**University of Alberta**

# Wetland Spider Diversity and Ecology in Alberta

by

Alice Katharine Graham ©

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# Abstract

The diversity and life-history traits of spiders in wetland ecosystems in central Alberta were investigated in two field experiments and one laboratory experiment.

Spider diversity was compared at six natural and nine restored prairie pothole wetlands of various ages. More spider individuals and species were collected at natural wetlands, and a succession of spider species was observable at restored wetlands as they aged.

Reproductive biology and life cycles of three species characteristic of wetlands were also examined. Two species, *Pirata piraticus* and *Tetragnatha extensa*, had annual life cycles and produced one egg sac per year, whereas *Pardosa fuscula* produced two egg sacs and showed a biennial life cycle.

Regulation of ballooning in the fishing spider *Dolomedes triton* was investigated in the laboratory by exposing juveniles to various environmental conditions and wind velocities. Juveniles displayed ballooning behaviour typical of members of other families, and temperature affected the proportion of individuals that ballooned.

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# 1. Introduction

## 1.1 A brief overview of Arachnology

Spiders are ubiquitous; they occupy all terrestrial areas, from icy slopes of Mount Everest to the deepest, darkest caves, and can be found underfoot in almost every area of the world (Foelix 1996). Most people seem to love or hate spiders, and, in my opinion, the majority of us, even in the scientific community, are mildly apprehensive or anxious around live spiders. In Great Britain a survey of arachnophobia showed that 50% of all women and 10% of men are mildly afraid of spiders (Hillyard 1994). Thus it was common for me, a graduate student studying spider biology, to encounter a wide variety of attitudes and opinions when discussing my work (Figure 1).

Arachnology, the study of spiders and their relatives, has increased in popularity and attracted serious attention in the past 100 years. Aristotle (384-322 B.C.E.) was the first to attempt to classify animals, and made many accurate observations about spider webs and prey capture, mating, and development of young (Savory 1961). Early Arachnologists such as Clerck began naming spider species in the 1700s, and in the 1800s, numerous volumes describing the spider fauna of Europe were published by Walckenaer, Koch, Blackwall and Simon (Savory 1961). The first systematic study of American spiders was completed by Hentz in 1875, and shortly after, foundations of American Arachnology were established by McCook, Peckham and Emerton (Bristowe 1958). Pioneer Arachnologists who sought, found and studied spiders outlined species lists and provided a solid taxonomic and ecological framework for more complex studies of the past century.

Approximately 40 000 species of spiders have been described (Coddington and Levi 1991, Marc *et al.* 1999), and that number, although it grows every day, is only a portion of the number of species that actually exist. Countless experiments have examined spider populations, behaviour, life cycles, silk, venom toxicity, and, in fact, few areas of spider biology remain wholly uninvestigated.

### 1.2 Water spiders

Although spiders are primarily terrestrial, some have developed associations with freshwater and marine ecosystems. Sea spiders exist; these are small, dorsoventrally flattened animals with large probosces, but they are not arachnids and instead occupy a separate taxon (Class Pycnogonida). Some true spiders, however, are able to live in intertidal habitats, where they are exposed to tidal inundation and frequent submersion (Barnes and Barnes 1954, McLay and Hayward 1987, Morse 1997). Salt marshes also contain a diverse spider fauna (Teal 1962, Dobel *et al.* 1990), and spiders are commonly encountered and abundant at freshwater habitats such as lakes, streams, and ponds (Bristowe 1939, Levi 1967, Graham *et al.*, in press).

*Argyroneta aquatica* Clerck, is a truly aquatic European species that swims readily and carries a diving bell to assist with hunting insect prey underwater (Kayashima 1991, Shunmugavelu and Palanichamy 1992). Spiders that live at or near the shores of freshwater bodies may be considered clearly semi-aquatic (Graham *et al.*, in press). However, criteria for a spider to be described as semi-aquatic have been reworked so a more precise definition is available (Graham *et al.*, in press). Semi-aquatic species in central Alberta include *Dolomedes triton*, *Pirata piraticus,* and *Pardosa fuscula* (Graham *et al.*, in press).

In spite of the vast array of information available about terrestrial spiders, surprisingly few studies of spiders have been conducted in wetland ecosystems.

## 1.3 Wetland ecology and spiders

Wetland ecosystems, whose ecological importance and future in the landscape are relentlessly debated, are vital to the health of our planet for many reasons (Semlitsch and Bodie 1998). First of all, they act as a sink for harmful gases emitted by industries (e.g., $CO_2$), especially in boreal regions (Schindler 1998). Wetlands have also been described as "nature's kidneys" for their ability to accept wastewater discharges and transform nutrients from these into less harmful by-products (Bastian and Benforado 1988). Since wetlands are transitional areas, they not only accept waste, but also act as buffers for lakes and oceans against agricultural and urban development (Bastian and Benforado 1988). In addition, wetlands provide habitats for migrating and breeding waterfowl, mammals, endangered macrophytes, and invertebrates, so they have significant intrinsic biological value (Walbridge 1993).

Unfortunately, the great majority of research in wetland ecology has focused on mammals, amphibians and waterfowl, even though invertebrates are ecologically significant and poorly known components of wetland ecosystems (Murkin and Wrubleski 1988). For example, wetland invertebrates provide the essential link between primary producers and higher order consumers (Murkin and Batt 1987). Fish, mammals, and especially waterfowl regularly feed on invertebrates during part or all of their life cycles. During the breeding season, ducks obtain protein-rich food required for gonadal development and egg-laying by consuming large quantities of spiders and insects (Murkin and Batt 1987). For this reason, waterfowl habitat selection during the spring breeding season may be strongly influenced by arthropod densities (Murkin and Kadlec 1986). Thus, arthropod diversity is an important factor in the conservation and production of waterfowl species. Although trophic interactions between vertebrates and invertebrates are critical to the structure and function of freshwater wetland ecosystems (Murkin and Batt 1987), the taxonomy and ecology of many wetland invertebrates is poorly understood.

Therefore, our first goal was to survey various wetlands in the prairie pothole region of central Alberta for spiders, and establish species lists for natural and restored wetlands. Central Alberta's prairie pothole region is characterized by abundant small, shallow wetlands that were formed during the Wisconsin period of glaciation 10,000 to 15,000 years ago (Gray *et al.* 1999). As the glacier disintegrated it deposited large ice chunks in the landscape, which slowly melted and formed depressions known as prairie potholes (Stewart and Kantrud 1971). This area includes south-central Saskatchewan and Manitoba, and extends south to the Dakotas, and eastward to Iowa, where it overlaps with the corn belt (Galatowitsch and van der Valk 1994). In Alberta, the prairie pothole region is an important source of cereal grains and grazing grasses, and vitally important habitat for breeding waterfowl (Gray *et al.* 1999).

A little understood aspect of conservation and biodiversity studies is how various arthropod species, especially spiders, have responded to changes in habitat associated with anthropogenic changes in prairie landscapes. In general, minor changes in habitat structure can have noticeable effects on relative abundance and species composition of spiders (McIver *et al.* 1992). In a 1998-1999 study of semi-aquatic spiders at a range of prairie wetlands I found that 10 species representing 4 families were associated with wetland habitats; some of these species (*e.g. Dolomedes triton*) were clearly semi-aquatic (Zimmermann and Spence 1992, 1998; Spence *et al.* 1996). Results of these studies also revealed significant differences in species richness between natural and restored areas and suggest that spider communities could be useful indicators for judging the success of wetland restoration projects.

### 1.4 Reproductive biology of wetland spiders

Despite the abundance, diversity and importance of spiders in natural systems, life histories of most species are poorly understood. Once a local fauna has been identified, understanding life histories and interspecific environmental relationships is the next essential step in assessing spacial and temporal changes in regional taxa. Shortage of such information hinders progress toward understanding the ecology of spiders (Aiken and Coyle 2000). Life history information is central to knowing when and where spiders can be found, and this, in turn, contributes to habitat choice of individuals, population dynamics, and other features that structure communities.

The life cycle of a spider may be described as a summary of important events from birth to death in an average generation (Dondale 1977). This type of information, generally missing for wetland spiders, is useful for characterizing populations, and leads to data useful in taxonomy and population dynamics (Dondale 1977, Zimmermann and Spence 1998).

Relationships between reproductive parameters such as egg size and clutch size with body size have been under intense investigation in evolutionary ecology (Eberhard 1979, Simpson 1995). Basic information about reproductive biology is important in developing an understanding of life histories for individual species, but little of this has been documented for wetland spiders.

I was interested in examining and comparing aspects of the biology of several selected wetland spider species, and in particular, their life cycles and reproductive effort. A comparative study will increase understanding of ecological adaptations to life around aquatic habitats, especially since spiders in this community have received relatively little concerted study. Ultimately, autoecology and life history information are required to pursue further studies of spider assemblages, and their connections to broader ecological communities.

### 1.5 Aerial dispersal of wetland spiders

After obtaining species lists for wetland spiders, and information about their life cycles and reproductive biology, I decided to further investigate their biology by examining behaviours associated with ballooning. Spiders associated with wetlands will have to recolonize newly restored ones, and this is usually achieved or accomplished by ballooning (Richter 1970). Ballooning is defined as the aerial displacement of a spider due to friction between air and silk threads emerging from the spider (Suter 1992). Although the ecological circumstances under which ballooning occurs are well documented, knowledge of spider aerial dispersal is based primarily on casual observations; controlled studies exist for only a small number of species (Richter 1970).

I attempted to estimate spider ballooning frequency in the field and examine the ability of ballooning spiders to colonize changing aquatic habitats. I designed and constructed a series of sticky traps at three newly restored wetlands using six foot long pieces of snow fence that had wooden planks tied to them. These traps had Tye-tac adhesive fastened to the planks, which worked to catch the sticky threads of balloon lines and eventually spiders as they pulled themselves to the point of contact along the line (Richter 1970). Unfortunately, these sticky traps meant to catch ballooning spiders were ineffective and trapped less than 10 spiders over five sampling dates.

Therefore, I decided to examine ballooning behaviour of one particular wetland species under more controlled laboratory conditions. *Dolomedes triton* was chosen because its life history and reproductive output have been thoroughly documented in central Alberta (Spence *et al*. 1996, Zimmermann and Spence 1992, 1998). It is established that juvenile *D. triton* are capable of dispersal by ballooning (Spence *et al*. 1996), but there is no information about the age range of ballooning juveniles, the proportion of juveniles from a given female that disperse aerially, or the environmental conditions that promoted ballooning behaviour. Thus, these were the questions I was interested in answering.

## 1.6 Summary

I sought to contribute to knowledge about wetland spider biology by determining which species were present in wetland ecosystems, and how wetland management affects them. Then I chose species that I knew were abundant and widespread in wetland ecosystems, and focused on examining their life cycles and reproductive effort, and how these were adapted to specific conditions associated with wetlands. Finally I concentrated on one wetland species, whose life cycle is well known, and investigated aerial dispersal behaviours.

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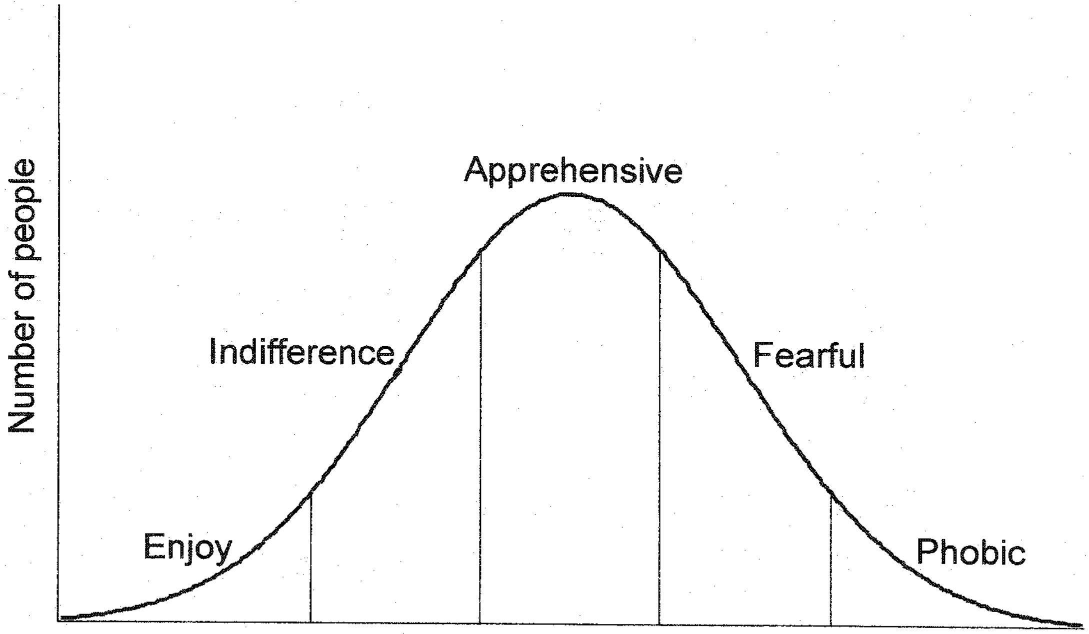
Figure 1.1. Results from an impromptu survey of a variety of people about their thoughts and opinions of spiders. (After Hillyard, 1994).



# 2. Responses of Spider Assemblages to Wetland Restoration Projects in Central Alberta

## 2.1 Introduction

Wetlands provide important animal habitat, accumulate atmospheric carbon, and protect uplands from flooding (Young 1996). Given the central role of wetlands in global carbon dynamics, restoration of altered wetlands may also slow climate change. However, over the past two centuries, one quarter of North America's wetland area has been lost to agricultural and urban development. Only recently have attempts been made to protect and restore these areas (Johnson 1994, Young 1996). Some restored wetlands are drained natural wetlands that have been allowed to fill again by removing drain tiles or plugging ditches that carry water away from the wetland basin (Gray *et al.* 1999).

Spiders are important elements in a variety of food webs, and should be sensitive indicators of disturbance (Wise 1993). Because they are ubiquitous and abundant at freshwater wetlands (Graham *et al.*, in press), spiders are also good model organisms for assessment of how wetland disturbances affect biodiversity. Before predictions can be made about spider responses, however, the fauna must be known and interspecific environmental relationships must be understood. Several lists of species have been compiled for spiders inhabiting bogs in boreal areas (Itamies and Jarva-Karenlampi 1989, Koponen 1994), but spider assemblages of non-peat forming wetlands have not been rigorously studied in Canada.

Dredging, draining, and filling of wetlands, as well as other disturbances associated with human activities, dramatically affect the diversity of wetland biota

(Gibbs 2000). These practices have seriously depleted wetland resources North America, and threatened many obligate wetland species (Boylan and MacLean 1997). Various arthropods serve as excellent indicators of both natural and anthropogenic disturbances in forest and peatland ecosystems (Schikora 1994, Nilsson and Svenson 1995, Hornberg *et al*. 1998,) and thus may be generally useful for monitoring ecosystem conditions; however their enormous potential in this regard is largely undeveloped for wetland habitats (Murkin and Wrubleski 1988, Galatowitsch and van der Valk 1994).

In this chapter, I consider how spiders could be useful in assessment of wetland disturbance. I have determined which spider species are present at natural and restored wetlands in central Alberta, and thus established the first complete systematic collection and inventory of wetland spider species for Alberta. Furthermore, I have explored how wetland management, particularly restoration, affects spider assemblages by asking if there were significant differences in spider abundance, diversity and species composition among natural wetlands and restored wetlands of several ages.

## 2.2 Materials and Methods

### 2.2.1 Study Sites

Two groups of wetland spiders characterized by pattern of habitat use (ground dwelling and semi-aquatic) were studied at natural and restored wetlands in the prairie pothole region of central Alberta during the summer of 2000. Subject to constraints on availability, we chose wetlands that were located in the same general area, and that had similar physical characteristics, such as size of basin, mean depth, and permanence. To examine variability between wetlands and minimize pseudoreplication (Streever *et al.* 1996), spiders were sampled at six natural wetlands and nine restored wetlands. Restored wetlands were sampled to compare spider communities among wetlands of three ages. We studied spiders at three wetlands restored in 1999, three wetlands restored in 1995, and three wetlands restored in 1993.

All 15 wetlands were located in a large triangle connecting New Sarepta, Camrose and Wetaskiwin, Alberta (Figure 2.1). Natural wetlands were randomly named N1 to N6, and restored wetlands were referred to by the year during which the ditch plugs were inserted and the basin began to flood, and given a letter (A, B or C) to indicate that three wetlands shared one date of restoration (Figure 2.1). All wetlands were on Ducks Unlimited Canada property, which was mainly pasture, and contained prairie grasses and meadow. Land use surrounding the wetlands supported beef and alfalfa production, haying, and roads. Natural wetlands ranged in size from 1 to 2 ha, but some of the restored wetlands were smaller, and ranged in size from < 1 ha to 2 ha. The complete history of all 15 wetlands, especially the exact date of original drainage for restored wetlands, is unknown.

The Stewart and Kantrud (1971) system for classifying prairie potholes according to the vegetation observed in the deepest part of the wetland was used to assess permanence for each wetland. There are five types of vegetation in freshwater prairie marshes: wet prairie, sedge meadow, shallow marsh, deep marsh and permanent open water. It follows that there are five classes of wetlands, ranging from ephemeral (Class I) to permanent (Class V), each with one of the above types of vegetation typically found at the marsh's center. All of the natural and restored wetlands used in this study were either Class III, seasonal ponds with a central shallow marsh zone dominated by bulrushes and other emergent marsh plants, or Class IV, semi-permanent ponds with a central deep marsh zone (Table 2.1).

### 2.2.2 Sampling Spiders

Ground dwelling spiders were collected in pitfall traps (Spence and Niemelä 1994). Pitfall trap captures depend on movement of individuals and therefore estimate activity and density of species, as well as their susceptibility to trapping (Topping and Sunderland 1992). Since pitfall traps measure this "activity-density", neither absolute abundance nor male to female ratios reflecting the presence of individuals can be detected (e.g., Topping and Sunderland 1992; Spence and Niemelä 1994). Even with these limitations, however, pitfall traps are still among the most commonly used and effective sampling techniques for collecting epigaeic spiders, and can offer significant insights into their biology, ecology, and habitat affinities (e.g., Uetz and Unzicker 1976; Pajunen *et al.* 1995; Buddle 2000; Buddle *et al.* 2000).

Each trap consisted of a plastic cup (10 cm diameter, 13 cm depth) containing a funnel that was buried in the soil so the open end of the cup was even with the ground surface. Plywood lids (15 cm x 15 cm) were placed above each trap to minimize disturbance by weather and large animals. Preservative was not added to the traps because we were able to empty them frequently, so most invertebrates caught in the traps were alive. Eight traps, arranged in two 2 m x 2 m plots of four traps each, were set at each wetland for a total of 120 traps (Figure 2.2). Within each plot, two traps were placed 2 m apart at the shoreline, and another two traps were set 2 m further away from the shore (Figure 2.2). Pitfall traps were open from mid-May to late August 2000, and spiders collected from them once per week. In early July, however, heavy rainfall prompted the relocation of all terrestrial pitfall traps to accommodate expanding shorelines.

Assemblages of spiders associated with water have been described for a freshwater pond in central Alberta using floating pitfall traps (Graham *et al.*, in press). These traps were similar to standard terrestrial pitfall traps, but the plastic container was held afloat in a thick piece of Styrofoam ™ (15 cm x 15 cm) that was tied to an anchoring pole. Four such floating traps were established in the open water of each marsh, and two were set near each grid of ground traps, for a total of 60 traps (Figure 2.2). In previous studies, floating traps caught fewer individuals and fewer species than ground traps (A. Graham, personal observation). Therefore, ethylene glycol was added to each floating trap as a preservative, and the traps were checked less frequently.

Individual spiders of both habitat guilds were identified to species according to the literature (*e.g.,* Opell and Beatty 1976, Dondale and Redner 1978, 1990), as well as reference collections at the University of Alberta Strickland Museum. Problematic linyphiid and theridiid specimens were sent to Don Buckle of Saskatoon, Saskatchewan, for confirmation or identification.

Since most species identifications are based primarily on genitalia, only sexually mature spiders can be accurately identified to species. Juveniles were identified to genus, and recently emerged spiderlings to family level.

### 2.2.3 Assessment of Environmental Conditions

Prolonged rainy weather and flooding of all study areas contributed to a noticeable increase in maximum depth at all wetlands after June 2000. The Camrose, Alberta area received 207 mm of rain in July 2000 (Environment Canada 2000), and this certainly affected spider assemblages of the wetlands studied here. The shorelines fluctuated markedly at all of the study sites from May to August because of rain and flooding. Pitfall traps that filled with water shortly after they were set were relocated, and all traps were replaced in mid-July to accommodate the expanding shorelines. In addition, surveys were conducted to describe the terrestrial and emergent vegetation for each plot.

Habitat use of particular species was characterized by associating abiotic variables with abundance and composition of spider communities. Several limnological parameters, such as specific conductance and maximum depth, were measured weekly and compared among wetland types and individual marshes. Two water samples were taken per pond on every occasion that specific conductance was measured, and these were kept at room temperature and assessed for specific conductance using a conductivity meter.

Many spiders are sensitive to changes in soil moisture (Schikora 1994), and so I evaluated seasonal and wetland site differences in this parameter. Small plastic soil corers (12 cm length, 5 cm diameter) were used to take two soil samples within each 2 m x 2 m plot at 10 of the marshes, (*i.e.,* 40 samples) five times between June and August. Samples were weighed, dried two days at 40°C, and then re-weighed to obtain estimates of per cent soil moisture (dry weight/wet weight) and relate those to the abundance of individuals and species caught in selected traps on those respective five sampling dates.

### 2.2.4 Data Analyses

Effects of wetland management practices on both common and rare wetland spider species were of interest, especially in the context of nature conservation. To simplify data analysis and interpretation, all species were included in a summary table (Appendix I), but only the most abundant spider species (*i.e.*, those comprising > 5% of the total catch) were used in species-level analyses.

Analysis of variance was used to examine differences in spider abundance among sites and wetland type. For these analyses, it was assumed that treatment and environmental effects were additive, and that experimental errors were random, independent and normally distributed about a mean of zero, *i.e.*, means and variances were uncorrelated. One-factor ANOVAs were used to compare total spider abundance among restored and natural wetlands, and also to analyse the development of spider communities at restored wetlands of various ages. Nested ANOVAs were used to compare variance in spider catch between natural and restored wetlands, among different ponds of both wetland types, and among traps at each wetland.

Pitfall trap data and environmental conditions at each marsh were also examined using Detrended Correspondence Analysis (DCA), an ecological ordination technique useful in revealing variations among data and identifying critical factors associated with species distributions (Jongman *et al.* 1995). Ordination analyses were done using the program PC-ORD (McCune and Mefford 1999); all species were included in these analyses but rare species were downweighted or selectively included to interpret their contribution to the patterns discovered. For these analyses, rare species were defined as those represented by less than F/5, where F represents the frequency of the most common species collected (McCune and Mefford 1999).

Linear regression was used to test if soil moisture was related to abundance of selected spider species in live capture traps.

## 2.3 Results

### 2.3.1 Abundance and diversity

Altogether, 65 species and over 7500 mature and immature specimens from 15 families were collected from pitfall traps between May and August 2000 (Appendix I). Wolf spiders (Lycosidae) were numerically dominant (Table 2.2), and accounted for over 80% of the total catch. *Pardosa fuscula* (Thorell) was particularly abundant, and represented almost half of the total catch (3725 individuals). Nineteen species of Linyphiidae were collected from pitfall traps, so it may be considered the most diverse family, followed by Lycosidae (12 species). Despite their high diversity, however, only 63 linyphiids were trapped over the entire course of the study, so they were not included in any of the species level analyses of habitat association. Over one third of the 65 spider species collected were rare, *i.e.* 22 species collected in pitfall traps were represented by only one individual, and 6 species were represented by two individuals.

### 2.3.2 Differences between restored and natural wetlands

Although the number of natural and restored wetlands sampled was unequal, significantly more individuals (mean trap total +/- SE, x.x +/- y.yy) were collected from live capture traps at natural wetlands (84.7 +/- 5.99) than restored wetlands (49.7 +/- 4.89) (Figure 2.3). In addition, several significant patterns were observable among species and families. Wetland type significantly affected wolf spiders (Lycosidae), and more were trapped at natural ponds than restored ponds (Table 2.3a).

The most abundant species, *Pardosa fuscula* (Lycosidae), was strongly associated with natural wetlands (Figure 2.3). The same pattern was found for two other fairly abundant wolf spiders, *Pardosa moesta* Banks, and *Alopecosa aculeate* (Clerck) (Table 2.3a). Several other species, in particular the wolf spider *Pardosa groenlandica* (Thorell), were significantly more abundant at restored wetlands (Figure 2.3). However, wetland type had no significant effect on the abundance of the wolf spiders *Pardosa modica* and *Pirata piraticus*, or the hahniid *Neoantistea magna* (Appendix I).

Significantly more species were also trapped at natural wetlands (Table 2.3a). When all sampling dates were included, 12.0 +/- 0.48 species were collected per trap at natural wetlands, while restored wetlands yielded 10.0 +/- 0.40 species per trap.

A Nested ANOVA to examine variation in spider catch between wetland types, among wetlands within each treatment, and among traps at each wetland showed that the greatest amount of variance in spider catch occurred between natural and restored wetlands (73.6%) (Table 2.4). Less variation in the spider catches was due to differences among wetlands within a restoration category, and differences between traps at the same wetlands (Table 2.4). The same was true when variance was examined for individual species; in general, the largest variation in abundance was due to wetland type, and variance within traps was usually greater than variance among ponds (Table 2.4). The total number of individuals, as well as abundances of the family Lycosidae and all of the species examined separately were significantly affected by differences among wetlands within each treatment. For *A. aculeata, P. modica, P. piraticus* and *N. magna* these local effects were more important than wetland type. However, for the other four species, wetland type absorbed more variance than did local differences among wetlands.

Site effects were highly significant when pitfall trap totals were analyzed ($F_{14,105}=5.94$, $p<0.0001$). Among the six natural wetlands, there were remarkable differences in the total number of spiders caught per trap, and the same was true for wetlands restored in 1995 and 1999. Similar numbers of spiders were trapped at wetlands restored in 1993, though, even though one wetland was located 14 km from the other two. Therefore, there are significant differences in spider abundance among the various wetlands, but, as the results from the nested ANOVA suggest, these differences are generally overshadowed by whether or not the wetland was restored.

Floating traps collected 812 individuals and 15 species during the summer of 2000 (Appendix I). Unlike the pattern observed for the terrestrial pitfall traps, significantly more individuals were trapped in restored wetlands than in natural ones (Table 2.3b). This result was likely because *Pirata piraticus* dominated the entire floating trap catch, and significantly more individuals of this species were collected at restored wetlands (Figure 2.4b). None of the other four common species investigated were significantly affected by wetland type (Figure 2.4b). Site effects were also significant for floating traps; the total number of individuals trapped per wetland differed markedly among individual wetlands ($F_{14,45}=5.71$, $p<0.0001$).

### 2.3.3 Restored wetland age classes

Effects of restored wetland age on spiders were less striking. It was apparent that more individuals and fewer species were collected at wetlands restored in 1999 than at wetlands restored in 1995 or 1993. Nonetheless, neither the total number of individuals nor the number of wolf spiders differed significantly among restored wetland age classes. Several species of wolf spider, including *Pardosa fuscula* and *Pirata piraticus,* were significantly affected by wetland age class, and were more abundant at newer wetlands (Table 2.3). Two other species of lycosid, *Pardosa modica* and *Alopecosa aculeata*, as well as *Gnaphosa parvula* (Gnaphosidae) and *Neoantistea magna* (Hahniidae), were most frequently collected at wetlands restored in 1995. Only one species, *Pardosa groenlandica*, was more abundant at the three older restored wetlands. Species richness (number of species collected in live capture traps), differed significantly among age classes; more species were collected at wetlands restored in 1995 than at those restored in 1999 or 1993 (Table 2.3a).

### 2.3.4 Environmental variables

In general, few environmental variables measured in this study were correlated with overall spider abundance, species richness, or relative abundance of the eight most commonly captured species. It is likely that heavy rains severely disrupted wetland shorelines and spider habitat, and that this effect may have blurred the normal pattern of seasonal population dynamics. Spider catches in pitfall traps tend to peak in June, at the height of the mating season, and then decline through July and August, barring any major fluctuations in temperature or precipitation (Dondale 1977).

During the three sampling dates in June, an average of 74.6 adult spiders were trapped per wetland; this number declined to 19.7 for the four sampling dates in July and 7.8 over the last four collections in August. This drastic decrease in spider abundance with increasing pond depth over the field season may have happened because shorelines expanded and many of the spiders living there either drowned or dispersed to a more suitable area.

Linear regression analysis showed that several spider species were associated with soil moisture. Significantly more *P. fuscula* individuals were collected from areas where soil was moist, i.e. above 50% soil moisture (Figure 2.5A). *Pardosa fuscula* was associated with moist soil in an earlier study

(Graham et al., in press), and may be considered semi-aquatic. *Pardosa modica* were negatively associated with moist soil (Figure 2.5B). Distributions of both species against soil moisture were somewhat triangular, though, and indicate that high soil moisture did not guarantee an abundance of lycosids. In fact, little of the variation in spider catch was explained by soil moisture since the $R^2$ values were <5% (Figure 2.5). When separate linear regressions were done using spider abundance at individual wetlands, and total spider catch per season (*i.e.*, May, June, July and August) there was no significant relationship between spider abundance and soil moisture. Realistically, though, soil moisture estimates used here are probably an unreliable indicator of spider habitat associations because rainy conditions made it impossible to take the samples after a standardized number of dry days. Also, there was considerable variability in moisture among the different wetlands, which made it difficult to assess patterns in species responses to this variable.

Average specific conductance at natural ponds (807 microsiemens/cm) was over six times higher than at restored ponds (123 microsiemens/cm). Pure water has a low salinity, and hence greater resistance to electrical flow, or specific conductance, than ponds with low ion concentrations (Rodhe 1949). Therefore, restored wetlands contain lower concentrations of ions, and thus have lower specific conductance than the older, more stable natural wetlands. It is unclear whether spiders are affected by specific conductance of ponds, but few of the spider species we trapped actively use the water surface, so specific conductance probably is not an important variable in the habitat choice of most wetland spiders. In addition, conductivity data were confounded with wetland type, so these data were not examined further.

The vegetation survey revealed some differences in ground and emergent plant species between wetland types and age classes. The predominant vegetation at natural wetlands consisted of shrubs (e.g. *Salix* sp.), slough grass (*Beckmannia syzigachne*) and aquatic plants such as cattails (*Typha latifolia*) and duckweed (*Lemna minor*) (Figure 2.6). The latter two aquatic plants common at natural wetlands are indicative of permanent water (Voigts 1976). Fewer plants were present at wetlands restored in 1999 and 1995, although more bulrushes (*Scirpus validus*), which are tolerant of a wide variety of conditions, were noticed (Figure 2.6a, b). Wetlands restored in 1993, however, resembled natural ones more closely in terms of vegetation cover; there were fewer bulrushes, and more aquatic plants (Figure 2.6c).

### 2.3.5 Succession and community patterns

Detrended Correspondence Analysis (DCA) was used to compare spider species composition in each of the 120 live capture traps (Figure 2.7). Two ordination analyses were done: one containing only common species, and another containing all species, including species represented by only one individual. In both cases, traps from natural wetlands occupied similar positions on DCA axis 1 (Figure 2.7), which separated traps mainly by wetland type and age. Positions of the sample scores from individual live capture traps suggest that natural wetlands have a different community composition than wetlands restored in 1995. In addition, wetlands restored in 1999 and 1993 were quite variable in terms of spider species composition because individual trap scores were randomly distributed across the ordination space (Figure 2.7).

Several species patterns within age classes were noticeable. Wetlands restored in 1999 tended to support more wolf spiders and fewer species than the other two age classes, whereas wetlands restored in 1995 supported both common and rare species. Wetlands restored in 1993, however, contained fewer species than those restored in 1995, but still more species than those restored in 1999. Wetlands restored in 1999 were primarily dominated by *Pardosa fuscula* and *Pardosa groenlandica*, whereas *Pardosa modica*, *Alopecosa aculeata* and *Gnaphosa parvula* were more common at wetlands restored in 1995. Spider assemblages at wetlands restored in 1993 were similar to those at wetlands restored in 1995 since wolf spiders were abundant, but fewer rare species were present.

## 2.4 Discussion

### 2.4.1 Differences between natural and restored wetlands

*Common species.* Serious biodiversity investigation must begin with firm knowledge of the species present. This study has provided a thorough introduction to wetland spider diversity, and suggests that spider communities in newly flooded and long established wetlands differ in terms of abundance and diversity, especially when common species are considered.

The eight dominant spider species responded differently to wetland type and age class. *Pardosa fuscula* dominated the entire live capture trap catch, with over 3700 individuals collected, and was significantly more abundant at natural than restored wetlands (Figure 2.3). Since *P. fuscula* was so abundant at natural wetlands, it follows that significantly more lycosids and individuals in total were collected from natural wetlands. *Pardosa fuscula* probably requires a stable habitat with few fluctuations in shoreline, and long-established, diverse vegetation cover and insect prey. Restored wetlands seem to accumulate less nitrogen in soils, and support less vegetation (Streever *et al.* 1996). As a result, perhaps, invertebrate counts are lower (Malakoff 1998). *Pardosa moesta* and *Alopecosa aculeata* are also dependent on vegetation (Dondale and Redner 1990), so their habitat affinities also contributed to the abundance of individuals and greater species richness at natural wetlands.

*Pardosa groenlandica* is commonly found in unstable habitats such as cobblestone beaches and gravel bars of rivers (Dondale and Redner 1990). Only nine of the 320 individuals collected were found at natural wetlands, so this species showed a distinct association with restored wetlands. It seems to thrive in unstable, transient habitats, so it was able to tolerate the low specific conductance and developing vegetation at the new wetlands. Since so many *P. groenlandica* were collected at the newly restored sites (Table 2.2), this species was probably able to persist during flooding, and rapidly colonize the new wetland habitats. Consequently, *Pardosa groenlandica* contributed to the influx of lycosids at wetlands restored in 1999.

*Pirata piraticus* is semi-aquatic with respect to habitat use (Graham *et al.*, in press) and is more closely associated with wetland shorelines than any of the other dominant species. *Pirata piraticus* was the most abundant species caught in floating traps, and significantly more individuals were trapped in restored wetlands (Figure 2.4B). Previous work about *P. piraticus* provides no reasons for why this should be so. Wallace (1978) noted that the species is found in moist areas such as bogs, ponds, and lakeshores, and Nørgaard (1951) indicated that it requires a free water surface. However, these conditions are satisfied at both natural and restored wetlands. None of the other species captured in floating traps were numerous enough to detect habitat associations, although there was a tendency toward higher capture rates in restored wetlands. The larger number of individuals at restored wetlands may be a result of ballooning spiders taking advantage of these new habitats shortly after they become available, and readily establishing initial populations there.

Captures of several species commonly encountered in terrestrial traps, including *Pardosa modica*, *Pirata piraticus*, and *Neoantistea magna* were not significantly affected by wetland type. *Pirata piraticus* did not show a significant habitat association when ground trap data were analysed, and thus it appears that populations only use the water surface more frequently in restored sites. Perhaps the microclimatic conditions necessary for this species to feed and reproduce on land were satisfied at both wetland types. The same may be true for *Neoantistea magna*, which is commonly found in areas where there are suitable depressions on which to anchor small sheet webs (Opell and Beatty 1976). These depressions are available at both natural and restored wetlands. *Pardosa modica* is found in swamps and salt marshes, and is common in Canada's prairie pothole region (Kaston 1936). All three of these species may be adapted to the fluctuating conditions of wetland shores, and any damp area, regardless of vegetation cover, and stability of environmental conditions may suffice for growth and reproduction.

### 2.4.2 Differences between natural and restored wetlands

*Communities.* More spider species (11.9 +/- 0.48 species/trap) were captured at natural wetlands than at restored sites (10.0 +/- 0.40 species/trap). The average species richness differed significantly between natural and restored wetlands (Table 2.3A), and may be indicative of a major difference in diversity between the two wetland types.

Differences in assemblages of invertebrates other than spiders among natural and restored wetlands have been detected; fewer individuals and species are collected at restored areas (Brown *et al.* 1997, Voigts 1976, LaGrange and Dinsmore 1989, Streever *et al.* 1996). These differences are usually explained by lack of plant diversity at restored wetlands, since many invertebrate taxa are closely associated with aquatic vegetation (LaGrange and Dinsmore 1989, Raizer and Amaral 2001). Links between vegetation type or structure and spider communities have been demonstrated (Robinson 1981, Riechert and Gillespie 1986, Raizer and Amaral 2001). Our vegetation survey hinted at these links since changes in vegetation with wetland type and time after restoration were accompanied by changes in spider abundance. The sparse vegetation cover at wetlands restored in 1999 may have been reflected in the low species richness, which increased with vegetation cover at wetlands restored in 1995. Recently restored wetlands may not support sufficiently diverse plant and insect communities for spiders with specific habitat and prey requirements.

Also, non-aerial invertebrate taxa were rare or absent at newly restored wetlands because they were unable to arrive at and colonize these sites as fast as flying insects (Brown *et al.* 1997). Spider colonization may be limited by both ballooning and the time required to develop a diverse array of species once initial colonists arrive. It is likely that spider colonization contributed to differences in spider fauna among natural and restored wetlands.

Our Nested ANOVA results confirm that there were significant effects of wetland type on abundance of all individuals and most of the common species. Whether the pond was natural or restored explained more about spider assemblages than did site characteristics such as wetland size or permanence. This seems odd because site effects were apparent within each wetland type, *e.g.*, several of the natural wetlands were over 20 km apart (see Figure 2.1), and quite different in size and vegetation cover. In addition, positions of terrestrial traps at each wetland contributed more to variance in species abundance than did the wetland sites themselves. The latter variance in species abundance may have been observed because two of the four terrestrial traps per grid were placed at the shore, and the second pair was placed 2 m away from shore. Apparently, this small difference in trap position was important in the habitat choices of wetland spiders.

### 2.4.3 Restored wetland age classes

Within restored habitats, there was no significant effect of wetland age on the total number of individuals or lycosids collected (Table 2.3a). Wetland age, however, significantly affected abundance of all of the common species examined, and peak numbers of each occurred at one of the age classes. Spider assemblages respond to disturbance, and often show changing species patterns with time after a disturbance. For example, open areas resulting from clear-cuts are quickly populated by fast-moving wolf spiders (Huhta 1971). As these areas grow to approximate natural forests in terms of tree diversity and cover, species inhabiting tree canopies and those requiring complex microhabitats can proliferate, so a more diverse spider fauna develops (McIver *et al.* 1992, Buddle *et al.* 2000).

A general succession of species was somewhat noticeable in our different wetland age classes. Spider abundance was similar, but species richness differed somewhat among the three wetland age classes. An average of 8.1 +/- 0.63 species was collected per trap at wetlands restored in 1999, in comparison with 12.1 +/- 0.63 species per trap at wetlands restored in 1995, and 10.0 +/- 0.63 species per trap at wetlands restored in 1993. Given the published nature of spider responses to disturbance, one would expect the largest number of species at wetlands restored in 1993, since they were oldest and would approximate natural wetlands more closely in terms of environmental conditions. Instead, the largest number of species was noted at wetlands restored in 1995, and this was the same value observed at natural wetlands.

Wetlands restored in 1995 had a spider fauna, vegetation structure and environmental conditions that were dissimilar to the other two restored wetland age classes, and instead resembled more closely those at natural wetlands. These three wetlands were dominated by wolf spiders, but also contained many linyphiid singletons, and cursorial species such as *Alopecosa aculeata*, *Pardosa modica*, *Neoantistea magna*, and *Gnaphosa parvula*. Thus, it seems that only five years are necessary for spider assemblages to recover to a natural state in terms of species richness. Nevertheless, there were still far fewer individuals at wetlands restored in 1995 than at natural ones, even after adjusting trap catch for dissimilar sample sizes (Appendix I). It is likely that spider communities are more stable at natural wetlands, and may be climax communities, while 1995 wetlands are still accumulating spider individuals and building up populations, so fewer individuals are present.

Wetlands restored in 1993 likely included early colonists as well as specialist species that arrived later. The observed decline in species richness following the 1995 peak in diversity may be due to a delay in spider population growth caused by slow colonization of insect prey (Greenstone *et al.* 1985), and site-specific environmental conditions.

Restored wetland age had a significant effect on the abundance of only two species collected in floating traps, *P. fuscula* and *D. triton* (Figure 2.4a). Both species were caught most frequently at wetlands restored in 1999, and, furthermore, *D. triton* adults were scarce at wetlands restored in 1995, and none were captured at wetlands restored in 1993 (Figure 2.4a). Only adult *D. triton* were captured and identified in this study. It is clear that these did not arrive as balloonists at wetlands restored in 1999 because only early instars are able to disperse by ballooning (A. Graham, personal observation- see Chapter 4). In addition, Zimmermann and Spence (1998) have shown that *D. triton* has a two-year life cycle in central Alberta, and if juvenile *D. triton* had ballooned into wetlands restored in 1999, we would have noticed these and not adults in our floating traps. Adults likely wandered onto the newly restored wetlands from neighbouring wetlands, and thus, adult *D. triton* are able to actively colonize new areas. *Dolomedes triton* is often absent or rare at old marshy areas (J. Spence, personal communication), and one reason for this may be that insectivorous fish are also absent from newly restored wetlands, but are able to proliferate and deplete aquatic spider populations as wetlands age.

### 2.4.4 Succession and community patterns

There are notable differences in the spider fauna between natural and restored wetlands, and a marked succession in community composition as restored wetlands age. Spiders are capable of arriving at disturbed areas faster than many other groups. For example, an immature web-building spider was the first sign of life on Rakata, Indonesia nine months after the eruption of Krakatoa in 1883 (Wilson 1992). Newly restored wetlands are colonized by certain wolf spider species (e.g., *Pardosa modica*) which tend to dominate the initial fauna, and after a few years have passed, more web-building species (e.g., *Bathyphantes pallidus*) arrive and re-establish populations. Oddly enough, this successional pattern resembled that of spiders sampled in clear-cut forests

(Huhta 1971, McIver *et al.* 1992), and in forests following wildfire and harvesting (Buddle 2000). In other words, recently clear-cut areas and newly restored wetlands tend to attract large numbers of wolf spiders, which rapidly establish initial populations. As time passes after disturbance, other hunting and web-building species arrive to join the lycosids, and spider diversity increases. Even though wetlands differ vastly from forest ecosystems in terms of spider fauna, inhabitants of each seem to respond to disturbances in a similar manner.

Linyphiids and other web-building species take longer to arrive at and re-establish populations, *i.e.,* recover, at a new wetland than fast-moving wolf spiders. Ineffective colonization abilities might account for delays in the appearance of these species until five years post-restoration. Some studies suggest that invertebrate populations do not fully recover and approximate those at natural wetlands, even after 30 years (Smith and Tome 1992, Malakoff 1998). Others suggest that although invertebrate populations may differ between the two wetland types, restored populations will come to approximate natural ones after a few years if certain management techniques are implemented (Brown *et al.* 1997, Voigts 1976, LaGrange and Dinsmore 1989). According to Brown *et al.* (1997), for example, soil transplanted from remnant wetlands into restored areas promotes a more diverse plant community, which, in turn, leads to a more diverse invertebrate community.

Ordination analyses suggest that spider community composition differs between wetland types and ages of restored wetlands. Although there are noticeable differences in trap scores when rare species are added to the ordination, traps in natural wetlands still appear together in the ordination space, as do traps from wetlands restored in 1995 (Figure 2.7). This suggests that the distinctiveness of assemblages in natural wetlands is not driven mainly by rare species.

A wider range of microhabitats is probably available for spiders at natural wetlands, especially since vegetation cover was more substantial in these areas. Since wetlands restored in 1999 and 1993 had fewer species and were dominated by several species of wolf spider, their trap scores were noticeably different from natural wetlands and those restored in 1995. Several species of ground spider, including *Gnaphosa parvula*, *Neoantistea magna* and *Xysticus ferox* were abundant at natural and 1995 wetlands and scarce at wetlands restored in 1999 and 1993 (Appendix I), and may have accounted for the overlap in species compositions between the former two.

## 2.5 Summary

Prairie pothole wetlands are dynamic habitats that support diverse spider assemblages. Altogether, in this study I collected 65 spider species from 15 natural and restored wetlands in central Alberta, and five of these species were previously undescribed in Canada (see Appendix I). It was apparent that there were noticeable differences in spider abundance and diversity at the two wetland types, and in particular we noticed that natural wetlands supported larger and more diverse communities of spiders. Ultimately, habitat changes such as wetland drainage and restoration are important in regulating spider communities in northern prairie wetlands. More field experiments must be completed in order to fully understand spider responses to wetland restoration, and provide more information about species recovery to natural levels after disturbance. Studies such as those described in Chapter 3 will help to provide basic biological information about constituent wetland species and tease apart interactions between wetland spiders and their habitats.

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Table 2.1. Basic information about all 15 wetlands, including general and specific (i.e. quarter section of land, township road, range road and W) locations, UTM coordinates, year of restoration, and class according to Stewart and Kantrud (1971).

| **Wetland** | **Sec** | **Twp** | **Rg** | **W** | **UTM Coordinates** | **General location** | **Wetland type** | **Date restored** | **Wetland class** |
|---|---|---|---|---|---|---|---|---|---|
| A&A Johnson A (N1) | SE 29 | 46 | 22 | 4 | 12 3558 58729 | 7km W of Bittern Lake | Natural | | IV |
| Blue Sky Z (N2) | NE 29 | 46 | 21 | 4 | 12 3655 58734 | 9.2km W of Camrose | Natural | | IV |
| Blue Sky B (N3) | NE 30 | 46 | 21 | 4 | 13 3655 58734 | 9.2km W of Camrose | Natural | | III |
| Hagstrom B (N4) | SW 31 | 47 | 22 | 4 | 12 3521 58844 | 13km N of Gwynne | Natural | | IV |
| Hagstrom C (N5) | SW 31 | 47 | 22 | 4 | 12 3521 58844 | 13km N of Gwynne | Natural | | IV |
| Lyseng 45 (N6) | SW 24 | 48 | 21 | 4 | 12 3623 58858 | 13.3km SE of Hay Lakes | Natural | | IV |
| Rettaler-1 (1999A) | S1/2 | 48 | 22 | 4 | 12 3502 58992 | 7.5km W of Hay Lakes | Restored | 1999 | III |
| Rettaler-2 (1999B) | S1/2 | 48 | 22 | 4 | 12 3502 58992 | 7.5km W of Hay Lakes | Restored | 1999 | III |
| Rettaler-3 (1999C) | S1/2 | 48 | 22 | 4 | 12 3502 58992 | 7.5km W of Hay Lakes | Restored | 1999 | III |
| Lyseng 44 (1995A) | SW 24 | 48 | 22 | 4 | 12 3623 58858 | 13.3km SE of Hay Lakes | Restored | 1995 | III |
| Maruschak-8 (1995B) | NW 26 | 48 | 22 | 4 | 12 3589 58931 | 5.8km SW of Hay Lakes | Restored | 1995 | III |
| Maruschak-12 (1995C) | NW 26 | 48 | 22 | 4 | 12 3589 58931 | 5.8km SW of Hay Lakes | Restored | 1995 | III |
| Beck-22 (1993A) | NE 15 | 47 | 21 | 4 | 12 3675 58799 | 8.3km S of Armena | Restored | 1993 | IV |
| Mittelstadt-13 (1993B) | NE 27 | 48 | 22 | 4 | 12 3581 58931 | 5.8km SW of Hay Lakes | Restored | 1993 | III |
| Mittelstadt-8 (1993C) | NE 27 | 48 | 22 | 4 | 12 3581 58931 | 5.8km SW of Hay Lakes | Restored | 1993 | III |

Table 2.2. Summary of spider species and adult individuals collected per family from A) live capture traps and B) floating traps at natural and restored wetlands during summer 2000. CV (coefficient of variation) describes the variance in catch among species within each family.

**A) Live capture traps**

| | **Natural (n=48)** | | | **Restored (n=72)** | | |
|---|---|---|---|---|---|---|
| **Family** | No. species | No. individuals | CV | No. species | No. individuals | CV |
| Agelenidae | | | | 1 | 1 | 1 |
| Amaurobiidae | 1 | 1 | 1 | 1 | 9 | 1 |
| Araneidae | 1 | 1 | 1 | 2 | 2 | 0 |
| Clubionidae | 3 | 7 | 0.25 | 3 | 9 | 1.16 |
| Dictynidae | | | | 1 | 1 | 1 |
| Gnaphosidae | 4 | 45 | 1.65 | 6 | 149 | 2.18 |
| Hahniidae | 1 | 53 | 1 | 1 | 128 | 1 |
| Linyphiidae | 9 | 33 | 1.22 | 13 | 23 | 0.7 |
| Liocranidae | 1 | 4 | 1 | 2 | 8 | 1.06 |
| Lycosidae | 10 | 3426 | 2.24 | 11 | 1634 | 1.57 |
| Philodromidae | 2 | 2 | 0 | 1 | 1 | 1 |
| Pisauridae | 1 | 1 | 1 | 1 | 5 | 1 |
| Tetragnathidae | 2 | 45 | 1.29 | 1 | 38 | 1 |
| Theridiidae | 3 | 16 | 0.6 | 3 | 5 | 0.69 |
| Thomisidae | 4 | 71 | 1.32 | 7 | 131 | 1.45 |
| **TOTAL** | 42 | 3705 | | 53 | 2143 | |

**B) Floating traps**

| | **Natural (n=24)** | | | **Restored (n=36)** | | |
|---|---|---|---|---|---|---|
| **Family** | No. species | No. individuals | CV | No. species | No. individuals | CV |
| Clubionidae | 1 | 1 | 1 | 2 | 5 | 0.28 |
| Linyphiidae | 2 | 2 | 0 | 4 | 9 | 0.56 |
| Lycosidae | 2 | 73 | 1.43 | 4 | 469 | 1.85 |
| Pisauridae | 1 | 5 | 1 | 1 | 33 | 1 |
| Tetragnathidae | 2 | 48 | 0.29 | 2 | 89 | 0.55 |
| Theridiidae | | | | 1 | 2 | 1 |
| **TOTAL** | 8 | 129 | | 14 | 607 | |

Table 2.3. One-factor (wetland type, restored wetland age class) ANOVA results for activity-abundance of the 8 most common species, and number of species collected by a) live capture traps and the five most common species, and number of species collected by b) floating traps. NS indicates non-significance, *i.e.* $p>0.05$.

| | Wetland type | Restored wetland age |
|---|---|---|
| **a) Pitfall traps** | | |
| Total number collected | $F_{1,118}=20.5$, $p<0.0001$ | NS |
| Lycosidae | $F_{1,118}=23.1$, $p<0.0001$ | NS |
| *Alopecosa aculeata* | $F_{1,118}=5.52$, $P=0.02$ | $F_{2,69}=9.15$, $p<0.000$ |
| Pardosa fuscula | $F_{1,118}=27.0$, $p<0.0001$ | $F_{2,69}=4.27$, $p=0.018$ |
| *Pardosa groenlandica* | $F_{1,118}=15.9$, $p<0.0001$ | $F_{2,69}=3.64$, $p=0.03$ |
| *Pardosa modica* | NS | $F_{2,69}=17.8$, $p<0.000$ |
| *Pardosa moesta* | $F_{1,118}=5.98$, $p=0.016$ | NS |
| *Pirata piraticus* | NS | $F_{2,69}=11.1$, $p<0.0001$ |
| *Neoantistea magna* | NS | $F_{2,69}=4.02$, $p=0.02$ |
| *Gnaphosa parvula* | NS | $F_{2,69}=25.5$, $p<0.0001$ |
| Number of species | $F_{1,118}=9.42$, $p=0.003$ | $F_{2,69}=9.95$, $p<0.0001$ |
| **b) Floating traps** | | |
| Total number collected | $F_{1,58}=17.1$, $p<0.0001$ | NS |
| Lycosidae | $F_{1,58}=12.5$, $p=0.001$ | NS |
| *Pirata piraticus* | $F_{1,58}=12.5$, $p=0.001$ | NS |
| *Pardosa fuscula* | NS | $F_{2,33}=3.49$, $p=0.042$ |
| *Pachygnatha clercki* | NS | NS |
| *Pachygnatha dorothea* | NS | NS |
| *Dolomedes triton* | NS | $F_{2,33}=3.18$, $p=0.05$ |

Table 2.4. Nested (wetland type, ponds within each wetland type) ANOVA results for activity-abundance of the 8 most common species, and number of species collected by live capture traps. NS indicates non-significance, *i.e.* $p>0.05$. Per cent variance contributed by each level in the hierarchy, including traps within wetlands, is also indicated.

| | Wetland type (% of variance) | Pond (wetland type) (%) | Trap(Pond) (%) |
|---|---|---|---|
| **Pitfall traps** | | | |
| Total number collected | $F_{1,13}=27.8$, $p<0.0001$ (73.6%) | $F_{13,105}=4.26$, $p<0.0001$ (7.6%) | 18.7% |
| Lycosidae | $F_{1,13}=33.5$, $p<0.0001$ (75.8%) | $F_{13,105}=5.07$, $P<0.0001$ (8.15%) | 16.0% |
| *Alopecosa aculeata* | $F_{1,13}=8.45$, $P=0.025$ (21.5%) | $F_{13,105}=5.81$, $p<0.0001$ (29.5%) | 49.0% |
| *Pardosa fuscula* | $F_{1,13}=47.8$, $p<0.0001$ (78.0%) | $F_{13,105}=8.00$, $p<0.0001$ (10.3%) | 11.8% |
| *Pardosa groenlandica* | $F_{1,13}=20.0$, $p=0.001$ (68.2%) | $F_{13,105}=3.37$, $p<0.0001$ (7.26%) | 24.6% |
| *Pardosa modica* | NS | $F_{13,105}=3.90$, $p<0.0001$ | |
| *Pardosa moesta* | $F_{1,13}=12.6$, $p=0.005$ (42.3%) | $F_{13,105}=5.67$, $p<0.0001$ (21.3%) | 36.4% |
| *Pirata piraticus* | NS | $F_{13,105}=3.88$, $p<0.0001$ | |
| *Neoantistea magna* | NS | $F_{13,105}=2.50$, $p=0.005$ | |
| *Gnaphosa parvula* | $F_{1,13}=12.2$, $p=0.005$ (35.7%) | $F_{13,105}=6.53$, $p<0.0001$ (26.2%) | 38.0% |
| Number of species | $F_{1,13}=12.9$, $p=0.005$ (50.0%) | $F_{13,105}=4.39$, $p<0.0001$ (14.9%) | 35.1% |

Figure 2.1. Locations of natural and restored wetlands sampled in the prairie pothole region of central Alberta during summer 2000.

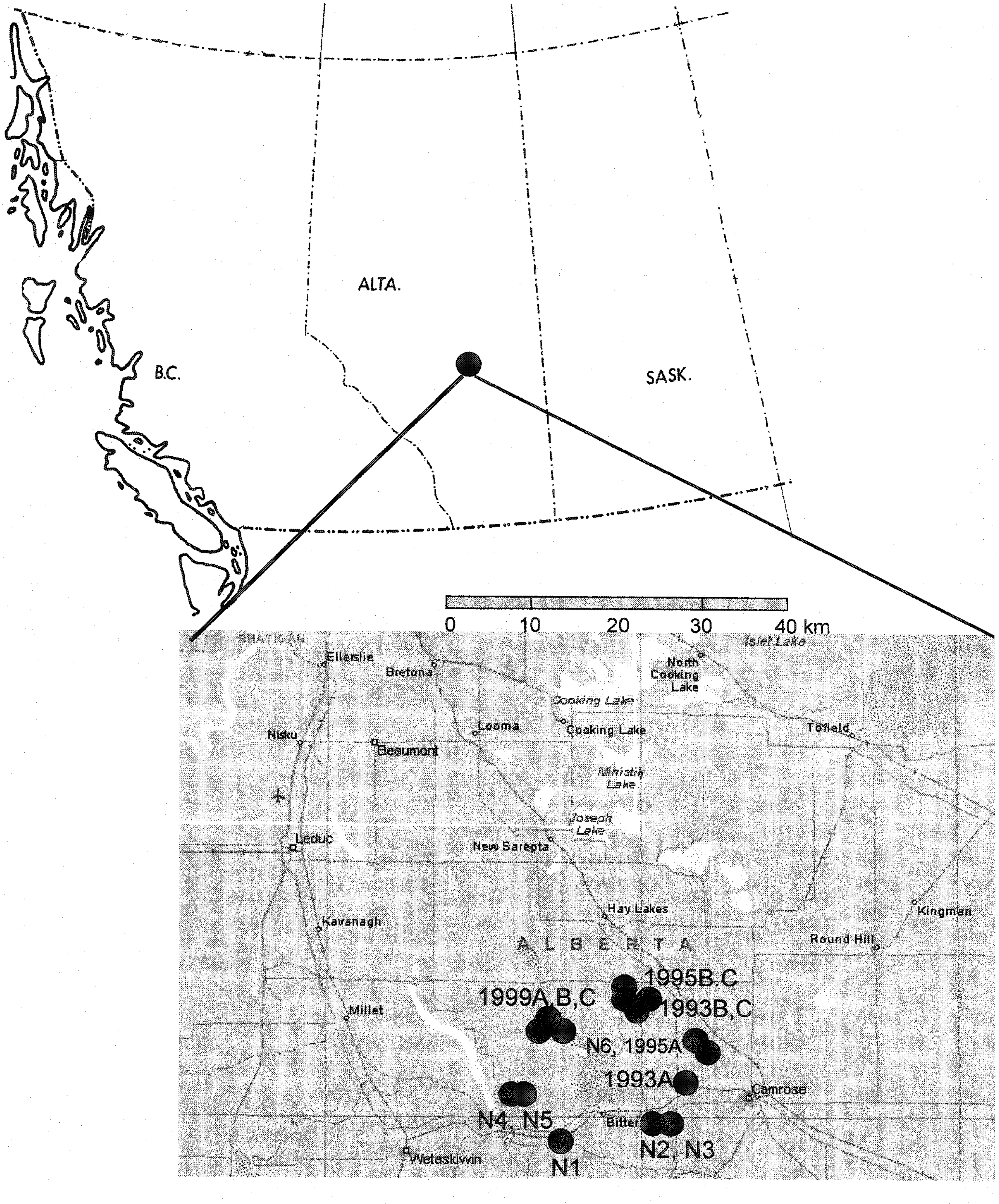


Figure 2.2. Sampling design; circles represent pitfall traps (8 at each wetland, 120 total), and circles within squares represent floating traps (4 at each wetland, 60 total).

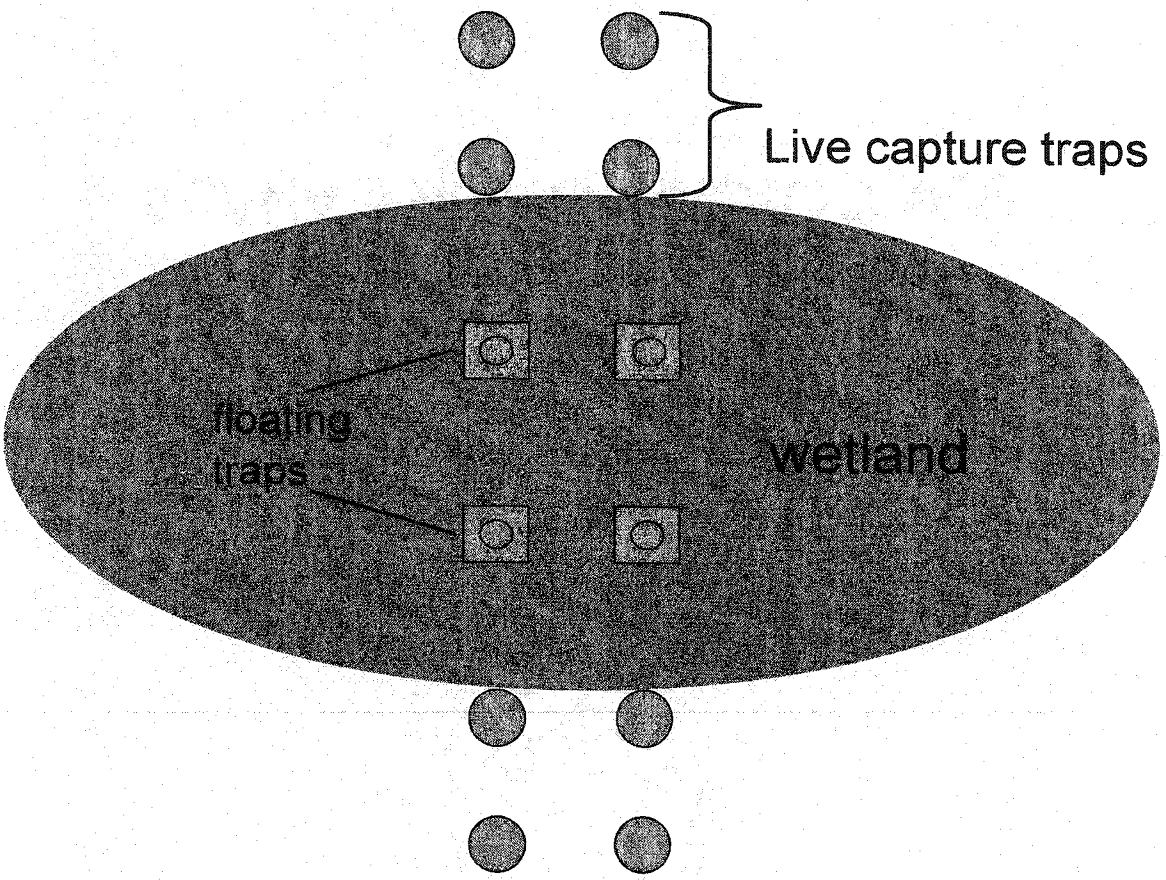


Figure 2.3. Mean (+ standard error) abundance of all individuals, lycosids, and three species of lycosid at natural and restored wetlands. Mean species richness at each wetland type is also shown.

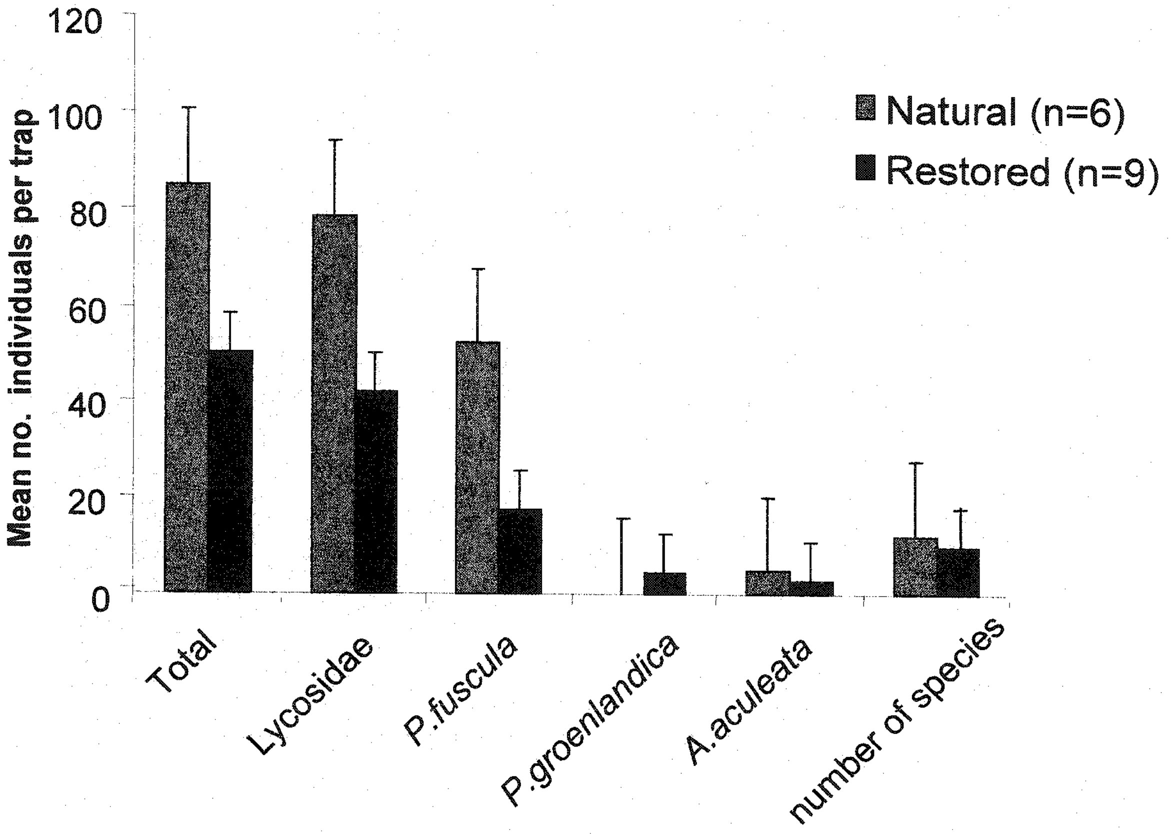


Figure 2.4. Mean (+ standard error) abundance of spiders caught in floating traps: two species at wetlands restored in 1999, 1995 and 1993 (A), 5 common species at natural and restored wetlands (B).

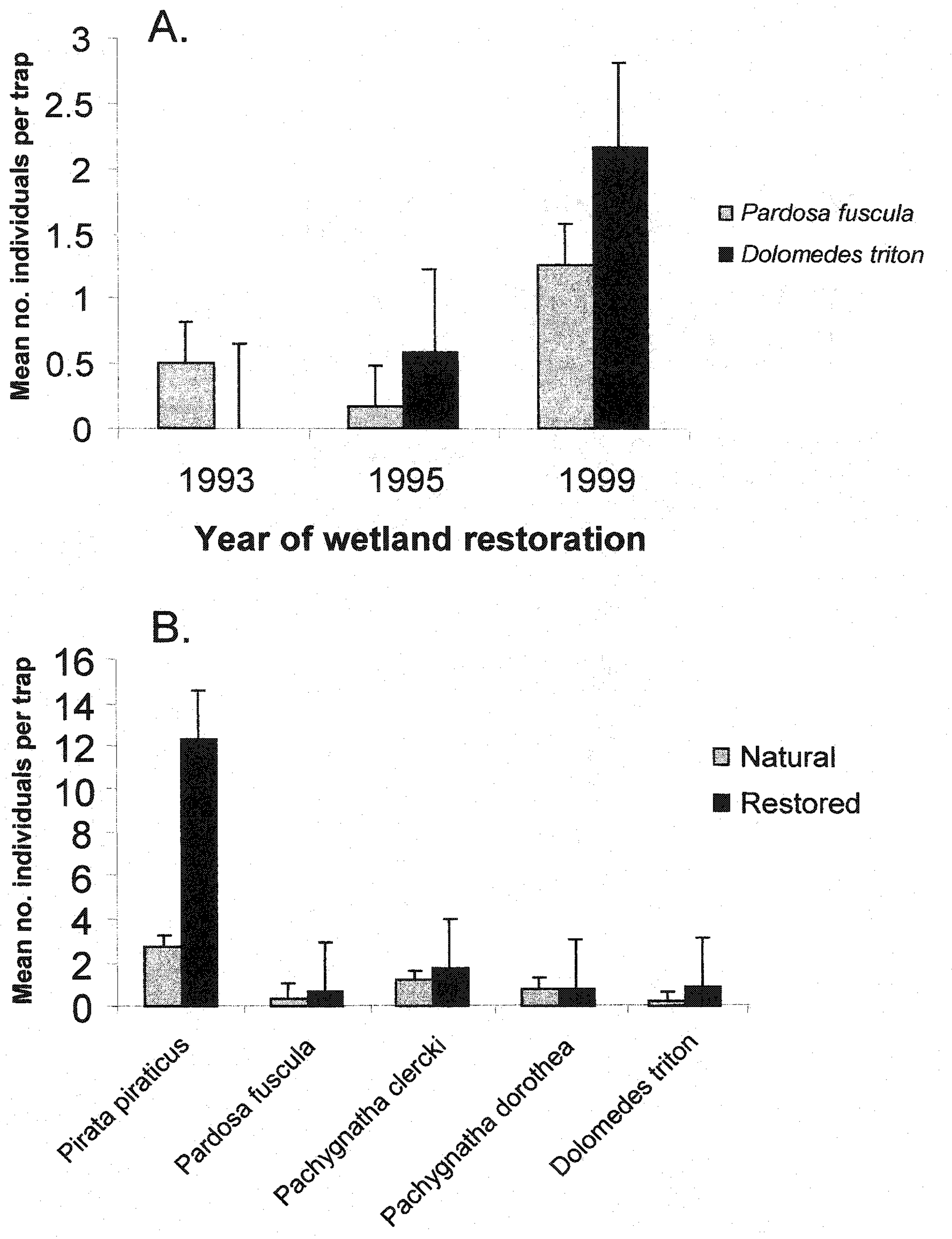
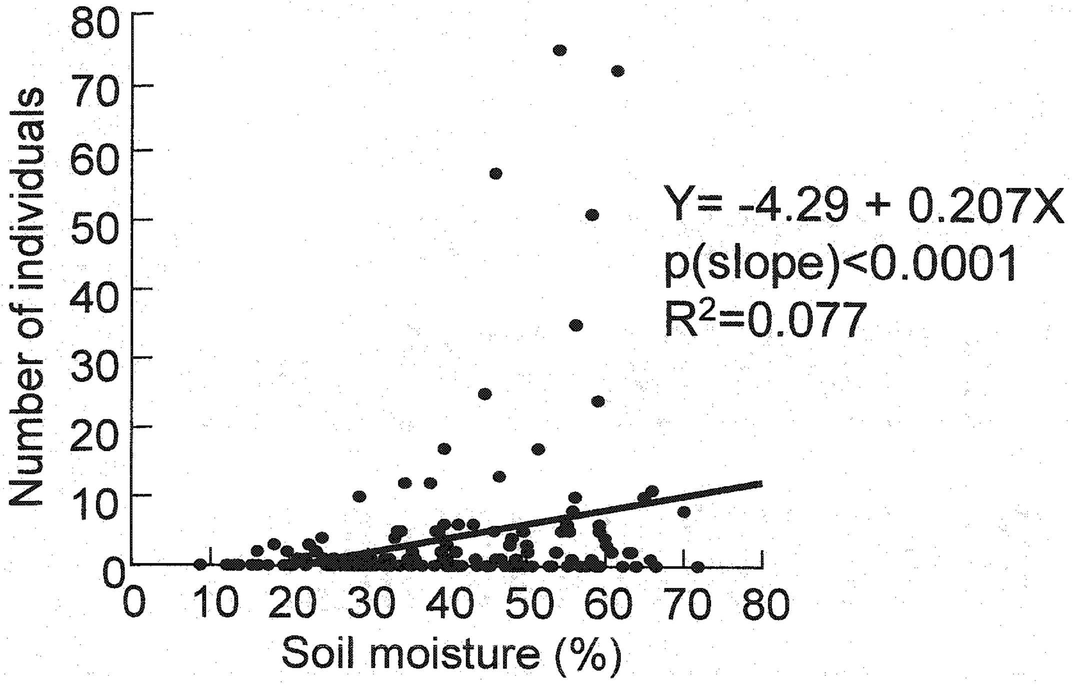


Figure 2.5. Linear regression of spider abundance (number of individuals per live capture trap) against relative soil moisture near each pitfall trap; n=163.

A. *Pardosa fuscula*



B. *Pardosa modica*

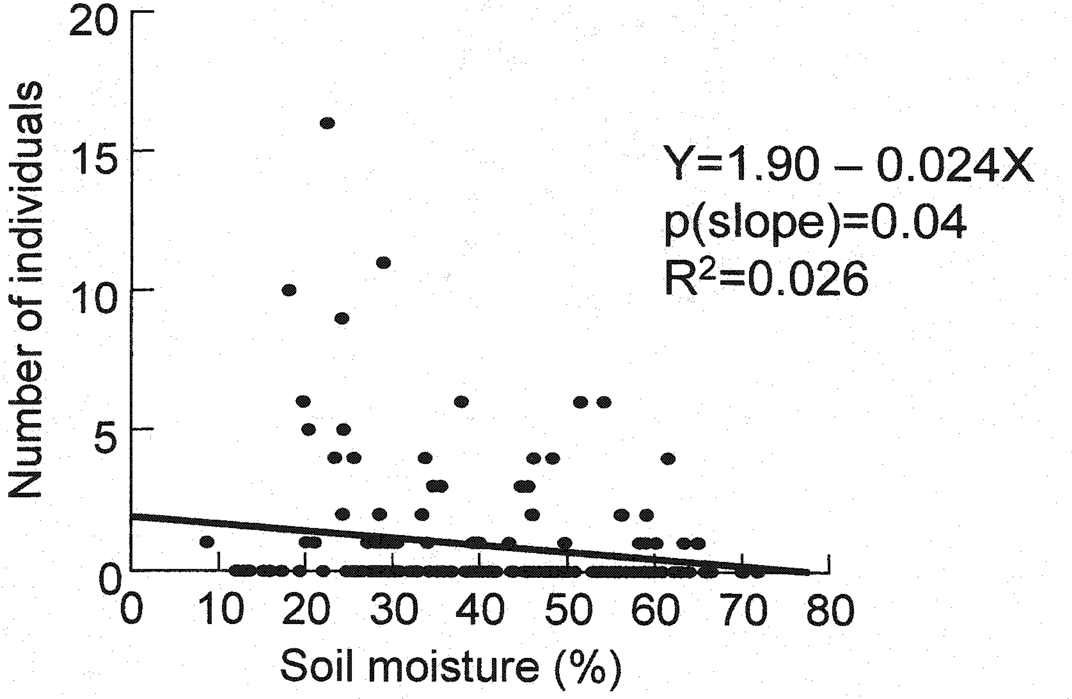
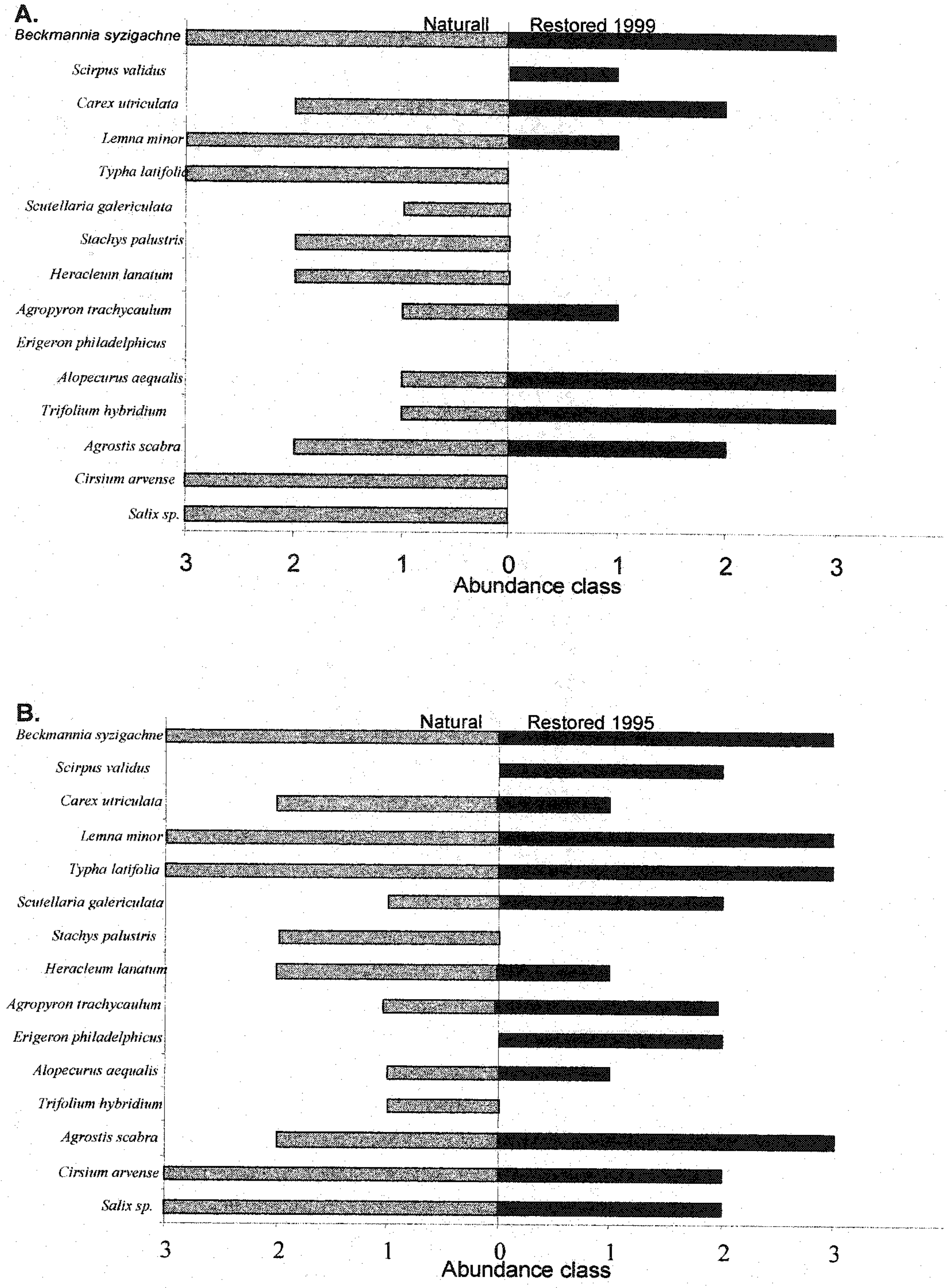


Figure 2.6. Comparison of the abundance of 15 dominant plant species at natural and restored wetlands. Abundance classes are based on the relative coverage of vegetation in the wetland itself, and within each 2m x 2m grid of live capture traps: 0- absent, 1- <20% cover, 2- 20-50% cover, 3- >50% cover. A) natural vs. 1999 wetlands, B) natural vs. 1995 wetlands, C) natural vs. 1993 wetlands.



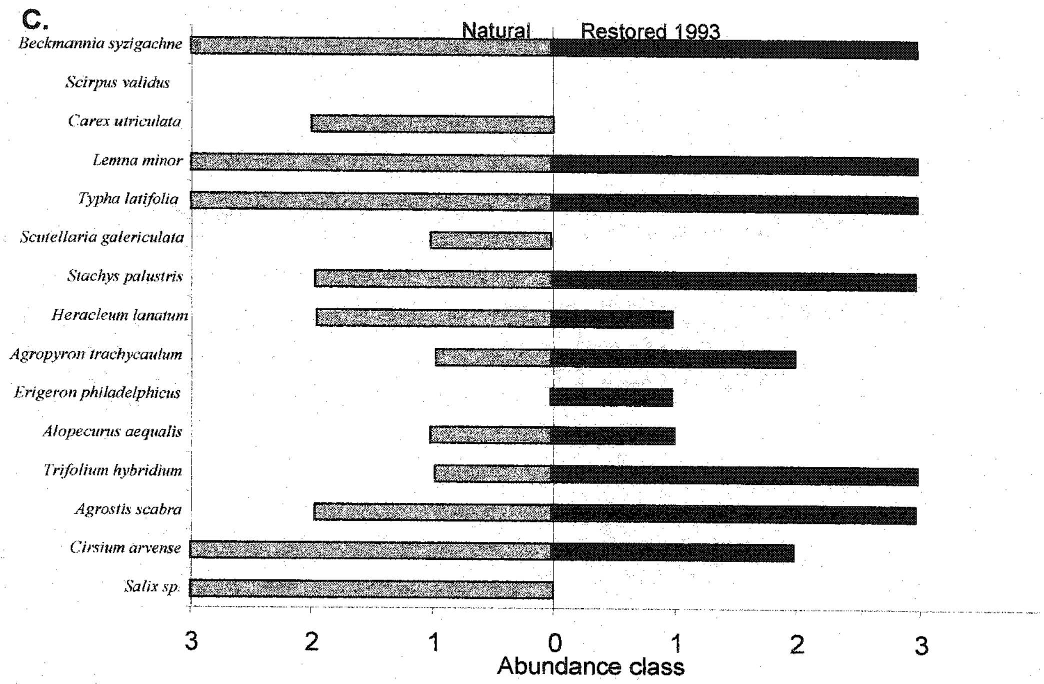
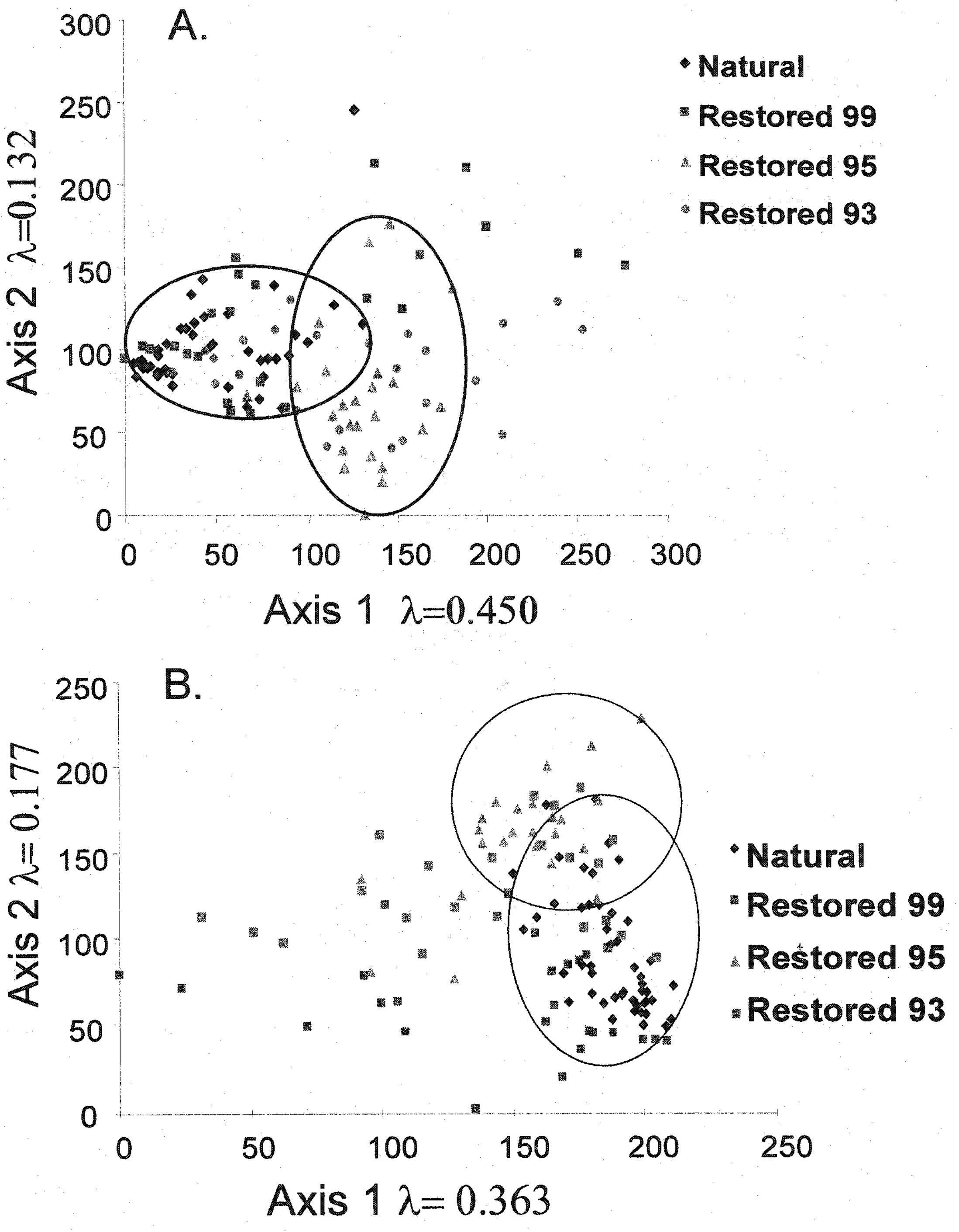

C.
Natural
Restored 1993
Beckmannia syzigachne
Scirpus validus
Carex utriculata
Lemna minor
Typha latifolia
Scutellaria galericulata
Stachys palustris
Heracleum lanatum
Agropyron trachycaulum
Erigeron philadelphicus
Alopecurus aequalis
Trifolium hybridium
Agrostis scabra
Cirsium arvense
Salix sp.
3
2
1
0
1
2
3
Abundance class

Figure 2.7. Sample scores from DCA ordination (axes 1 and 2) derived from 120 live capture traps and 65 species: common species only (A), all species, including rare species (B). Traps from natural wetlands and wetlands restored in 1995 that occupied similar positions in the ordination space have been circled to show similarities in species composition.



# 3. A Comparison of Life History and Reproductive Strategies of Wetland Spiders in Central Alberta

## 3.1 Introduction

Despite the existence of a rich Nearctic boreal fauna, interest in life history studies of northern spiders is relatively recent. For example, although the life cycle of *Dolomedes*, a fishing spider genus common in semi-aquatic habitats, is well known in Alberta, and in other parts of the world (Miyashita 1986, Zimmermann and Spence 1992, 1998), relationships between adult size and fecundity and how these vary temporally remain uninvestigated for *Dolomedes triton* (Zimmermann and Spence 1992). Species of *Tetragnatha* (Tetragnathidae) have also been studied quite recently (LeSar and Unzicker 1978, Williams *et al.* 1995, Aiken and Coyle 2000), and there is a large amount of literature about life histories and phenology of spiders in the genus *Pardosa,* (*e.g.* Edgar 1972, Van Dyke and Lowrie 1975). One study has compared the life histories of two species of *Pardosa* in central Alberta (Buddle 2000). Such research should be extended to encompass poorly understood species. In particular, much knowledge about ecological adaptations may be gained by comparative life history studies that include poorly understood taxa.

There is no published life cycle information for *Pirata piraticus*, a widespread lycosid species that is a conspicuous part of boreal semi-aquatic communities. Spiders of the genus *Pirata* are often found near bodies of water, including ponds, lakes, bogs, swamps and marshes (Wallace and Exline 1978). Although most *Pirata* species have been described (Wallace and Exline 1978), only scattered information is available about life cycles, fecundity, and phenology of these spiders. Therefore, I was interested in compiling life history and fecundity information for *P. piraticus* in central Alberta and comparing it to those of two other spider genera [*Pardosa* (Lycosidae) and *Tetragnatha* (Tetragnathidae)] that occur in similar habitats, and about which there is more information.

The purpose of this study was to examine patterns of fecundity and juvenile development that characterize three spider species living on or near water: *Pirata piraticus, Pardosa fuscula, Tetragnatha extensa.* To provide fecundity and life history information for these species, I sought to determine: 1) reproductive output in terms of number of eggs per egg sac and number of egg sacs produced per female, 2) relationships between female size and fecundity, and 3) body size, number of instars, and generalized life cycles for *Pirata piraticus, Pardosa fuscula,* and *Tetragnatha extensa.* Fecundity data was also collected for *Dolomedes triton*, so reproductive output and relationships between female size and fecundity were also determined for this species.

## 3.2 Materials and Methods

### 3.2.1 Study sites and species descriptions

For the life history work, spiders were sampled at two permanent, freshwater ponds in central Alberta. Sivers Pond, which is near George Lake Field Station, was built in 1994 as a "borrow pit" during road construction, and a large area of continuous hardwood forest dominated by *Populus* trees begins 30-40 m from the pond's edge. Maruschak-8 is a Class III wetland that was restored in 1995. See Table 3.1 for location and descriptive details about both ponds.

*Pirata piraticus* (Clerck 1757), *Pardosa fuscula* (Thorell 1875), *Tetragnatha extensa* (Linnaeus 1758) and *Dolomedes triton* (Walckenaer 1837) are among the most abundant spiders found at the shores of ponds in central Alberta (Graham *et al.*, in press); other species, such as *Pachygnatha tristriata*, C. L. Koch 1845 and *Neoantistea magna*, (Keyserling 1887) frequent the area, but are encountered less often. *Pirata piraticus* is usually found near water (Wallace and Exline 1978, Dondale and Redner 1990, see Table 3.2). *Dolomedes triton* is also collected on or near ponds, lakes and streams throughout North America (Carico 1973).

*Pardosa fuscula* is found in a wide variety of moist habitats (see Table 3.2), and hence is common at the George Lake Field Station (Buddle 2000). According to Lowrie (1973), *Pardosa fuscula* is generally associated with wet areas at various elevations, and at the George Lake Field Station it was concentrated near the shores of several ponds (Graham *et al.* in press).

*Tetragnatha extensa* build their webs in meadows, bushes and long grass near water (Levi 1981). This species may be numerically dominant in some habitats (see Table 3.2). However, despite its abundance there is only scattered information about its life history in North America.

Juveniles of these three species are easily distinguishable in the field based on their habitat, size and coloration. *Pirata piraticus* has two pale lateral bands on its carapace, and a distinct V-shaped mark extending from the posterior eyes to the dorsal groove (Wallace and Exline 1978). In moist areas, immature *Pardosa fuscula* are easily spotted because of their relatively large size and pale lateral bands on the carapace (Dondale and Redner 1990). *Tetragnatha extensa* is a long-legged spider, and all life stages can be recognized by an elongate abdomen marked with a silver folium ringed in black (Levi 1980).

### 3.2.2 Spider sampling

A team of two people collected spiders at weekly intervals for four months during summer 2001. Two fences, constructed of small wooden stakes held together with rope, were placed around the perimeter of the ponds, 2 m and 4 m from shore, to establish 12 large quadrats for sampling (Figure 3.1). Previous studies have shown that the semi-aquatic spider community occurs within discrete boundaries (Zimmermann and Spence 1992, Graham *et al.* in press), and in this way it may be partitioned from the grassland community and sampled exclusively. Sampling consisted of searching below knee level, on hands and knees, and examining grass, shoreline vegetation, and overhanging vegetation for spiders. Spiders were collected by hand using plastic film vials.

### 3.2.3 Life history

Live-collected spiders were sorted to identify and sex the three species of interest. Juvenile spiders were preserved in 70% ethanol before they were measured. Other spiders brought back to the laboratory were held and released during the next visit to the site of their capture. Since the three species of interest were quite distinctive in appearance, even as juveniles, we were able to visually separate them from similar looking species in the same genera during hand collecting and sorting.

To estimate the number and length of instars for each species, the carapace width/length of the left tibia on leg I of juvenile spiders were measured using a dissecting microscope and ocular micrometer at 12X. For many species, leg measurements provide a much clearer separation of consecutive instars than cephalothoracic measurements, which tend to overlap between instars (Toft 1976, Aiken and Coyle 2000).

### 3.2.4 Fecundity

Female *Pirata piraticus* and *Pardosa fuscula* that were carrying egg sacs on their spinnerets or that had swollen abdomens and appeared ready to produce egg sacs were transferred to opaque plastic film cans with moistened Plaster of Paris ™. They were held individually at constant conditions (22°C and 16L:8D) and reared without food until they produced egg sacs. Early season egg sacs were taken from females collected in the field so that clutch size, *i.e.,* number of eggs per egg sac, could be determined by counting.

Many *Pardosa* species produce multiple egg sacs in one snow-free season (Buddle 2000), but this has not been confirmed for *Pardosa fuscula* or *Pirata piraticus*. Females of *P. piraticus* and *P. fuscula* whose egg sacs were removed were marked with brightly colored model paints, one dot placed at the center of the carapace, and released in the same quadrat they were collected. If marked *Pirata piraticus* or *P. fuscula* were recaptured with egg sacs, we concluded that they had produced a second egg sac in the interim.

*Tetragnatha* species deposit egg cocoons on leaves or other vegetation (LeSar and Unzicker 1978). We tried to collect egg cocoons that had a female *T. extensa* nearby, guarding the eggs. Large, mated female *T. extensa* were also collected, and isolated in vials with Plaster of Paris ™ so egg sacs could be produced in the laboratory and kept to determine fecundity.

Adult female *Dolomedes triton* that were carrying egg sacs in their chelicerae were caught on an opportunistic basis at a variety of aquatic environments (ponds) across central Alberta. Spiders were collected by J. Spence and associates over seven consecutive summers between 1987 and 1993, and by Alice Graham and associates in 2001. Pond locations for each year of collection are shown in Table 3.3, and data are available for Gate and Experiment Ponds at George Lake Field Station each year between 1987 and 1993.

To assess relationships between female size and clutch size, adult females of the three species that had produced egg sacs were measured for carapace width. Carapace width, or the distance across the widest part of a spider's cephalothorax, is a good indicator of adult spider size (Hagstum 1971). Individual egg weight was determined by removing the egg mass from the silken sac, weighing the two separately on a Cahn ™ Electrobalance, and dividing the egg mass by clutch size (Zimmerman and Spence 1992).

In 2001, adult female *D. triton* and their egg sacs were reared in large glass jars with water and aquatic grasses at 22°C and 16L:8D until their eggs hatched. After hatch, spiderlings were used in ballooning experiments described in Chapter 4, and then counted and released. Carapace width of females was determined after they died. For methods detailing egg sac rearing and cephalothoracic measurements of female *D. triton* collected between 1987 and 1993, see Zimmermann and Spence (1992, 1998).

### 3.2.5 Data Analyses

Regression analyses were used to assess relationships between female size (carapace width) and clutch size (number of eggs) for each species, as well as between female size, clutch size and mean egg weight for *P. piraticus*. ANCOVAs were executed to examine the influence of carapace width on clutch sizes of the lycosids, and *Dolomedes triton*. Frequency distribution histograms were generated for size (CW and tibia I length) of immature spiders collected. These histograms revealed the phenology of each species through the spring, summer and fall, and the total number of instars for each species, as well as generation time. All data analyses were done in SYSTAT 9.0 (REF?).

## 3.3 Results

### 3.3.1 Fecundity

*Pardosa fuscula* was larger-bodied than *Pirata piraticus*, both in terms of carapace width (Table 3.4) and tibia I length; *P. fuscula* had a mean (+/- SD) tibia I length of 2.07 +/- 0.03 mm, while *P. piraticus* had a mean tbia I length of 1.68 +/- 0.01 mm. *Pardosa fuscula* tended to have larger clutches of eggs than *P. piraticus* (Table 3.4), although the mean clutch sizes per female were not significantly different for these two species ($t= 0.241$, $p>0.05$).

Although several dozen large female *Tetragnatha extensa* were collected and reared in a laboratory environment, only a few produced egg sacs in late June and early July. Female *T. extensa* had the smallest average CW of our four wetland species, and produced about 65 eggs per clutch, although clutch size was quite variable (Table 3.4).

*Dolomedes triton* was the largest and most fecund of the four species; females produced nearly 400 eggs per clutch on average (Table 3.4).

To examine effects of CW on clutch size, an ANCOVA was done using all females of both lycosid species. Carapace width was used as the covariate because tibia I length was not significantly related to fecundity for *P. fuscula*. The covariate was significant ($n=196$, $F_{1,192}=32.9$, $P<0.0001$). The slopes of the regression lines for the two lycosid species were not significantly different from each other (Figure 3.2A).

*Dolomedes triton* showed a significant positive relationship between female size, as measured by carapace width, and clutch size using linear regression (Figure 3.2B). The $R^2$value was relatively high, indicating that ~35% of the variation in clutch size was explained by female size.

Fecundity of *Dolomedes triton* varied markedly by year at George Lake (Figure 3.3a), and among other sites (Figure 3.3b). Both one-factor ANOVAs examining effects of year on fecundity were significant (Figure 3.3), which suggests that clutch sizes of *D. triton* vary with changing conditions each year. In 1989, *D. triton* fecundity was much higher at other sites than at George Lake, and from 1990 to 1993 fecundity of *D. triton* was considerably higher at George Lake than at the other sites studied (Figure 3.3). In addition, an ANCOVA was done using clutch sizes of female *Dolomedes triton* collected at George Lake Field Station from 1987 to 1993, and using CW as the covariate. The covariate was significant (n=149, F=69.0, $p<0.0001$), but the regression slopes for each year were not significantly different from each other.

In contrast, egg masses of *P. piraticus* did not vary in a predictable way. Size (CW) of female *P. piraticus* did not significantly affect mean egg mass ($R^2$=0.09, $p>0.05$), and there was no significant negative effect of clutch size on mean egg weight (R =0.02, $p>0.05$). Thus, there was no apparent trade-off between egg number and egg size for this species. There was not enough data to do a similar analysis for *P. fuscula* (n=6).

### 3.3.2 Life history: A) Juvenile phenology and population dynamics

I estimated the number of instars and general life cycles for the three wetland species based on size-frequency histograms, and literature available on life histories of related species or genera.

I graphically analysed immature *P. piraticus* of unknown sex with penultimate stage males and females over four separate time periods. The distribution of carapace widths of immature *P. piraticus* of unknown sex revealed about five peaks in the graph, each of which could be considered an instar (Figure 3.4). Each 'instar' therefore encompassed a range of about 0.4mm in size, although this range was probably smaller in the earlier instars.

In May, the penultimate stages were dominant, and most frequently collected, so it is likely that this was the overwintering stage. The first adults were observed near the end of May. In June and July, more immatures of undetermined sex were present in field collections than subadults (Figure 3.4). In August, however, subadults of both sexes were much more frequently encountered, although immatures of undetermined sex were still present. Thus, it is likely that there is one cohort of immatures produced each summer and most of these are able to develop to the subadult stage by September, when ambient temperatures drop and spiders must prepare to overwinter.

Frequency histograms of immature unknown *Pardosa fuscula* suggest a life history somewhat different to that observed for *Pirata piraticus* (Figure 3.5). These two species have virtually identical size ranges for immatures of unknown sex; *P. piraticus*: 0.41mm- 2.33mm, range of 1.92mm, *P. fuscula*: 0.75mm- 2.66mm, range of 1.91mm. As for *P. piraticus*, data suggest that there are about five post-emergent instars (instars living outside the egg sacs) of *P. fuscula* in central Alberta between May and August (Figure 3.5). Adult

*P. fuscula* were present at the beginning of May 2001, when we began our sampling, but it seems likely that there are two cohorts or groups of juveniles present during spring and summer (Figure 3.5). It is likely that some *P. fuscula* overwintered as young immatures in their first year of development and the rest as subadults during their second year of development. Also, no adult male *P. fuscula* were collected after mid-July, so males of this species are probably short-lived, and die soon after mating.

Unlike the two species of wolf spider, sizes of immature *Tetragnatha extensa* of unknown sex were not normally distributed, and instead were randomly distributed over a wide range of tibia I lengths (Figure 3.6). Tibia I lengths are a better estimate of size for this species because they are long spiders with narrow carapaces and extremely long legs. Thus, carapace width measurements tend to overlap and fall within a narrow range, which may not represent intraspecific variability in size. During spring, immatures of undetermined sex dominated field collections of this species (Figure 3.6). Large numbers of juveniles were still present during early and late summer, but we did not collect many penultimate stage males and females at any one time. In fact, no penultimate adults were collected after the end of July (Figure 3.6).

### 3.3.2 Life History: B) Adult population dynamics

Male and female *P. piraticus* were most active in mid-June and early July, although the first adults were observed at the end of May 2001. The first female carrying an egg sac was collected at Sivers Pond on 12 June 2001, but the first egg sac we saw was produced in the lab on 06 June 2001 by a large, gravid female that was collected the day before. The reproductive period was lengthy, as females were collected with egg sacs on 28 August 2001, our last sampling date.

Adult females that had produced egg sacs were marked and released approximately once per week between 26 June and 14 August 2001. Although several dozen marked female *P. piraticus* were recaptured during this time, none were recaptured with egg sacs, so apparently they did not produce a second egg sac later in the summer

Adults of *P. fuscula* were collected all summer, even at the beginning of May, although they were most common in June and early July. Females with egg sacs were collected from the end of May until our last sampling date in late August 2001. Two females of *P. fuscula* that had produced one egg sac and were subsequently marked and released were recaptured with egg sacs; and thus at least two egg sacs may be produced in one snow-free season. However, clutch sizes of both females recaptured with egg sacs (43 and 40 eggs) were smaller than the average for first egg sacs of *P. fuscula* in 2001 (see Table 3.4).

The first adult *Tetragnatha extensa* were observed at the beginning of June, and adult females were collected until the end of August 2001. Females began producing egg sacs in late June, and were likely still producing them in late August, because we noticed them in field collections, and they are known to die soon after egg sac production (Foelix 1996). No adult males of *T. extensa* were collected after the first week of August, so they probably died shortly after mating.

## 3.4 Discussion

### 3.4.1 Fecundity

Generally, clutch size increases with female body size within and across spider taxa (Enders 1976, Wise 1993, Marshall and Gittleman 1994, Simpson 1995). This is certainly true for the three species considered here, but the relationship was more sharply increasing for *D. triton*. *Pirata piraticus* females were the smallest of the three spider species, and, on average, they produced the fewest eggs. Females of *Pardosa fuscula* were slightly larger and produced more eggs. Females of *D. triton* were much larger still and had disproportionately large clutches of several hundred eggs.

The relatively low coefficient of variation for CW measurements suggested little variation in sizes of adult *Pardosa fuscula* and *Pirata piraticus* in central Alberta (Table 3.4). However, females of both species were somewhat larger than the averages previously reported for Canada. Dondale and Redner (1987, 1990) reported the average CW for *Pirata piraticus* and *Pardosa fuscula*, respectively, as 2.13 +/- 0.23 mm and 2.67 +/- 0.22 mm. On average, the carapaces of Alberta spiders were several tenths of a millimeter wider for both species. A similar trend was noticed when *Pardosa mackenziana* and *Pardosa moesta* were collected and measured at George Lake; these specimens were substantially larger than the national average (Buddle 2000). As far as we know, there have been no published measurements of tibia I length for lycosids, so we have no studies with which to compare our data.

Although there is some information for related species, we know of no other studies that have investigated clutch size for *Pirata piraticus*. *Pirata sedentarius,* which is about 0.3mm larger than *P. piraticus* (average CW), produced 10 more eggs per clutch (Whitcomb 1967). *Pirata minutus*, as its name suggests, is a tiny spider whose adult carapace is less than 1mm wide. This small spider produced only 24 eggs per clutch (Dondale 1977), which is much fewer than observed for *P. piraticus*. *Pirata subpiraticus* (CW 2.0 mm) is slightly smaller than *P. piraticus* (Table 3.4), and egg sacs contained slightly more eggs on average (Hamamura 1971).

A positive relationship exists between female size and clutch size for 14 species of *Pardosa,* and female size of each species accounts for almost two thirds of the variation in clutch size (Buddle 2000). Size and fecundity data for *P. fuscula* fell within the 95% confidence limits of the linear regression of 14 *Pardosa* species.

Since the $R^2$ value for the ANCOVA examining female size and fecundity was relatively high ($R^2$=0.195), size accounted for some of the variation in fecundity observed for *P. fuscula* and *P. piraticus*. Other factors may have contributed to variation in spider fecundity as well. The George Lake area received 50% of the average expected precipitation during winter 2000 and spring 2001 (Environment Canada 2001), and this may have affected the spiders' ability to produce large clutches of eggs, or consistent clutch sizes. Also, food supply is known to determine clutch size and number in spiders (Enders 1976, Eberhard 1979, Briceno 1987, Anderson 1990). Spence *et al.* (1996) showed that food limitation and individual condition of female *D. triton* can drastically affect reproductive output, especially of larger females.

Therefore, clutch size of lycosids and pisaurids is dependent on a number of factors, including female size, female health as determined by food supply and foraging ability, climate, and habitat type. Spiders that were unable to capture prey or had less food available to them, perhaps because of deficiencies in their habitats, may have been limited in the number of eggs they could produce (Shine 1988).

*Dolomedes triton* is a robust spider, and the largest collected regularly in Alberta (Dondale and Redner 1990, Zimmermann and Spence 1989, 1992). Therefore it is not surprising that females of *D. triton* are able to produce such large clutches of eggs, and up to three clutches in a season (Zimmerman and Spence 1998). Spence *et al.* (1996) observed that reproductive output of larger female *D. triton* was significantly higher than that of smaller females. Fecundity data from female *D. triton* over seven different years showed a significant positive relationship between female size and number of eggs produced per sac. Over 35% of the variation in fecundity was explained by female size, so, as with *P. piraticus* and *P. fuscula*, other factors beside female size contributed to variation in *D. triton* fecundity.

I also observed that average fecundity of *D. triton* varied by year of collection at George Lake and other sites. Low fecundity at George Lake tended to coincide with locally dry years, as was the case in 1988, 1989 and 2001. In 1987, females were larger and quite fecund, and after extreme drought in central Alberta the following year, juvenile growth was depressed and females were about half as fecund (Spence *et al.* 1996). 2001 was also a dry year (Environment Canada 2001) and fecundity was lower than that of all other years except 1988. Differences in fecundity each year are probably due to site and climate differences, as well as a number of other factors, including female size and food availability. At other sites, fecundity was lowest in 1991, and that year spiders were collected predominantly in southern Alberta. In general, southern Alberta has a drier climate than central Alberta, and this may have been a factor in the low *D. triton* fecundity there.

There is no apparent size-number trade-off in spiders so that egg size remains generally constant with clutch size (Marshall and Gittleman 1994). Our results support this conclusion for lycosids since clutch size had no effect on mean egg weight for either species. Spence *et al.* (1996), however, found a significant negative effect of clutch size on mean egg weight for *Dolomedes triton,* and apparently this species is able to maintain large clutches by producing smaller eggs. In general, spiders do not show a size-number trade off with offspring, and females of most species tend to lay as many eggs as possible, given that a minimum egg mass and maximum clutch mass exist (Marshall and Gittleman 1994).

### 3.4.2 Life history

There is a confusing array of spiders of different sizes present at any given time of year, so it is difficult to determine the number and duration of instars for spider species from field collections alone. Since spiderlings hatch at different times over the summer, instar number and adult body size can vary greatly, even within the same species (Dondale 1961).

It seems that we collected five-six instars of *P. piraticus* from May to August, which is in keeping with the number of instars typically seen in one snow-free season for other wolf spider species (Edgar 1972). In addition, I think that *P. piraticus* has a one-year life cycle because distributions of juvenile carapace widths over summer 2001 were consistently unimodal (Figure 3.4). If this species had a two-year life cycle, two distinct size groups would be noticeable in the size-frequency histograms, *i.e.*, distributions would be bimodal (Edgar 1971, 1972).

A substantial number of female *P. piraticus* with egg sacs and immatures of unknown sex were collected at the end of August 2001. These immature spiders and those hatching from late egg sacs would be at a disadvantage for efficient growth and development because ambient temperatures would begin to get cooler relatively soon after hatch. In Ontario, however, eggs of *Pirata minutus* hatch at the same time as those of *P. piraticus*, and females were seen carrying egg sacs as late as October (Dondale 1977). Immatures collected in autumn were likely penultimate adults, which indicated that juveniles reached the penultimate stage after only a few weeks of life and the species has an annual life cycle (Dondale 1977). I suggest that the life cycle of *P. piraticus* in Alberta is as follows: spiderlings hatch between June and September, mid-late instars overwinter, immatures grow to subadults the following spring and subsequently develop into adults and mate during the summer.

We found no evidence that female *P. piraticus* produced more than one egg sac during the summer. However, because some females still carried egg sacs at the end of August; it is possible that this species produces two egg sacs per summer. In Arkansas, female *Pirata sedentarius* produce an average of 2.5 clutches in a lifetime (Whitcomb 1967), which means they are substantially more fecund than *P. piraticus*. In addition, female *Pirata subpiraticus* produced up to three egg sacs when reared under laboratory conditions in Japan (Hamamura 1971).

In general, species of *Pardosa* live for only one year, except in northern Canada where some species may require an additional year for development (Gertsch 1949, Schmoller 1970). It seems reasonable to suggest that most *Pardosa* species overwinter as sub-adults, and mature and mate in late spring (Vlijm and Kessler-Geschiere 1967, Dondale 1977, Buddle 2000). Females carry egg sacs from June to August, and spiderlings from early season egg sacs hatch and undergo a variable number of instars in a given summer (Edgar 1971). In Canada, *P. fuscula* egg sacs have been collected from June to September (Dondale and Redner 1987), so it is likely that spiderlings hatching in September overwinter as early instars and complete development after they have overwintered a second time as subadults. According to our size-frequency histograms for *P. fuscula*, there was one large cohort of young juveniles and a second smaller cohort of larger juveniles present during our sampling period (Figure 3.5). Therefore, *P. fuscula* probably has a biennial life cycle. I suggest that the life cycle for *P. fuscula* in Alberta is as follows: spiderlings hatch between May and September, early season spiderlings overwinter as mid-instars, and late season ones as early instars, then immatures develop to the subadult stage by the next autumn, overwinter again, and complete development and mate the following spring.

Life cycles of *P. piraticus* may be shorter than those of *P. fuscula* because the former is a smaller spider, and also because the two occupy different microhabitats in wetland ecosystems. *Pirata piraticus* is frequently collected on aquatic macrophytes, including wet stems of *Sphagnum* mosses, on bare areas at pond shores, and is even encountered skating across the water surface and diving underneath the water surface in search of aquatic prey (A. Graham, personal observation).

Although female *P. piraticus* with egg sacs prefer to remain along pond shores and expose their egg sacs to the sun (Nørgaard 1951), they were also observed diving underneath the water whilst carrying egg sacs. This set of microclimatic conditions may be less stable and support fewer prey items than the moist areas frequented by *P. fuscula*, which does not often venture onto the water surface. Perhaps *P. fuscula* has a wider range of areas in which it can overwinter, so conditions permit a longer development time than for *P. piraticus*.

Size frequency histograms of immature *T. extensa* of unknown sex indicate a non-normal size distribution, unlike that of *P. piraticus*. I suggest that there were about six instars collected at our ponds during summer 2001, and this may not include the penultimate stage, since few of these were observed in August (see Figure 3.6).

In central Illinois, *Tetragnatha laboriosa* undergoes nine instars, including the adult stage (LeSar and Unzicker 1978). Field collections of *T. straminea* in North Carolina revealed an annual life cycle with six post-emergent instars (Aiken and Coyle 2000), while laboratory reared *T. laboriosa* had eight post–emergent instars (LeSar and Unzicker 1978). In Denmark, *T. extensa* exhibited an annual life cycle, where spiderlings grew rapidly to the mid-to-late juvenile stages by winter, and matured and mated the following spring and summer (Toft 1967). The study area in Denmark where the spiders were collected was at a latitude similar to that of Sivers Pond at George Lake Field Station, but with a milder, coastal climate (Zimmermann and Spence 1998). Therefore it is likely that our central Alberta populations of *T. extensa* have an annual life cycle, especially since the first adults were observed at the end of June 2001, and mid-to-late instars were present in late August 2001.

Other studies examining north temperate *Tetragnatha* species have determined that these spiders have annual life cycles, and this may be the norm for the entire genus (Toft 1976, LeSar and Unzicker 1978, Aiken and Coyle 2000). In southern France, however, *Tetragnatha* species grow rapidly and have two generations per year (Juberthie 1954).

We now have basic information about the total development time for *P. piraticus*, *P. fuscula* and *T. extensa*. In addition, estimates of instar number were determined from spiders collected in the field, and these allowed us to piece together the life histories and phenology for each species. However, laboratory rearing experiments are necessary to supplement life history information gathered from field collections of wetland spider species, and obtain comprehensive estimates of instar number and size.

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Table 3.1. Location and descriptive information for ponds at which juvenile and adult spiders were collected during summer 2001.

| **Wetland** | **Location** | **Latitude/ Longitude** | **Year built/ restored** | **Basin size** | **Maximum depth** | **Vegetation** |
|---|---|---|---|---|---|---|
| Sivers | 83 km NW of Edmonton | 53°57'N, 114°06'W | 1994 | 75m x 30m | >1m | grazing grasses, short shrubs |
| Maruschak-8 | 5.8 km SW of Hay Lakes | 53°08'N, 113°06'W | 1995 | 28m x 15m | <1m | slough grass, cattails |

Table 3.2. Habitat, distribution and published life history information for the four wetland spider species collected during 2001.

| Species | Usual habitats | Distribution | Published life history work (region) |
|---|---|---|---|
| *D. triton* | open water broken by plants; ponds, lakes, slow-moving streams | N. America | Zimmermann and Spence (1998), Alberta |
| *T. extensa* | wet meadows, aspen understory | N. America (circumboreal) | Toft (1976), Denmark |
| *P. fuscula* | fresh and saline marshes, bogs, meadows | N. America | None |
| *P. piraticus* | swamps, bogs, moist shores of lakes and streams | N. America, Europe, Asia | None |

Table 3.3. Location information for ponds at which female *Dolomedes triton* with egg sacs were collected during 1987-1993 and 2001.

| **Year** | **Site** | **Location** | **Latitude/Longitude** | **No. females collected** |
|---|---|---|---|---|
| **1987** | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 18 |
| 1987 | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 16 |
| 1987 | Ditch | Arvilla, Alta., 9.96 km NE GLFS | 53°59' N, 114°01' W | 1 |
| **1988** | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 9 |
| 1988 | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 1 |
| 1988 | Manola, Alberta | 6.64 km NW of GLFS | 54°05' N, 114°12' W | 1 |
| **1989** | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 22 |
| 1989 | Tomahawk | 1 km S Seba Beach, Alberta | 53°32' N, 114°44' W | 1 |
| 1989 | Alderflats | Alderflats, Alberta | 53°32' N, 114°44' W | 10 |
| 1989 | Modeste Creek | Rural Route #57 Crossing, B.C. | 53°15' N, 114°42' W | 6 |
| 1989 | Sion | 2.34 km SW GLFS | 53°56' N, 114°08' W | 5 |
| 1989 | Golden | 3 km E of Golden, B.C. | 51°18' N, 116°55' W | 2 |
| 1989 | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 12 |
| 1989 | Meadow Pond | George Lake Field Station | 53°57' N, 114°06' W | 3 |
| 1989 | Swan Hills | Swan Hills, Alberta | 54°43' N, 115°24' W | 7 |
| 1989 | Wagner Bog | Hwy 16X, 10km W of Edmonton | 53°31' N, 114°14' W | 5 |
| **1990** | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 12 |
| 1990 | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 9 |
| 1990 | Op Cresc | N of Riske Creek, B.C. | 51°58' N, 122°31' W | 7 |
| 1990 | Sunset | N of Riske Creek, B.C. | 51°58' N, 122°31' W | 5 |
| 1990 | CMR | N of Riske Creek, B.C. | 51°58' N, 122°31' W | 11 |
| **1991** | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 11 |
| 1991 | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 9 |
| 1991 | Nanton | Nanton, Alberta | 50°21' N, 113°45' W | 11 |
| **1992** | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 11 |
| 1992 | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 10 |
| 1992 | Swan Hills | Swan Hills, Alberta | 54°43' N, 115°24' W | 9 |
| **1993** | Experiment Pond | George Lake Field Station | 53°57' N, 114°06' W | 12 |
| 1993 | Gate Pond | George Lake Field Station | 53°57' N, 114°06' W | 6 |
| 1993 | Hinton | 10 km E Hinton Hwy 16 | 53°27' N, 117°28' W | 11 |
| **2001** | Meanook | Meanook Biological Station | 54°37' N, 113°21' W | 5 |
| 2001 | Sivers Pond | George Lake Field Station | 53°57' N, 114°06' W | 2 |
| 2001 | Swan Hills | 38.4 km N Swan Hills, Alberta | 55°03' N, 115°19' W | 4 |
| 2001 | Ditch | Arvilla, Alta., 9.96 km NE GLFS | 53°59' N, 114°01' W | 3 |

Table 3.4. Size and fecundity data for four wetland spider species.

| **Species** | **CW (mm)** | **CW (mm)** | **No. eggs** | | **Egg mass (g)** | **n** |
|---|---|---|---|---|---|---|
| | range | (mean +/- SE) | (mean +/- SE) | CV | (mean +/- SE) | |
| *Pirata piraticus* | 1.67-3.17 | 2.46 +/- 0.02 | 44.7 +/- 1.62 | 0.488 | 0.082 +/- 0.002 | 181 |
| *Pardosa fuscula* | 1.75-3.33 | 2.86 +/- 0.04 | 56.0 +/- 3.78 | 0.482 | 0.148 +/- 0.026 | 51 |
| *Dolomedes triton* | 4.40-7.38 | 5.92 +/- 0.03 | 387.5 +/- 8.37 | 0.352 | | 266 |
| *Tetragnatha extensa* | 1.17-1.83 | 1.46 +/- 0.03 | 64.6 +/- 13.9 | 0.568 | | 7 |

Figure 3.1. Quadrat design for hand collecting spiders at Sivers Pond and Maruschak-8 during summer 2001.

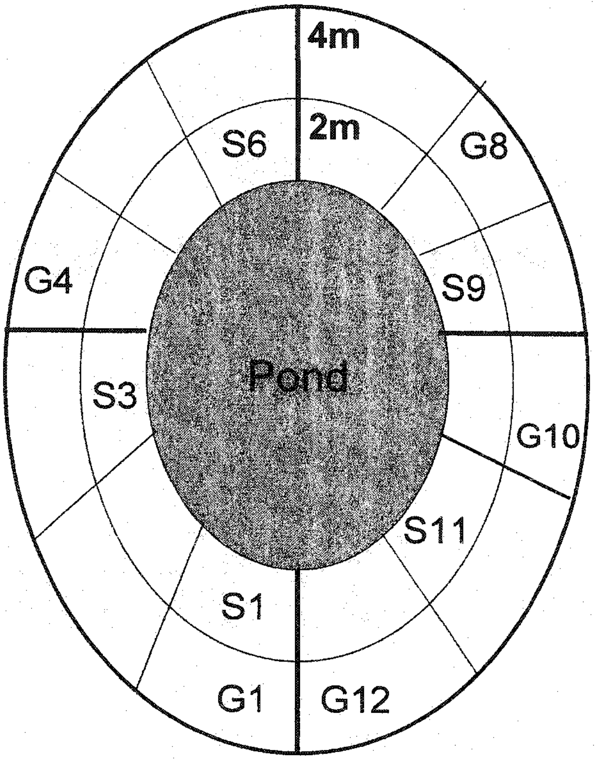


Figure 3.2. (A) ANCOVA for carapace width and fecundity of all females of *P. piraticus* (n=152) and *P. fuscula* (n=44). $F_{1,458}=224.6$, $p<0.0001$. (B) Linear regression of clutch size (number of spiderlings or eggs per egg sac) against carapace width (mm) for all females of *D. triton* (n=266).

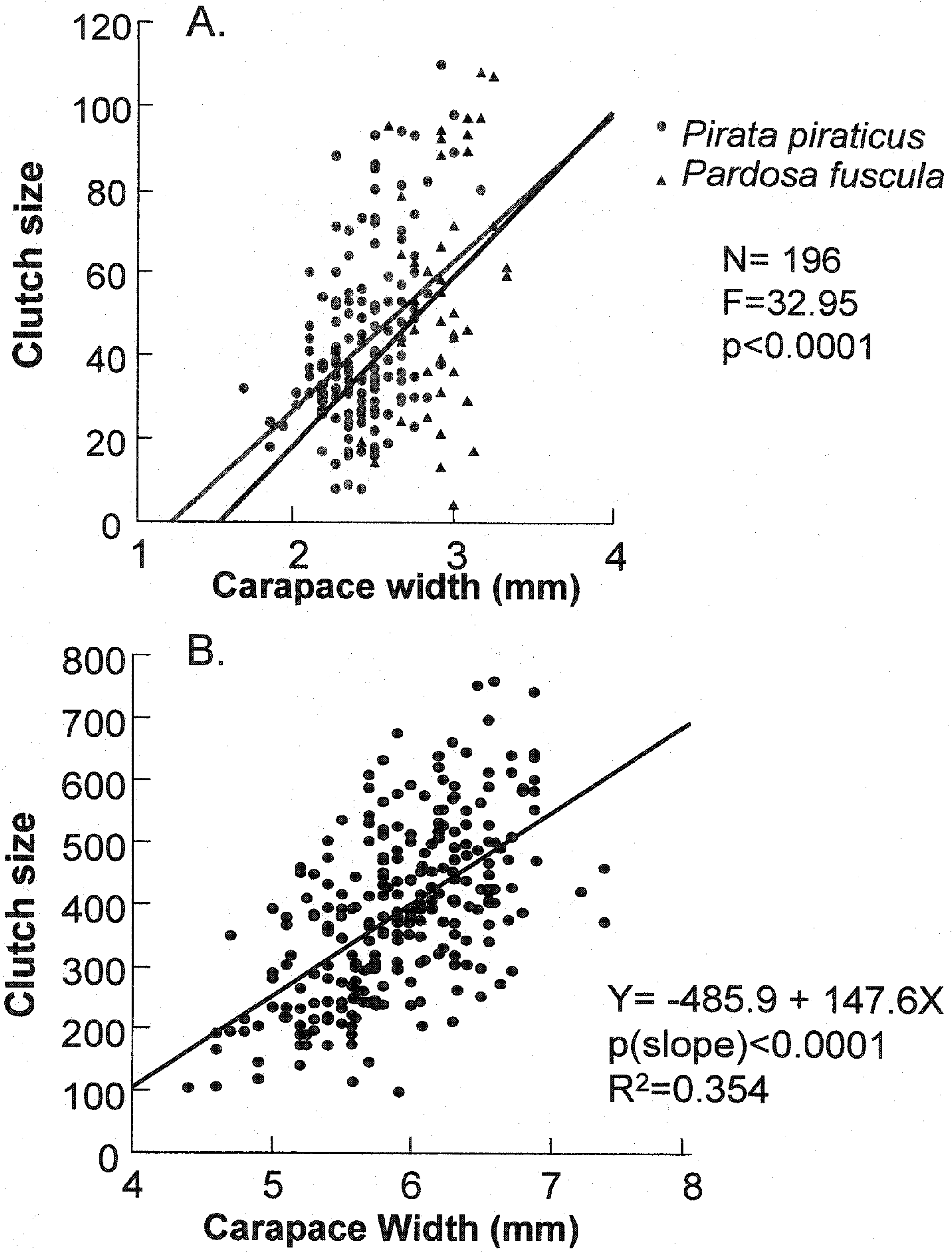
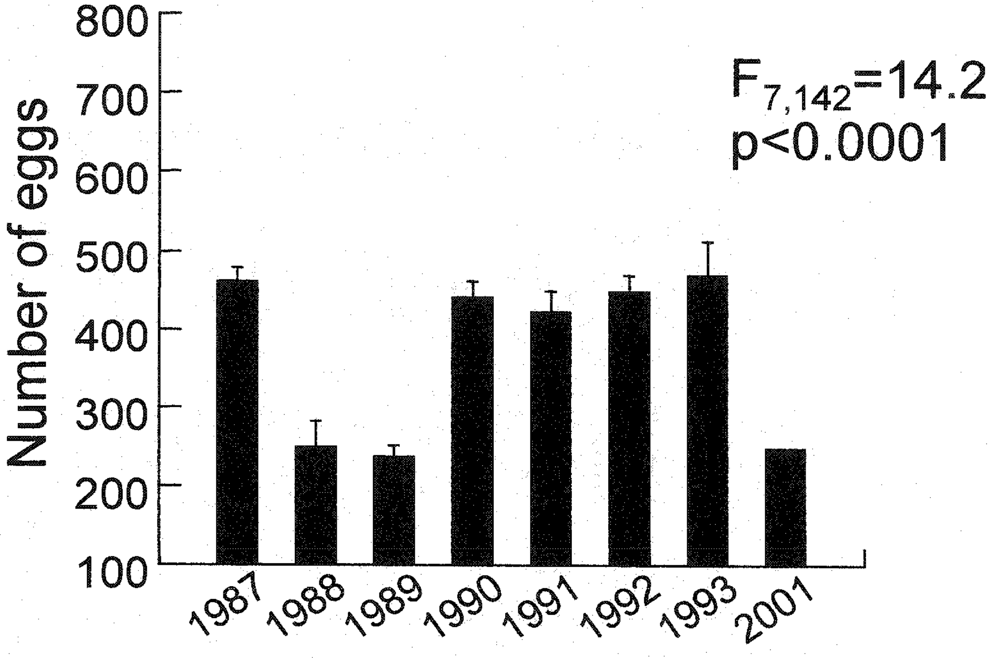


Figure 3.3. Differences in fecundity of *Dolomedes triton* by year for females collected at George Lake Field Station (A), and females collected from other sites in Alberta and British Columbia (B).

**A.** George Lake



**B.** Other sites (Alta. and B.C.)

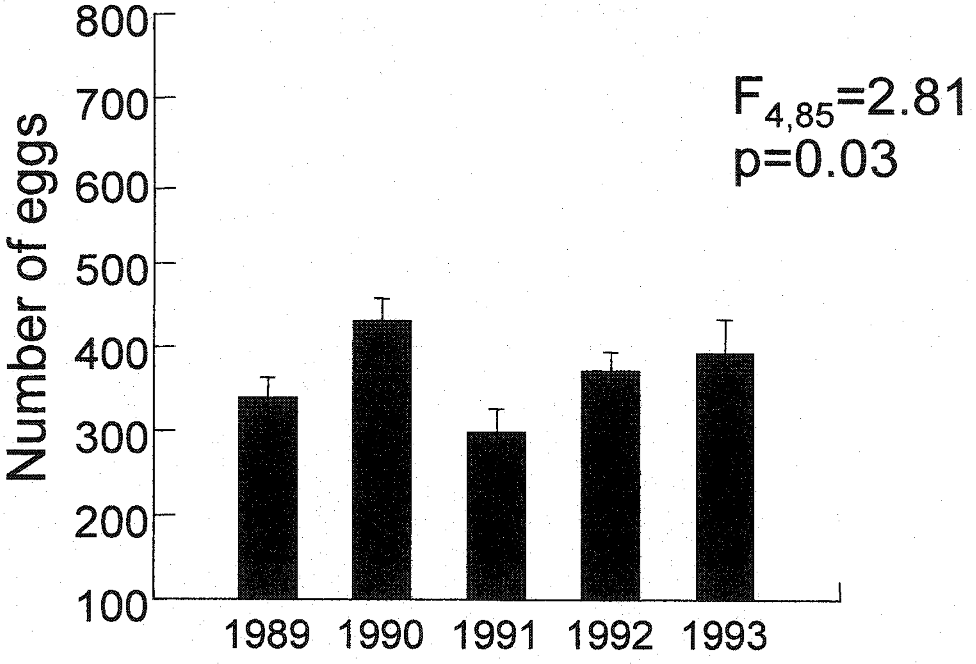


Figure 3.4. Size (CW) frequency distribution histograms of seasonal subsets of all 1366 immature *Pirata piraticus* individuals collected at the two wetland sites during 2001. Individuals too young to be sexed are graphed together using black bars, penultimate females are shown in grey, and penultimate males in white bars. Size ranges of adult males and females collected during each time period are indicated together using horizontal bars. A) 09- 31 May 2001, B) 05- 28 June 2001, C) 03- 31 July 2001 and D) 01- 28 August 2001.

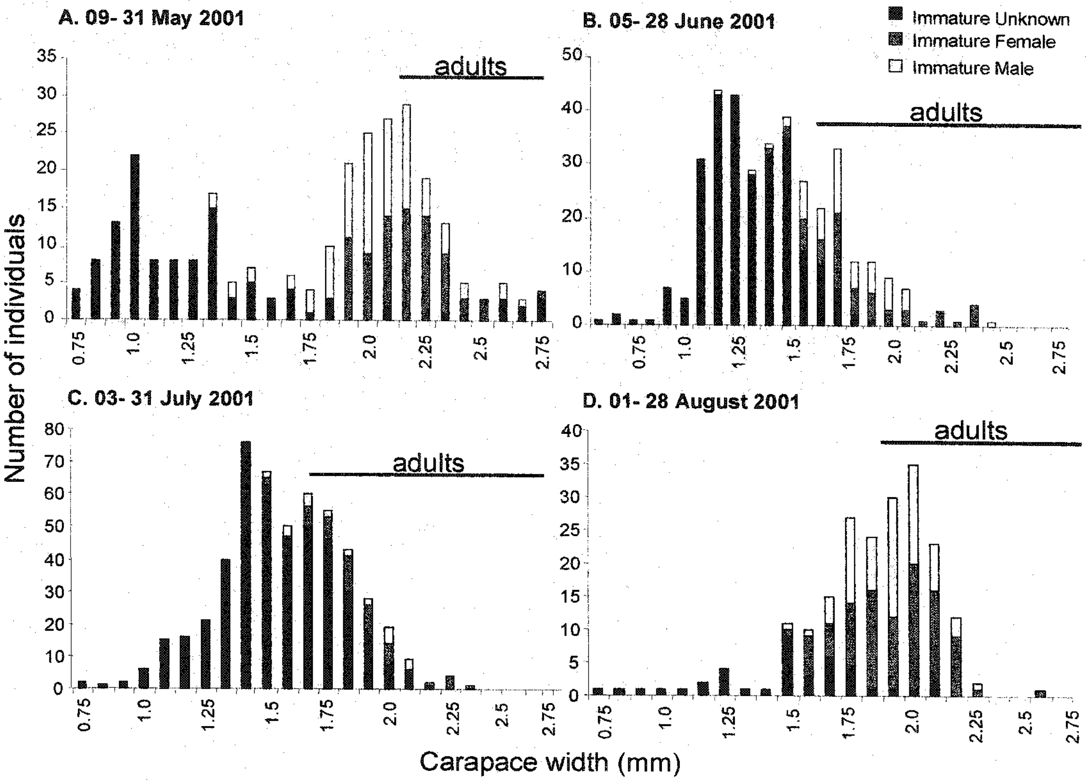


Figure 3.5. Size (CW) frequency distribution histograms of seasonal subsets of all 239 immature *Pardosa fuscula* individuals collected at the two wetland sites during 2001. Individuals too young to be sexed are graphed together using black bars, penultimate females are shown in grey, and penultimate males in white bars. Size ranges of adult males and females collected during each time period are indicated together using horizontal bars. A) 09 May- 14 June 2001, B) 19 June- 25 July 2001, and C) 26 July-28 August 2001.

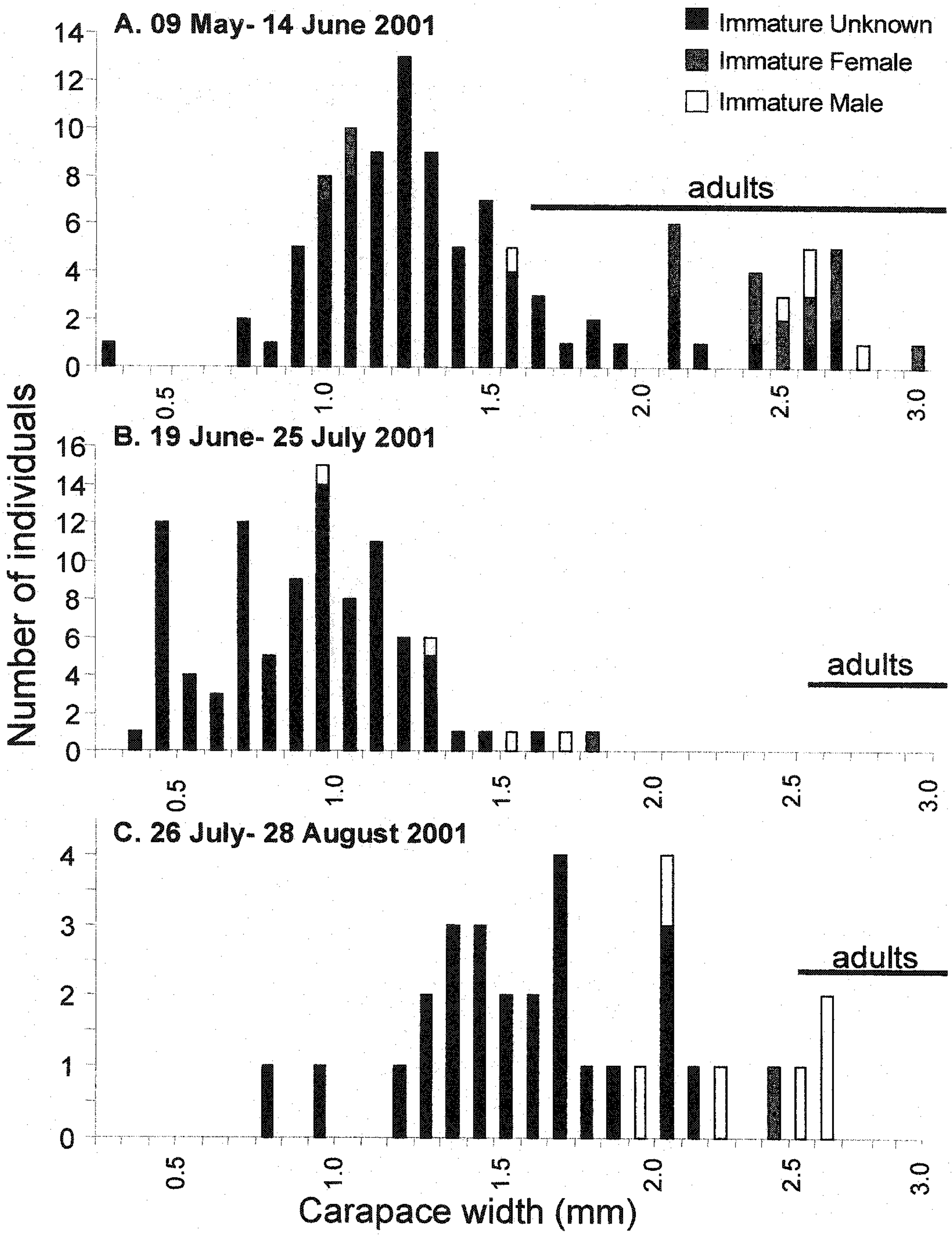
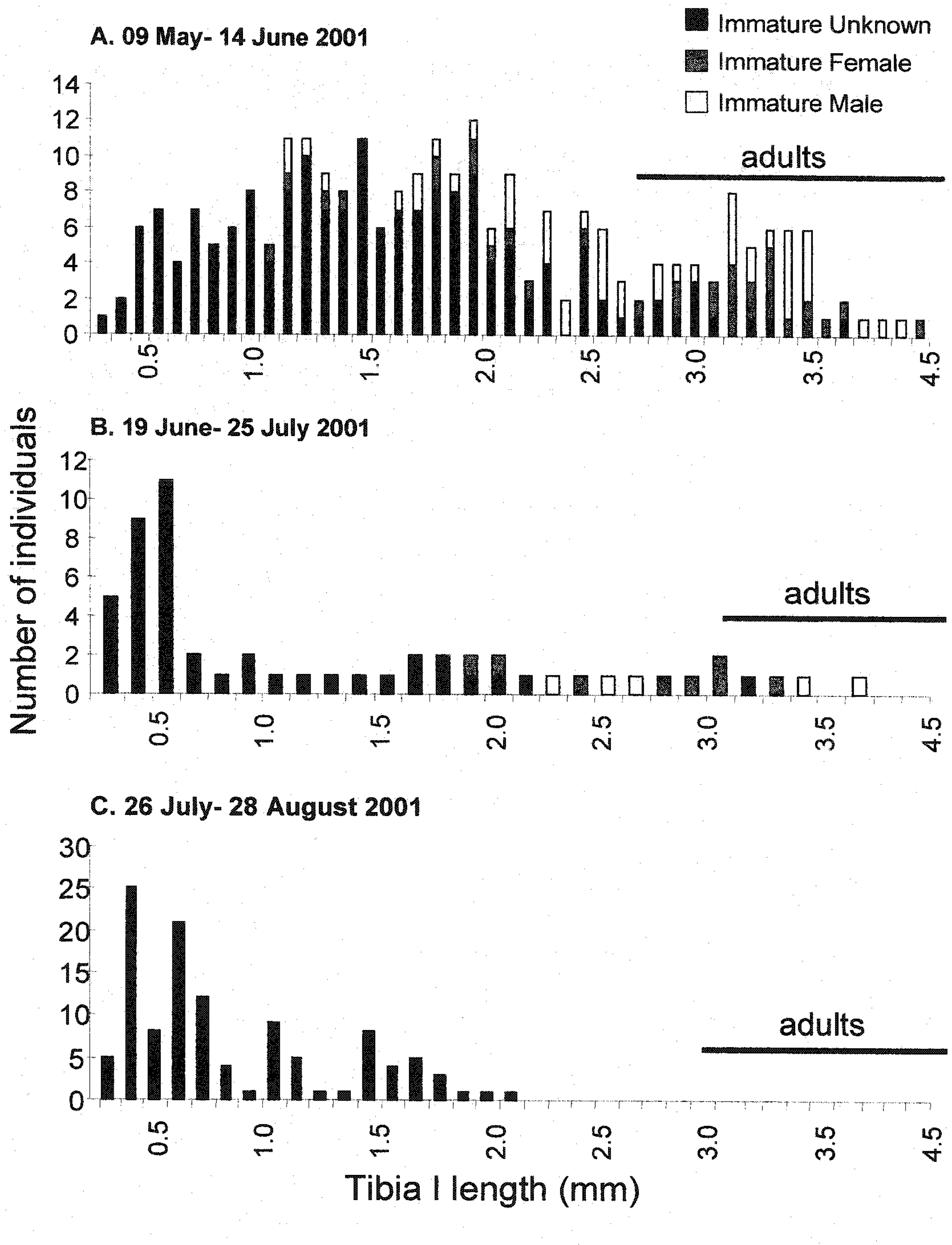


Figure 3.6. Size (tibia I length) frequency distribution histograms of seasonal subsets of all 425 immature *Tetragnatha extensa* individuals collected at the two wetland sites during 2001. Individuals too young to be sexed are graphed together using black bars, penultimate females are shown in grey, and penultimate males in white bars. Size ranges of adult males and females collected during each time period are indicated together using horizontal bars. A) 09 May- 14 June 2001, B) 19 June- 25 July 2001, and C) 26 July- 28 August 2001.



# 4. Mechanisms and Regulation of Ballooning in the Fishing Spider *Dolomedes triton* Walckenaer (Araneae: Pisauridae)

## 4.1 Introduction

The nursery web spider *Dolomedes triton* Walckenaer 1837 is a widespread species that is common along lakes, ponds and quiet areas of streams in North America (Carico 1973). Adults live at the water surface and are known for preying on insects such as water striders and whirligig beetles, and can occasionally subdue fish that outweigh them 4-5 times (Zimmerman and Spence 1989). *Dolomedes triton* has a biennial life cycle in central Alberta, and adult females carry their egg sacs for some time before suspending them in a tent-like web in which the spiderlings remain for several days post-hatch (Zimmermann and Spence 1998).

After moulting, spiderlings gradually disperse, some by "ballooning", *i.e.,* they ride on an exuded thread of silk that, if caught by the slightest air current, lifts the spider and carries it away from the natal habitat (Greenstone *et al.* 1985, Plagens 1986, Zimmermann and Spence 1992). In general, this passive dispersal mechanism seems to be employed shortly after juvenile spiders emerge from their egg sacs, and, in most cases, only juvenile spiders balloon because adults are too heavy (Decae 1987, Foelix 1996).

Changes in micro-climatic conditions are often thought to precipitate aerial dispersal, which serves as a way to travel long distances to more suitable habitats (Richter 1970). In fact, spiders associated with unstable habitats are known to invest heavily in aerial dispersal; for example, *Pardosa purbeckensis* F. O. P. Cambridge is an intertidal species that can survive for a limited time underwater, but young juveniles usually balloon to drier areas when their habitats become partially flooded (Richter 1970). Little is known about this method of dispersal in *D. triton*; however, preliminary observations suggest that it is associated with variation in quality of habitats (Spence *et al* 1996).

To assess ballooning behaviour in juvenile *D. triton*, we sought to determine: 1) if variation in temperature, humidity, and wind speed affect ballooning, 2) the average time between hatching and dispersal, and 3) the percentage of juveniles that disperse from the egg sac by means of ballooning.

## 4.2 Materials and Methods

A team of two people collected 12 *D. triton* females with egg sacs during summer 2001, from various ponds across central Alberta. Pond location information is given in Table 4.1. We used offspring of one female to develop our experimental design, and one of the other females died before her eggs hatched. Thus, altogether juveniles from 10 different mothers were available for experiments.

Females with egg sacs were kept in large jars containing water and aquatic plants in the laboratory at a controlled temperature (22°C) and high humidity until egg sacs were hung in nursery webs constructed inside the jars, and spiderlings hatched. Several (2-5) days after hatch, juveniles were separated into groups of ten, and groups were exposed to different temperatures and humidities before being tested for ballooning under three different wind speeds.

Three temperatures were used: 5°C, 21-22°C and 30°C in an attempt to represent the range of temperatures to which ballooning spiders would be exposed in the field. Spiderlings were exposed to each temperature treatment for one hour before they were transferred to the test apparatus. We chose one hour for the length of these treatments because many spiderlings left at either 5°C or 30°C overnight died. Light intensity, humidity, and wind velocity were kept constant while temperature was varied.

Humidity was manipulated as follows: groups of 10 spiderlings were kept in empty vials for the low humidity treatment (control), vials containing moistened Plaster of Paris ™ for the medium humidity treatment, and vials containing 2.5 mL of water for the high humidity treatment. Light intensity, temperature (21-22°C) and wind velocity were kept constant for all humidity treatments. Each humidity treatment lasted one evening, and spiderlings were tested on the ballooning apparatus the following day.

We used a hairdryer to manipulate the wind velocity to which spiderlings were exposed. Our hairdryer had two settings, which were used for the medium (0.35- 0.75 m/sec) and high (1.5-3 m/sec) wind velocities, respectively. The hairdryer was turned off for the no wind treatment. An animometer was used to determine wind velocity in front of the hairdryer and on top of the ballooning platform. For all three levels (low, medium and high) of each treatment (temperature, humidity and wind speed) we attempted to use three sets of 10 spiderlings.

Sets of 10 spiderlings were kept in plastic film containers during temperature or humidity treatments, and later brought to the apparatus that was established to measure ballooning. We enclosed a large area (1.9 m x 1.5 m) around the ballooning platform with cardboard so we could observe and catch any juveniles that ballooned from the platform, and flew a few meters into the air. Spiderlings had enough space to release silk draglines and balloon freely from the tower until they reached the ceiling or the boundaries of our enclosure. Vials containing spiderlings were placed atop the 40 cm platform inside a plastic container (9 cm diameter, 8 cm height) with a hole cut in the top, so the lip of the vial was even with the top of the platform (Figure 4.1). The hairdryer was positioned (40° angle, 90 cm from ballooning tower) and then taped to a scaffold so that the emitted wind current blew directly across the top of the platform. Each vial of ten juveniles was then exposed to air movement for 20 minutes at a time, except during the no wind treatment.

## 4.3 Results and Discussion

**4.3.1. Ballooning behaviour.**------Spiderlings that ballooned released silk from their spinnerets after thrusting their abdomens into the air and wiggling. After this, spiderlings caught the air current and flew at least 50 cm above the tower. Actual ballooning was distinguished from pre-ballooning behaviour, which involved crawling out of the vial and onto the tower, thrusting abdomens into the air and releasing silk from spinnerets in six or eight threads. Some spiderlings then stood on their front two pairs of legs and wiggled their abdomens around in an apparent effort to catch the wind current, but did not actually take flight.

We called the pre-flight sequence of events “tip-toe” behaviour (Richter 1970). Tip-toe behaviour always preceded ballooning, but some spiderlings exhibiting this behaviour remained on the tower for the entire 20 minute duration of the experiment. Spiderlings crawled out of the vial and onto the platform almost immediately after the hairdryer was turned on. Most of the spiderlings that ballooned did so within the first five minutes of the trials; those that spent ten or more minutes crawling around the platform possibly seeking an optimal place to take off rarely ballooned.

Altogether, 700 spiderlings from ten different mothers were tested, and nearly half of these (341) ballooned. Our results agree with those found for *Pardosa purbeckensis*, where approximately 50% of the young instars tested showed aeronautic behaviour in the laboratory (Richter 1970).

**4.3.2 Response to treatments.**-----We were able to compete temperature treatments on spiderlings from almost all of the mothers, but we obtained little data for humidity or wind speed treatments.

We discovered that more spiderlings flew if they were they were taken from nursery webs 3 or 4 days after hatch; very few flew if we waited only two days, or five days after hatch. In some cases 8, 9 or 10 of the spiderlings in one vial ballooned if they were three days old (Table 4.2). Although small, our data set suggests that the tendency of spiderlings of *D. triton* to balloon peaks about three days after hatching.

Temperature clearly affected spiderling ballooning frequency (Table 4.2). There was a significant difference in the mean number of ballooning spiderlings after exposure to low, medium and high temperatures (ANOVA: $F_{2, 24}=3.53$, p=0.04). Similar proportions of juveniles ballooned after exposure to low and medium temperatures, but more ballooning was exhibited by spiderlings exposed to high temperatures (Table 4.2).

Although we had little data for our humidity treatments, one group of spiderlings showed slightly more ballooning behaviour after exposure to low humidites (Table 4.2). Few juveniles came out of their vials during the high wind treatments (2-3 m/sec), and those that did venture out did not perform "tip-toe" behaviour, and instead crept around attempting to avoid the strong air current. In clear contrast, most juveniles were able to balloon using the medium wind speed (0.35-0.75 m/sec).

In general, aerial dispersal by spiders occurs on unusually warm, calm days during the summer, or on sunny days during autumn, winter and spring for the family Linyphiidae, which are able to disperse by ballooning as adults in response to unfavourable environmental conditions (Duffey 1956). Our results are similar to those found for other spider species, in particular for lycosids. Richter (1970) manipulated temperature, humidity and wind speed for early instars of eight species of *Pardosa*, and found that all of these species had a particular set of environmental conditions that elicited tip-toe behaviour. Generally speaking, Richter (1970) found that warm, dry air, and wind speeds of 0.35-1.70 m/sec facilitated aerial dispersal in all juvenile wolf spiders. Results from our ballooning experiment support the conclusion that warm temperatures (ca. 30°C), low humidities and medium wind speeds approach the optimal conditions for aerial dispersal in juvenile *D. triton*.

Our results and conclusions cannot be supported by extensive statistical analysis, so they should be considered as general observations about ballooning behaviour in *D. triton*. Ultimately, more detailed experiments with larger sample sizes are required to substantiate our observations, and unravel the mysteries of ballooning in *Dolomedes triton*.

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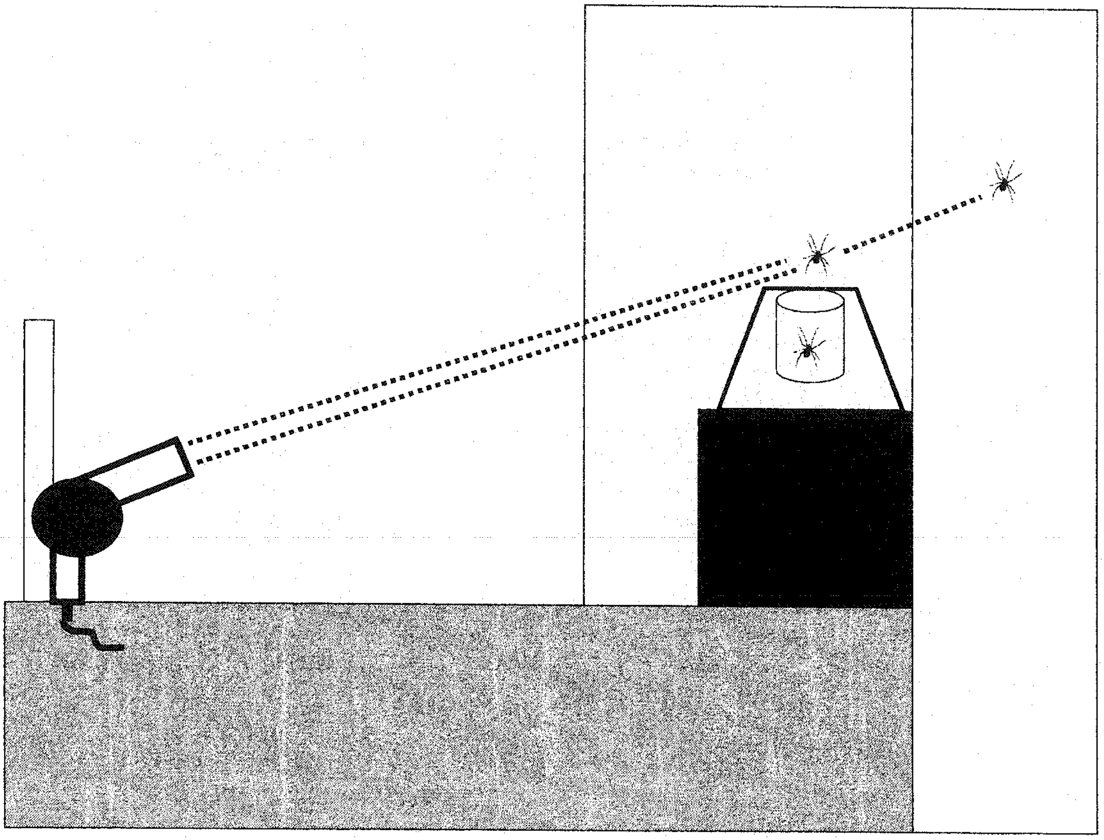
Table 4.1. Locations of ponds where female *Dolomedes triton* with egg sacs were collected during 2001.

| **Year** | **Date** | **Site** | **Location** | **Latitude/Longitude** | **No. females collected** |
|---|---|---|---|---|---|
| 2001 | 9-Jul | Meanook | Meanook Biological Station | 54°34' N, 113°19' W | 5 |
| 2001 | 1-Aug | Sivers Pond | George Lake Field Station | 53°57' N, 114°06' W | 1 |
| 2001 | 7-Aug | Ditch | Arvilla, Alta., 9.96 km NE GLFS | 53°59' N, 114°01' W | 2 |
| 2001 | 8-Aug | Swan Hills | 38.4 km N Swan Hills, Alberta | 55°03' N, 115°19' W | 4 |

Table 4.2. Proportion of *Dolomedes triton* spiderlings (1, 2 or 3 replicates of 10) that ballooned from a platform after exposure to various environmental conditions.

|  | **Days after** | **Temperature** |  |  | **Humidity** |  |  | **Wind speed** |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| **Mother** | **hatch** | HIGH | MED | LOW | HIGH | MED | LOW | HIGH | MED | NONE |
| Bernadette | 5 |  |  |  | 0.6 | 0.6 | 0.87 |  |  |  |
| Cassandra | 4 | 0.83 | 0.73 | 0.83 |  |  | 0.3 | 0 |  |  |
| Dita | 3 | 0.23 | 0.73 | 0.83 | 0.2 |  | 0.2 | 0.15 | 0.3 | 0.1 |
| Euphemia | 2 | 0.3 | 0.3 | 0.33 |  |  |  | 0.1 |  |  |
| Frances | 3 | 0.5 | 0 | 0 |  |  |  |  |  |  |
| Genevieve | 3 | 0.9 | 0.35 | 0.4 |  |  |  |  |  |  |
| Hella | 3 | 0.6 | 0.3 | 0.4 |  |  |  |  |  |  |
| Ingrid | 5 | 0.7 | 0 | 0.5 |  |  |  |  |  |  |
| Katharine | 3 | 0.8 | 0.2 | 0.5 |  |  |  |  |  |  |
| Lolita | 4 | 0.7 | 0.55 | 0.35 |  |  |  |  |  |  |
| AVERAGE | 3.5 | 0.58 | 0.45 | 0.52 | 0.4 | 0.6 | 0.46 | 0.08 | 0.3 | 0.1 |

Figure 4.1. Ballooning apparatus with tower, platform containing the plastic vial of spiderlings, and hairdryer used to initiate ballooning behaviour of juvenile *Dolomedes triton*.



# 5. Conclusions

## 5.1 Summary

Ultimately, three years of continuous work on a fairly small group of semi-aquatic spiders has yielded much information about diversity, ecology, and behaviour of these organisms. When this project began, no wetland spider communities from the Nearctic region had been described, but now Alberta's wetland spider fauna has been described for the prairie pothole region, and the reproductive biology of several constituent species has been examined. This thesis makes available species lists for both natural and restored wetlands and these will provide essential baseline data for future arthropod studies in the prairie pothole region. Therefore, these projects have expanded knowledge of the province's invertebrate diversity, and especially that of middle trophic levels in wetlands.

## 5.2 Spider diversity at natural and restored wetlands

Wetlands in their natural state are known to be optimal habitats for spiders, and to contain rich assemblages of species (Marc *et al.* 1999, A. Graham Chapter 2). Analyses of effects of wetland restoration on spider abundance and species richness indicate that there are consequences of wetland management for communities of ground-dwelling spiders. For example, natural prairie pothole wetlands harbored significantly more spider individuals and species than restored wetlands. I propose that differences in spider abundance and species richness between wetland types are due to developing vegetation cover and insect prey populations at restored wetlands, and spider colonization of restored wetlands. It is likely that drainage of wetlands induces migration of spiders to nearby undisturbed areas, and reflooding causes the inhabitants of the drained area to migrate to drier areas and be replaced by wetland spider colonists (Marc *et al* 1999).

Wolf spiders are often described as open habitat specialists (Lowrie 1973, Van Dyke and Lowrie 1975 , Dondale and Redner 1990, Buddle 2000). Lycosids were the most abundant family of spiders trapped at both wetland types, and although they were far less numerous at restored wetlands, they were the initial colonists of these areas. Thus, wolf spiders are sensitive to wetland management, and seem to respond to temporal changes in restored wetland habitats.

Comparison of natural communities with those at older restored areas indicated that spider communities can recover to an approximately natural state in terms of species richness after about five years. Spider diversity was greatest in prairie pothole wetlands 5 years post-restoration, and actually comparable to that at natural wetlands, but it was lower at wetlands 7 years post-restoration. Spider assemblages seven years after wetland restoration were less speciose than expected, and this may have been due to a decline in prey populations. This thesis prompts us to ponder some information about the course of invertebrate faunal succession in the first decade after wetland management, and these data will be of interest to managers, and critics who believe that restored wetlands will never be equivalent to natural wetlands in terms of animal and plant diversity (*e.g.* Smith and Tome 1992, Malakoff 1998).

It would be interesting to sample spiders in wetlands that are more than seven years post-restoration, and compare the fauna and species composition to that at natural wetlands, and seven year old wetlands. Such a comparison would give more complete information about spider succession at wetlands in the first decade after management activities.

We suggest that spiders are noticeably affected by wetland drainage and restoration, but that these disturbances do not destroy spider assemblages, they merely change them. Spiders are one of the first animal groups able to recognize and colonize new habitats such as wetlands (Plagens 1986, Wilson 1992, Weyman *et al.* 1995). They exhibit a typical succession of species as the newly restored wetlands age, and I predict that after a certain number of years the restored wetlands will become equal to natural wetlands in spider adundance and species composition. Some spiders are more particular than others about their habitat associations and requirements (Wise 1993), but essentially they are resilient creatures with short life cycles so many are able to tolerate unstable conditions and proliferate in habitats that are suboptimal. Spiders are polyphagous predators, and most do not have specialized diets so they can live anywhere there is an abundance of insect prey (Marc *et al.* 1999). Also, spiders require vegetation for web attachment sites and refugia, but may not be choosy about the plant cover or species present (Gillespie 1987).

Since there are important differences in spider abundance between natural and restored wetlands, there will be consequences of wetland management for animals that depend on spiders for food, and insect prey consumed by spiders. Studies have shown that wetland restoration negatively affects waterfowl health and diversity (Porter and van Kooten 1993, Taylor *et al.* 1993, Wandschneider 1993). Arthropods are an important food source for waterfowl (Murkin and Batt 1987) and the trophic interactions between these two groups in wetland ecosystems will have bottom-up effects on waterfowl.

Our results should be useful for assessment of current wetland management practices in Alberta. Until recently, wetlands were seen as wastelands, and only useful once converted into agricultural land (Wandschneider 1993). Now that their importance has been demonstrated and various organizations exist to protect them (*e.g.*, NAWMP, Ducks Unlimited Canada), wetland managers are aware of the consequences of restoration on ducks and amphibians. I have assessed the influence of wetland management on spiders, and in light of these analyses, I suggest that it is important for managers to see links between invertebrates and vertebrates and include these linkages in assessment of wetland restoration programs.

### 5.3 Life cycles and fecundity of wetland spiders

This research has provided new information about the life cycles and fecundity of four spider species characteristic of wetland habitats in Alberta's boreal ecosystem. In particular, I discovered that females of *Pirata piraticus* were somewhat less fecund than those of *Pardosa fuscula,* and that both species were markedly less fecund than *Dolomedes triton*. Data were not as extensive for *Tetragnatha extensa*, but there is still an indication of when egg sacs were produced and I provide several estimates of fecundity for this species. All species but *T. extensa* showed a significantly positive relationship between carapace width and clutch size, but other factors that vary annually, such as climate, may account for some of the variability in fecundity of these species.

Several patterns of fecundity and juvenile development characterize these four taxa that live in and around water. First, all are capable of producing many eggs, and, in some cases, multiple egg sacs in one summer (*e.g.*, *Pardosa fuscula* and *Dolomedes triton*). Also, moisture and complete submergence did not seem to adversely affect the egg sacs of these four species (A. Graham, personal observation). All spiders are capable of producing water-resistant silk for egg sac construction (Foelix 1996), but it is possible that these spiders use more of this silk, or a stickier type when constructing egg sacs that will be exposed to a semi-aquatic environment.

The two larger-bodied species, *Pardosa fuscula* and *Dolomedes triton* (see Zimmermann and Spence 1998), needed two full years to complete development. *Pardosa fuscula* adults were seen all summer, and females produced two egg sacs over the four month sampling period. Two size cohorts of *P. fuscula* juveniles of undetermined sex were observed from May to August 2001.

The two smaller-bodied species, *Pirata piraticus* and *Tetragnatha extensa*, had annual life cycles. *Pirata piraticus* adults appeared in late May, and females produced one egg sac over the summer: these were observed in early June through to August 2001. Approximately five juvenile instars were present from June to August, and these probably overwintered as penultimate adults. *Tetragnatha extensa* adults appeared in early June, and the first egg sacs were seen in the laboratory in mid-July. This species underwent an undetermined number of juvenile instars during 2001.

Certainly, these wetland spiders face challenges different than those of their upland relatives because their habitats are often transient, and much more island-like. Therefore, their reproductive biology and life cycles reflect these challenges, and are different than those of related terrestrial spiders since egg sacs can withstand submergence, and juveniles of some species balloon readily when habitats become unfavourable.

## 5.4 Ballooning behaviour of *Dolomedes triton*

My field studies of ballooning did not describe how spiders colonize newly available wetland habitats. These basic data still need to be gathered, especially since wetland spiders may be good subjects for developing metapopulation models to show how wetland restoration can most effectively contribute to conservation of wetland biotas.

Laboratory experiments involving regulation of ballooning in *Dolomedes triton*, however, were more useful in compiling behavioural data about aerial dispersal in spiders. We discovered that this species displayed “tip-toe” behaviour similar to that of some lycosids prior to ballooning, and that certain environmental conditions elicited actual ballooning. Juveniles that were several days post-hatch, and exposed to high temperatures, low humidites, and wind speeds of 0.35- 0.75 m/s showed the most ballooning behaviour, although juveniles only showed a clear effect of temperature in their ballooning frequency.

## 5.5 Final words

As we use knowledge gained from experiments with spiders and analyse their role as predators, prey, and indicators of disturbance in wetland ecosystems, we see wetlands in a larger picture, as components of landscapes that include upland, surface water and ground water (Johnson 1994). We are after improved understanding of the sources of disturbances to these spider assemblages, but also of potential solutions to maintaining their diversity, and hence the diversity of all animals affected by spider populations.

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Appendix I. Summary of spider species collected from a) live capture traps and b) floating traps at natural and restored wetlands. (65 species) * indicates the 8 most common species collected from live capture traps, and the 5 most common species collected from floating traps.

## a) Live capture traps

| | Traps at natural ponds (48 total) | Traps at restored ponds **(1999)** (24 total) | Traps at restored ponds **(1995)** (24 total) | Traps at restored ponds **(1993)** (24 total) | Total |
|---|---|---|---|---|---|
| **Agelenidae** | | | | | |
| *Agelenopsis utahana* (Chamberlin & Ivie 1933) | | | | 1 | 1 |
| **Amaurobiidae** | | | | | |
| *Cybaeopsis euopla* (Bishop and Crosby 1935) | 1 | 9 | | | 10 |
| immature | | | 1 | | 1 |
| **Araneidae** | | | | | |
| *Lariniodes cornutus* (Clerck 1757) | 1 | | | 1 | 2 |
| *Zygiella dispar* Kulzynskii 1885 | | | 1 | | 1 |
| immature | 1 | | 1 | | 2 |
| **Clubionidae** | | | | | |
| *Clubiona bryantae* Gertsch 1941 | 3 | | 4 | 3 | 10 |
| *Clubiona canadensis* Emerton 1890 | 2 | | | 1 | 3 |
| *Clubiona norvegica* Strand 1900 | 2 | 1 | | | 3 |
| immature | 1 | | 1 | | 2 |
| **Dictynidae** | | | | | |
| *Tricholathys dakota* Chamberlin & Gertsch 1958 | | | | 1 | 1 |
| **Gnaphosidae** | | | | | |
| *Drassyllus niger* (Banks 1896) | | | | 1 | 1 |
| *Gnaphosa borea* Kulczynski 1908 | | | | 2 | 2 |

| | | | | | |
|---|---|---|---|---|---|
| *Gnaphosa parvula* Banks 1896* | 39 | 2 | 74 | 51 | 166 |
| *Haplodrassus hiemalis* (Emerton 1909) | 1 | 1 | | | 2 |
| *Haplodrassus signifer* (C.L. Koch 1839) | 2 | | | 4 | 6 |
| *Zelotes fratris* Chamberlin 1920 | 3 | 1 | 3 | 1 | 8 |
| immature | 1 | | 5 | 4 | 10 |
| **Hahniidae** | | | | | |
| *Neoantistea magna* (Keyserling 1887)* | 53 | 23 | 54 | 51 | 181 |
| *Neoantistea* (immature) | 3 | | 5 | 8 | 16 |
| **Linyphiidae** | | | | | |
| *Bathyphantes gracilis* (Blackwall 1841) | 4 | 3 | | 1 | 8 |
| *Bathyphantes pallidus* (Banks 1892) | 15 | 3 | 1 | | 19 |
| *Ceratinella brunnea* Emerton 1882 | 2 | | | | 2 |
| *Ceratinopsis stativa* (Simon 1881) | | | | 1 | 1 |
| *Diplocentria bidentata* (Emerton 1882) | 1 | | | 1 | 2 |
| *Erigone atra* Blackwall 1833 | | 3 | | | 3 |
| Erigonine Sp. A (female) | | | 1 | | 1 |
| Erigonine Sp. B (female) | 1 | | | | 1 |
| Erigonine Sp. C (female) | | | | 1 | 1 |
| *Grammonota gentilis* Banks 1898 | | | | 1 | 1 |
| *Grammonota gigas* (Banks 1896) | | | | 1 | 1 |
| *Hypselistes florens* (O.P.C. 1875) | 1 | | | | 1 |
| *Kaestneria pullata* (O.P.C. 1863) | 4 | | | | 4 |
| *Meioneta* C. Sp. A | | 1 | | | 1 |
| *Neriene clathrata* (Sundevall 1829) | | 1 | 1 | 1 | 3 |
| *Pelecopsis mengei* (Simon 1884) | | | 1 | | 1 |
| *Scyletria inflata* Bishop and Crosby 1938 | | | | 1 | 1 |
| *Tapinocyba* Sp. A | 1 | | | | 1 |
| *Walckenaeria fusiceps* Millidge 1983 | 4 | | | | 4 |
| immature | 5 | | 1 | | 6 |
| **Liocranidae** | | | | | |

| | | | | | |
|---|---|---|---|---|---|
| *Agroeca ornata* Banks 1892 | | 1 | | | 1 |
| *Agroeca pratensis* Emerton 1890 | 4 | | 6 | 1 | 11 |
| **Lycosidae** | | | | | |
| *Alopecosa aculeata* (Clerck 1757)* | 231 | 5 | 109 | 66 | 411 |
| *Arctosa emertoni* Gertsch 1934 | 5 | | | | 5 |
| *Pardosa distincta* (Blackwall 1846) | 2 | | 1 | | 3 |
| *Pardosa fuscula* (Thorell 1875)* | 2498 | 705 | 214 | 308 | 3725 |
| *Pardosa groenlandica* (Thorell 1872)* | 9 | 117 | 33 | 161 | 320 |
| *Pardosa modica* (Blackwall 1846)* | 377 | 75 | 414 | 199 | 1065 |
| *Pardosa moesta* Banks 1892* | 162 | 35 | 64 | 21 | 282 |
| *Pardosa mulaiki* Gertsch 1934 | | 5 | 2 | 1 | 8 |
| *Pardosa tesquorum* (Odenwall 1910) | 2 | 6 | 1 | 1 | 10 |
| *Pardosa xerampelina* (Keyserling 1877) | | | 1 | | 1 |
| *Pirata piraticus* (Clerck 1757)* | 63 | 8 | 18 | 11 | 172 |
| *Trochosa terricola* Thorell 1856 | 77 | | 27 | 16 | 120 |
| *Alopecosa* (immature) | 1 | | 4 | | 5 |
| *Arctosa* (immature) | 2 | | | | 2 |
| *Pardosa* (immature) | 137 | 69 | 31 | 3 | 267 |
| *Pirata* (immature) | 38 | 17 | 8 | 4 | 67 |
| *Trochosa terricola* (immature) | 16 | 1 | 2 | 1 | 20 |
| **Philodromidae** | | | | | |
| *Philodromus* (immature) | | 1 | 1 | | 2 |
| *Thanatus formicinus* (Clerck 1757) | 1 | | | | 1 |
| *Thanatus striatus* C.L. Koch 1845 | | | 1 | | 1 |
| *Thanatus* (immature) | 1 | | 2 | | 3 |
| *Tibellus maritimus* (Menge 1875) | 1 | | | | 1 |
| **Pisauridae** | | | | | |
| *Dolomedes triton* (Walckenaer 1837) | 1 | 5 | | | 6 |
| **Tetragnathidae** | | | | | |
| *Pachygnatha clercki* Sundevall 1830 | 43 | 32 | 2 | 4 | 81 |

| | | | | | |
|---|---|---|---|---|---|
| *Pachygnatha dorothea* McCook 1893 | 2 | | | | 2 |
| *Pachygnatha* (immature) | | | 1 | | 1 |
| *Tetragnatha* (immature) | 1 | | | | 1 |
| **Theridiidae** | | | | | |
| *Enoplognatha marmorata* (Hentz 185) | | | 1 | | 1 |
| *Euryopsis argentea* Emerton 1882 | 3 | | | | 3 |
| *Robertus riparius* O.P.C. | 9 | | 3 | | 12 |
| *Thymoites minnesota* Levi 1964 | 4 | | | 1 | 5 |
| **Thomisidae** | | | | | |
| *Ozyptila gertschi* Kurata 1944 | 14 | 1 | 6 | 1 | 22 |
| *Xysticus britcheri* Gertsch 1934 | | | 1 | | 1 |
| *Xysticus chippewa* Gertsch 1953 | | | 1 | | 1 |
| *Xysticus discursans* Keyserling 1880 | 1 | | 1 | 2 | 4 |
| *Xysticus elegans* Keyserling 1880 | | 1 | | 2 | 3 |
| Xysticus emertoni Keyserling 1880 | 52 | 4 | 45 | 17 | 118 |
| *Xysticus ferox* (Hentz 1847) | 4 | 1 | 34 | 14 | 53 |
| immature | 2 | 1 | | 3 | 6 |
| damaged spiders | | | | | 264 |
| Total | 4066 | 1025 | 1229 | 1044 | 7589 |

## b) Floating traps

| | | | | | |
|---|---|---|---|---|---|
| **Clubionidae** | | | | | |
| *Clubiona canadensis* Emerton 1890 | | 2 | | | 2 |
| *Clubiona norvegica* Strand 1900 | 1 | 1 | | 2 | 4 |
| immature | | | 1 | | 1 |
| **Hahniidae** | | | | | |
| immature | | 1 | | | 1 |
| **Linyphiidae** | | | | | |
| *Bathyphantes gracilis* (Blackwall 1841) | 1 | 1 | | 1 | 3 |

| | | | | | |
|---|---|---|---|---|---|
| *Bathyphantes pallidus* (Banks 1892) | | 2 | | 2 | 4 |
| *Erigone atra* Blackwall 1833 | | 1 | | 1 | 2 |
| *Pelecopsis* sp. A | 1 | | | | 1 |
| *Walckenaeria spiralis* | | 1 | | | 1 |
| immature | | 1 | 1 | 1 | 3 |
| **Lycosidae** | | | | | |
| *Pardosa fuscula* (Thorell 1875)* | 7 | 15 | 2 | 6 | 30 |
| *Pardosa groenlandica* (Thorell 1872) | | 2 | | 1 | 3 |
| *Pardosa moesta* Banks 1892 | | 1 | | | 1 |
| *Pirata piraticus* (Clerck 1757)* | 66 | 142 | 96 | 204 | 508 |
| *Pardosa* (immature) | | | | 2 | 2 |
| *Pirata* (immature) | 14 | 12 | 2 | 3 | 31 |
| **Pisauridae** | | | | | |
| *Dolomedes triton* (Walckenaer 1837)* | 5 | 26 | 7 | | 38 |
| *Dolomedes* (immature) | 1 | 11 | 4 | | 16 |
| **Tetragnathidae** | | | | | |
| *Pachygnatha clercki* Sundevall 1830* | 29 | 24 | 21 | 16 | 90 |
| *Pachygnatha dorothea* McCook 1893* | 19 | 8 | 10 | 9 | 46 |
| *Pachygnatha* (immature) | 1 | 1 | | | 2 |
| **Theridiidae** | | | | | |
| *Euryopsis argentea* Emerton 1882 | | 2 | | | 2 |
| damaged | | | | | 10 |
| Total | 150 | 262 | 146 | 254 | 812 |

Appendix IIA. Raw One-factor ANOVA tables for effects of wetland type on various spider species captured in live capture (df=1,118) and floating (df=1,58) traps.

| Source | Sum-of-Squares | df | Mean-Square | F-ratio | p |
|---|---|---|---|---|---|
| **i) Pitfall traps** | | | | | |
| Total abundance | 35322.0 | 1 | 35322.0 | 20.49 | <0.0001 |
| Lycosidae | 37656.7 | 1 | 37657.7 | 23.11 | <0.0001 |
| *Alopecosa aculeata* | 152.17 | 1 | 152.17 | 5.52 | 0.02 |
| *Pardosa fuscula* | 34555.8 | 1 | 34555.8 | 27.0 | <0.0001 |
| *Pardosa groenlandica* | 515.11 | 1 | 515.11 | 15.9 | <0.0001 |
| *Pardosa modica* | 83.37 | 1 | 83.37 | 1.09 | NS |
| *Pardosa moesta* | 72.2 | 1 | 72.2 | 8.34 | 0.005 |
| *Pirata piraticus* | 1.17 | 1 | 1.17 | 0.204 | NS |
| *Neoantistea magna* | 1.01 | 1 | 1.01 | 0.289 | NS |
| *Gnaphosa parvula* | 25.31 | 1 | 25.31 | 7.57 | 0.007 |
| Number of species | 105.8 | 1 | 105.8 | 9.42 | 0.003 |
| **ii) Floating traps** | | | | | |
| Total abundance | 2121.9 | 1 | 2121.9 | 17.1 | <0.0001 |
| Lycosidae | 1476.2 | 1 | 1476.2 | 12.5 | 0.001 |
| *Pirata piraticus* | 1307.2 | 1 | 1307.2 | 12.5 | 0.001 |
| *Pardosa fuscula* | 1.74 | 1 | 1.74 | 2.04 | NS |
| *Pachygnatha clercki* | 3.40 | 1 | 3.40 | 1.11 | NS |
| *Pachygnatha dorothea* | 0.03 | 1 | 0.03 | 0.02 | NS |
| *Dolomedes triton* | 7.22 | 1 | 7.22 | 2.15 | NS |

Appendix IIB. Raw One-factor ANOVA tables for effects of wetland age on various spider species captured in live capture (df=2,117) and floating (df=2,57) traps.

| Source | Sum-of-Squares | df | Mean-Square | F-ratio | p |
|---|---|---|---|---|---|
| **i) Pitfall traps** | | | | | |
| Total abundance | 1511.0 | 2 | 755.5 | 0.584 | NS |
| Lycosidae | 2746.8 | 2 | 1373.4 | 1.26 | NS |
| *Alopecosa aculeata* | 223.0 | 2 | 111.5 | 9.15 | <0.0001 |
| *Pardosa fuscula* | 6320.2 | 2 | 3160.1 | 4.27 | 0.02 |
| *Pardosa groenlandica* | 361.6 | 2 | 180.8 | 3.64 | 0.03 |
| *Pardosa modica* | 2451.7 | 2 | 1225.8 | 17.8 | <0.0001 |
| *Pardosa moesta* | 35.6 | 2 | 17.8 | 2.24 | NS |
| *Pirata piraticus* | 120.2 | 2 | 60.1 | 11.2 | <0.0001 |
| *Neoantistea magna* | 34.1 | 2 | 17.0 | 4.02 | 0.02 |
| *Gnaphosa parvula* | 110.1 | 2 | 55.0 | 16.9 | <0.0001 |
| Number of species | 192.3 | 2 | 96.1 | 9.95 | <0.0001 |
| **ii) Floating traps** | | | | | |
| Total abundance | 701.0 | 2 | 350.5 | 1.94 | NS |
| Lycosidae | 605.2 | 2 | 302.6 | 1.70 | NS |
| *Pirata piraticus* | 489.6 | 2 | 244.8 | 1.52 | NS |
| *Pardosa fuscula* | 7.39 | 2 | 3.69 | 3.49 | 0.04 |
| *Pachygnatha clercki* | 2.72 | 2 | 1.36 | 0.38 | NS |
| *Pachygnatha dorothea* | 0.16 | 2 | 0.083 | 0.09 | NS |
| *Dolomedes triton* | 30.2 | 2 | 15.1 | 3.18 | 0.05 |