridion	*aurantium*	Emerton			1	1					2
Theridion	*sexpunctatum*	Emerton				2					2
Theridula	*emertoni*	Levi							1		1
Thomisidae											
Ozyptila	*sincera*	Dondale & Redner	170	135	68	191	15	34	22	40	675

			Experiment 1			Experiment 2					
			Pre	Con	Rem	Pre	Con	Rem	Add	Dis	Total
	canadensis										
Xysticus	*elegans*	Keyserling	1	3	5	2		3	2	7	23
Xysticus	*emertoni*	Keyserling				1		2	2		5
Xysticus	*luctuosus*	(Blackwall)	24	22	15	46	1	16	15	9	148
Xysticus	*obscurus*	Collett		7	11	5			3	4	30