Spider (Araneae) assemblages in the Carmanah Valley on Vancouver Island: Composition, habitat preferences, and phenology

by

Claudia Copley
B.Sc., University of Victoria, 1993

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University of Victoria

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Abstract

Spiders of the Carmanah Valley, Vancouver Island, British Columbia were examined to determine differences in species assemblages in a regenerating clearcut and an ancient forest, and characterize life histories of the different species. Twenty-three families (113 species, 76 genera) were collected using Malaise traps. Diversity was greater in the regenerating clear-cut than in the ancient forest. The latter was dominated by the web-building guild. Assemblages in the two habitats were significantly different and species that preferred the regenerating forest tended toward spring/summer stenochronous life histories compared to fall stenochronous in the ancient forest. Eight species showed non-random distribution patterns relative to the riparian corridor formed by Carmanah Creek. Species that used both habitats did not show a shift in timing of reproduction despite differences in abiotic conditions. More adults were collected in the ancient forest habitat than in the regenerating clear-cut, while more immatures were found in the regenerating clear-cut.

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Chapter 1. General Introduction

Deforestation has led to landscape-level changes, altering diversity patterns and causing significant species loss (Soulé 1991; Vitousek *et al.* 1997; Sala *et al.* 2000). More than a century of logging along the northwest coast of North America has converted vast tracts of mature temperate rainforest ecosystems into a fragmented patchwork of forests in various stages of succession, urban areas, and agriculture. Forests that contain trees that are 300 years old, or older, and have 60 metre-high canopies, contain structural heterogeneity that cannot be replicated in the logging rotation of managed stands. Moss mats centimetres-thick and suspended soils in the canopy form microhabitats that result in extensive specialization of arthropods (Campbell and Winchester 1993; Schowalter 1995; Winchester and Ring 1996a, 1996b; Behan-Pelletier and Winchester 1998; Winchester *et al.* 1999; Lindo and Winchester 2006).

In ancient temperate forests, Asquith *et al.* (1990) found that arthropods comprise 80 to 90% of the total known species present. This diversity is recognized as a priority for conservation (Dunn 2005; Losey and Vaughan 2006; Samways 2007). Despite this, basic information about forest arthropod communities is lacking (Schowalter *et al.* 1986; Schowalter 1989, 1995; Didham *et al.* 1996; Winchester 2006). How arthropods respond to habitat changes in temperate forests is of particular importance in British Columbia because of the conversion of ancient forests to young managed forest plantations (Saunders *et al.* 1991; Winchester and Ring l996a, 1996b; Winchester 1997, 1998). On Vancouver Island, only five of 89 watersheds larger than 5000 hectares remain intact (Western Canada Wilderness Committee 2005).

The abundance of arthropods and relative ease in they can be sampled make them ideal candidates for investigations into the effects of disturbance on community structure in these forests. Work on Vancouver Island has been undertaken with relatively well-known taxa such as the ground-dwelling spiders and carabid beetles (Brumwell *et al.* 1998), while difficult taxa such as Acarina, Collembola, Staphylinidae, and Sphaeroceridae are reserved for specialists in their fields (Behan-Pelletier and Winchester 1998; Marshall and Winchester 1999; Klimaszewski *et al.* 2000; Klimaszewski and Winchester 2002; Addison *et al.* 2003; Lindo and Winchester 2006).

Spiders constitute a major component of temperate forests (Schowalter 1995; Mason *et al.* 1997). For example, in mature stands of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) in the northwestern United States, spiders made up 54-68% of the arthropod predator guild (Schowalter 1995). Although there are 40,000 spider species described worldwide, the estimated total number of species is 170,000 (Coddington and Levi 1991). Of the 1500 species known to occur in Canada, 700 have been reported in British Columbia (Bennett 1999; Bennett *et al.* 2006). There are perhaps 100 species still to be described. Spiders provide a model taxon for community ecology research due to their ubiquitous distribution, wide range of habitats, and well-known position in the food web (Turnbull 1973; Bennett 1999).

Spider assemblages are known to change in response to habitat alterations in temperate forest systems. Medium to large-sized hunting spiders increase in abundance in areas that have been clear-cut logged, and web-builders and small moisture-preferring species decline (McIver *et al.* 1992, Pajunen *et al.* 1995; Buddle e*t al.* 2000; Huber *et al*. 2007).

Baseline information prior to disturbance is necessary to predict responses to ecosystem alterations by spider species assemblages.

This thesis examines the spider fauna of the Carmanah Valley on Vancouver Island, British Columbia, in terms of species occurrence, distribution patterns, and phenology. My objective is to understand how spider assemblages differ between an ancient forest and a regenerating clear-cut. Chapter 2 summarizes the impact of habitat conversion using comparisons of composition, diversity, abundance, and habitat distribution patterns relative to a riparian corridor. In Chapter 3, I examine the phenological patterns of the spider species assemblages in terms of reproductive timing, winter activity, and life history.

Chapter 2. The effect of logging on the spider species assemblage of a temperate rainforest ecosystem in the Carmanah Valley, Vancouver Island, British Columbia

Abstract

I characterize the spider species assemblage of an ancient forest and a regenerating clear-cut in the Carmanah Valley, Vancouver Island, British Columbia in terms of diversity, species composition, and patterns of distribution relative to a riparian corridor. Twenty-three families were represented, consisting 76 genera and 113 species, including 23 undescribed ones. In both the regenerating clear-cut and the ancient forest, a large proportion of the species were of the family Linyphiidae. Species abundance was similar in the two habitats but diversity was greater in the regenerating clear-cut. The ancient forest was dominated by the web-building guild. Species abundance patterns for both habitats appear similar to a log series model. Results of a spatial autocorrelation analysis revealed no overall pattern in the species assemblages relative to the riparian corridor of Carmanah Creek but eight species showed non-random distribution patterns. Bray-Curtis similarity measure and principal component analysis results indicate that spider assemblages in the two habitats were significantly different in composition. This study provides an exploratory view of the spider species assemblage a decade after an area of ancient forest was logged. The impact of the loss of these forests on arthropods has only begun to be explored, and only in a limited number of taxa.

Introduction

Deforestation has significant effects on diversity patterns (Soulé 1991; Vitousek *et al.* 1997; Sala *et al.* 2000) and much of the forests of Vancouver Island have already undergone extensive landscape-level conversion due to logging. The result is a shift away from climax forests (self-perpetuating and virtually unaltered except by local scale perturbations), to a fragmented mosaic of various age classes and successional stages (Trofymow *et al.* 1997; Lertzman *et al.* 2002). The habitat characteristics of second growth forests differ from ancient forest ecosystems in terms of their spatial and structural heterogeneity (Ishii *et al.* 2004).

Research into characteristics of the arthropod communities associated with temperate coastal rainforests on Vancouver Island has been underway for more than a decade, including investigations of the Carmanah Valley on Vancouver Island, British Columbia (Winchester 1997; Winchester *et al*. 2002). An estimated 10,000 arthropod species have been recorded from this area and many new species have been found, particularly those with specialized niches (Campbell and Winchester 1993; Winchester and Ring 1996a, 1996b, 1999; Behan-Pelletier and Winchester 1998; Winchester *et al.* 1999; Marshall and Winchester 1999; Klimaszewski and Pelletier 2004).Winchester (1997) concludes that to document and understand this biological diversity, we must focus research on species assemblages and conservation strategies at a landscape level.

The Canadian spider fauna is reasonably well known (Bennett 1999), and spiders are abundant, ubiquitous in their distributions, easy to sample, and readily assigned to a trophic level (Turnbull 1973; Wise 1993). Distinct habitat preferences have been demonstrated, allowing for divergent assemblages to form in response to habitat alterations (Huhta 1965; 1971; Buddle *et al.* 2000; Marusik and Koponen 2000).

Although many studies have examined the effects of habitat alterations on spider species assemblages in forested ecosystems, most have been conducted in heavily managed forests or disturbance-prone systems (Hippa and Mannila 1974; Pettersson 1996; Niemelä 1997; Logunov and Koponen 2000; Koponen 1987, 1993b, 2005; Thunes *et al.* 2004; Freitag *et al.* 1982; Pearce *et al.* 2004). Spider research in coastal temperate forests includes work by Mason (1992) and Halaj *et al.* (1996, 2000) and some successional work (McIver *et al.* 1992; Brumwell 1996; Brumwell *et al.* 1998).

Spiders are abundant and diverse in ancient forests (Winchester and Ring 1999; Humble *et al.* 2000), and this has been linked to the complex structural heterogeneity that includes branch architecture, needle structure (Halaj *et al*. 2000) and accumulations of moss and debris (Hauge 1976; Pajunen *et al.* 1995). For example, Kessler and van der Ham (1988) estimated the density of spiders to be as high as 500 individuals per metre squared, due to the many micro-habitats available. Prey items are readily available in these arthropod-dominated systems; habitat preferences by spiders have instead been shown to relate to temperature, humidity, and structural characteristics (Coyle 1981; Greenstone 1984; Buddle *et al.* 2000; Halaj *et al.* 2000).

Conversion of ancient forests changes abiotic characteristics and causes increased extremes in temperature and humidity (Huhta 1965; 1971; Coyle 1981; Winchester *et al.* 2002). Habitat structure is simplified through the lack of vertical stratification because only single age classes of trees are represented, stumps are at a similar stage of decay, there is a loss of epiphytic mosses and lichens due to canopy closure, and few to no standing dead trees occur (Winchester 1997; Wells *et al.* 1998). Spider assemblages are known to change in response to habitat alterations in temperate forest systems. Medium to large-sized hunting spiders increase in abundance in areas that have been clear-cut logged, and web-builders and small species preferring relatively high and constant humidity decline (McIver *et al.* 1992, Pajunen *et al.* 1995; Buddle e*t al.* 2000; Huber *et al*. 2007). Spiders can readily colonize newly disturbed areas (Crawford *et al.* 1995), and many spider taxa preferentially do so (Meijer (1977).

My objective in this chapter is to characterize the spider assemblage of the Carmanah Valley, Vancouver Island, British Columbia. Two habitats, an ancient forest and a regenerating clear-cut, are compared in terms of species diversity, a term that includes the total number of species (richness) as well as species abundance (evenness). Community composition and guild structure are summarized in each habitat. Seasonal and annual effects on the assemblage are examined, and distribution patterns relative to the riparian corridor are investigated.

Methods

Study Site

Carmanah Valley (48° 44' N; 124° 37' W) is within the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991) and is located on the south-west coast of Vancouver Island between the villages of Port Renfrew and Bamfield (Figure 2.1). A maritime climate prevails, with wet, humid cool summers and mild winters with little snow. The mean annual precipitation is 3000 mm (Winchester 1997).

This 6,731 hectare valley represents a virtually intact watershed dominated by ancient conifers that are approximately 700 years old and commonly exceed 60 meters in height

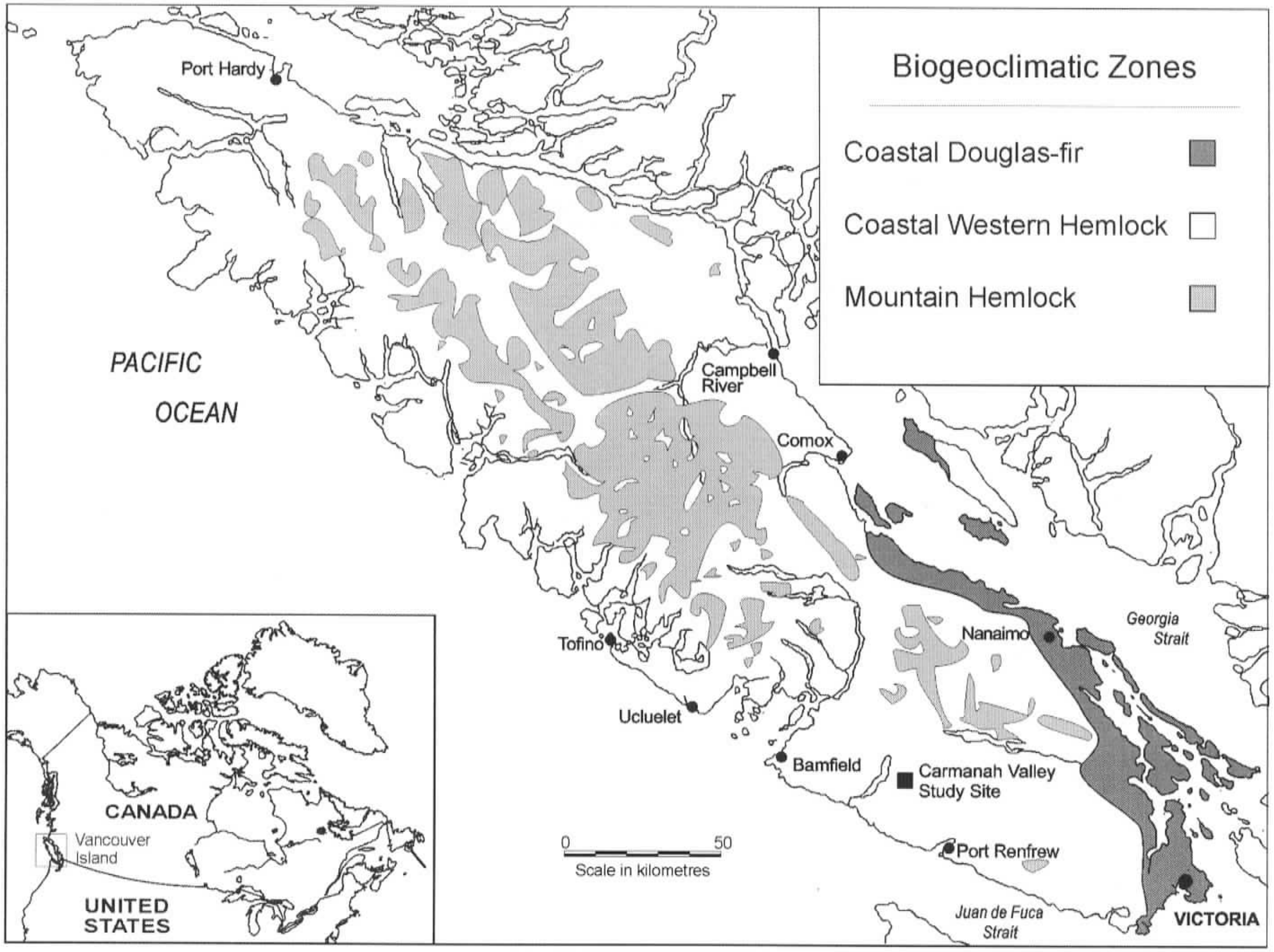


Figure 2.1. Location of the Carmanah Valley study site on Vancouver Island, British Columbia, Canada (modified from Winchester 1997).

with diameters at breast height in excess of one metre. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western redcedar (*Thuja plicata* Donn ex D. Don.), account for 30, 25, 25 and 10% of the total tree canopy, respectively (Winchester 1997). Salmonberry (*Rubus spectabilis* Pursh), devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell), false azalea (*Menziezia ferruginea* Sm.), and salal (*Gaultheria shallon* Pursh) are common in the shrub layer.

Approximately four hectares of the Carmanah Valley were clear-cut logged in 1985. Vascular plant species in the regenerating clear-cut were similar to those found in the ancient forest and described in Cross *et al.* (1999) as thick scrub and regenerating conifer growth.

Sampling Design

The spider specimens collected for this study were part of a larger project that examined the use of the Carmanah Creek riparian habitat by aquatic insects. On June 24, 1996, six randomly positioned transects, three in a regenerating clear-cut and three in the ancient forest, were established perpendicular to the stream. Ground Malaise flight interception traps (Townes 1962) were erected along each transect and cleared every two weeks until December 1997 (excluding late November 1996 through February 1997). Each transect was comprised of six traps positioned at 0, 10, 20, 30, 50, and 75 metres distant from the stream edge, for a total of thirty-six sampling locations. Specimens were collected into a mixture of 75% ethyl alcohol and 5 ml ethylene glycol.

All specimens were sorted into taxonomic groups of interest (Ephemeroptera, Plecoptera, Neuroptera, Coleoptera, Hymenoptera, Lepidoptera, Trichoptera, and Diptera

(Asilidae and Tipulidae) and stored in vials containing 75% ethanol. Arachnids were also among the initial taxa targeted in this study. Samples that contained both Araneae and Opiliones were stored for future taxonomic work. All 1996 arachnids were identified to species by D.J. Buckle. I identified the 1997 Araneae specimens to genus or species, using the reference collections held at the Royal British Columbia Museum and various taxonomic keys (Dondale and Redner 1978; 1982; 1990; Bennett 1991; Platnick and Dondale 1992; Paquin and Dupérré 2003; Dondale *et al.* 2003; Ubick *et al.* 2005). Spider species identifications require the examination of genitalic characters, so most immatures could only be identified to genus. Determinations were verified by D.J. Buckle and Dr. R.G. Bennett. All specimens collected in 1997 are deposited at the Royal British Columbia Museum. Nomenclature and classification follow Platnick (2008).

Data Analysis

The spider fauna of each habitat was compared in terms of species, the relative proportions of families and two broad guild categories based on foraging strategies: web-builders and cursorial predators (after Buddle *et al.* 2000). Species richness and abundance were standardized to the average number of species and individuals (respectively) captured in a two-week period and compared by habitat type and year.

Habitat "preferences" were based on adult spiders (Draney 1997). Species collected between 90-100% of the time in a particular habitat were associated with that habitat only. Species that were collected in both habitats between 40-60% of the time are listed as using both habitats equally. Symbols < and > were used if a species was found in one habitat 61-75% of the time more often then the other habitat, and >> and << were used for percentages between 76 and 89%.

I used the number of samples to construct cumulative species curves for each habitat and to determine whether or not sampling was sufficient to estimate species richness. Curves are based on the number of samples since sampling effort was the same for both habitats (see also Buddle *et al.* 2005). Diversity estimators were calculated for each location. These included abundance-based calculations (Chao 1 and Abundance-based Coverage Estimator (ACE)) and sample-based calculations (Chao 2, Incidence-based Coverage Estimator (ICE), first and second order Jackknives), using EstimateS (Colwell 2005).

Rank abundance plots of the log of the total abundance of adults for each species were used to determine the species abundance model for each habitat. Curves were compared to each other using the Kolmogorov-Smirnov two-sample test.

A community compositional similarity matrix was calculated using the Bray–Curtis index to compare spider species assemblages inhabiting the ancient forest and regenerating clear-cut. Habitat, season (spring, summer, and fall), and distances along each transect (0, 10, 20, 30, 50, and 75 m) were included in this analysis and the data were normalized by a log(x+1)-transformation. An analysis of similarity (ANOSIM) with 1,000 permutations was performed to assess the significance of the main factor affects: habitat type, season, and distance. Primer 5 for Windows was used for these analyses (2001).

Variation in spider assemblage composition was analysed using principal components analysis (PCA) in Statistica 7.0 (StatSoft Inc. 2004) with a significance level of α=0.05. Species with adult abundances equal to or greater than 10 individuals over all sampling periods were used to create the PC factors, forty species in total. These factors were then analysed with an analysis of variance (ANOVA) for main effects of habitat type, season, and distance from the riparian corridor. Factor coordinates, based on species correlations, were used to interpret the PCA.

To determine if there was an overall pattern in the distribution of spiders associated with the riparian corridor, the spatial autocorrelation of the assemblages along the horizontal distance from the Carmanah Creek boundary was evaluated. Standardized species abundance of the samples collected at the various distances along the transects were used as replicates. An assemblage compositional similarity matrix, based on Bray-Curtis similarity of $\log(x+1)$ spider species abundances, was compared with a geographical distance matrix based on the absolute Euclidean distances of the samples from the creek edge, using a Mantel test (Manly 1997) in Primer 5 (2001). The Mantel test produced a rank correlation coefficient *(rm)* that corresponded to the average magnitude of spatial autocorrelation of the community composition similarity over all sampling distances. The resulting value was not significant (r=0.236, P=0.256), allowing me to treat each of the samples along each transect as independent replicates for multivariate analyses. Individual species represented by 15 or more specimens were also examined for trends associated with the riparian corridor.

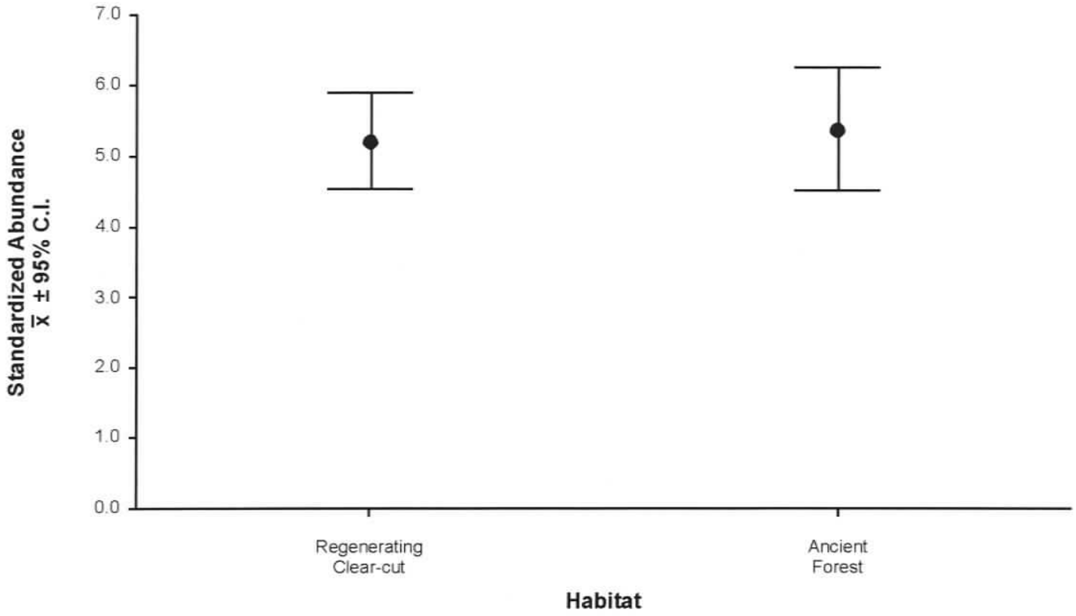
Two-sample Student's t-tests were used to compare spider species abundance in each habitat over the different years: 1996 and 1997. The months that were sampled in both years were compared, and abundance was standardized by determining the average number of spiders caught per day in each trap in both habitats and multiplying by the total number of trapping days. Rainfall and temperature data, taken from the Environment Canada website (Environment Canada 2002), were also compared between the two years over the same months. Rainfall data was based on information from the Carmanah Point weather station, and temperature data came from the Amphitrite Point weather station. Analyses were performed using Minitab 15.1.1.0. (Minitab 2007) with a significance level of α=0.05.

Results

Richness and abundance in the regenerating clearcut and ancient forest were similar (Figure 2.2) and years were pooled for assemblage-level analyses. A total of 113 spider species from 23 families and 76 genera were found (Table 2.1). Of these, 23 species are undescribed and all but one of these is in the family Linyphiidae. Two non-native Theridiidae are reported from the regenerating clear-cut: *Enoplognatha ovata* (Clerck) and *Neottiura bimaculata* (Linnaeus).

Seventy-four percent of the families are shared between the two habitats, and 52 % of all species reported were from the family Linyphiidae (Table 2.2). A higher percentage of the ancient forest assemblage was represented by this taxon. The regenerating clear-cut was numerically dominated by specimens in the family Clubionidae while the ancient forest had more Theridiidae specimens than any other family (Table 2.2). Almost one quarter of the specimens collected in this study were *Rugathodes sexpunctatus* (Table 2.2) and it was only reported in the regenerating clear-cut 36 times over the 15-month sampling period. The second most frequently collected species was *Clubiona trivialis*, accounting for 16% of all mature spiders collected, and it was only reported from the regenerating clear-cut (Table 2.1). The web-building guild dominated the ancient forest habitat compared to the regenerating clear-cut (Figure 2.3).

a) Abundance



b) Richness

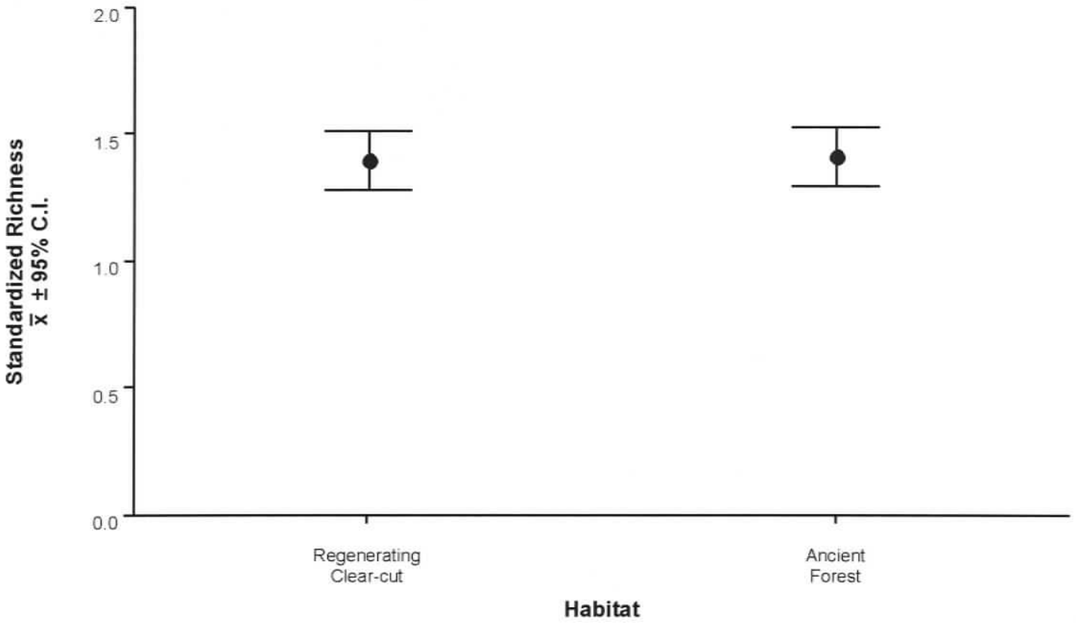


Figure 2.2. Standardized spider species a) abundance and b) richness over all sampling intervals and years combined. Means and 95% confidence intervals are presented.

Table 2.1. Habitat preference and guild placement of the spider fauna (Araneae) reported from the Carmanah Valley. Non-native species are indicated with an asterisk (*). Nomenclature and classification follow Platnick (2008). Data are based on all trap collections pooled over all time intervals.

Spider Species	**Habitat Collected**	**Number**			**Guild**
		♀	♂	**Imm.**	
ANTRODIAETIDAE					
Antrodiaetus pacificus (Simon)	Forest > Clear-cut	5	10	7	web
MECICOBOTHRIIDAE					
Hexura picea Simon	Forest = Clear-cut	10	0	6	web
TELEMIDAE					
Usofila pacifica (Banks)	Forest	1	0	0	web
MIMETIDAE					
Ero canionis Chamberlin & Ivie	Clear-cut	0	1	0	cursorial
ULOBORIDAE					
Hyptiotes gertschi Chamberlin & Ivie	Forest	0	1	1	web
THERIDIIDAE					
Achaearanea sp. 1	Clear-cut	1	0	0	web
**Enoplognatha ovata* (Clerck)	Clear-cut	0	2	0	web
**Neottiura bimaculata* (Linnaeus)	Clear-cut	2	1	0	web
Rugathodes sexpunctatus (Emerton)	Forest	821	425	160	web
Theridion californicum Banks	Clear-cut	0	1	0	web
Theridion saanichum Chamberlin & Ivie	Forest	3	2	0	web
PIMOIDAE					
Pimoa altioculata (Keyserling)	Forest = Clear-cut	31	26	60	web
LINYPHIIDAE					
Agyneta sp. 1	Clear-cut	49	1	0	web
Agyneta sp. 2	Forest	1	1	0	web
Bathyphantes alascensis (Banks)	Clear-cut >> Forest	3	2	0	web
Bathyphantes brevis (Emerton)	Clear-cut >> Forest	15	0	0	web
Bathyphantes keeni (Emerton)	Forest >> Clear-cut	22	6	4	web
Bathyphantes orica Ivie	Clear-cut > Forest	5	0	0	web
Ceraticelus atriceps (O.P.-Cambridge)	Clear-cut > Forest	5	0	0	web
Ceratinella acerea Chamberlin & Ivie	Forest	3	0	0	web
Ceratinella alaskae Chamberlin & Ivie	Forest > Clear-cut	2	1	0	web
Ceratinella cf. alaskana	Clear-cut	0	1	0	web
Ceratinella ornatula (Crosby & Bishop)	Clear-cut	0	1	0	web
Ceratinops inflatus (Emerton)	Forest >> Clear-cut	7	3	0	web
Ceratinopsis nr. *gosibia*	Forest	1	0	0	web

Table 2.1 (*continued*)

Spider Species	**Habitat Collected**	**Number**			**Guild**
		♀	♂	**Imm.**	
Disembolus sp. 1	Clear-cut	1	0	0	web
Erigone aletris Crosby & Bishop	Forest	0	2	0	web
Erigoninae sp. 1	Clear-cut	4	0	0	web
Erigoninae sp. 2	Forest	1	0	0	web
Erigoninae sp. 3	Clear-cut	1	0	1	web
Erigoninae sp. 4	Forest	1	0	0	web
Helophora reducta (Keyserling)	Clear-cut	7	8	0	web
Linyphantes nr. *eureka*	Clear-cut >> Forest	1	4	0	web
Linyphantes orcinus (Emerton)	Forest >> Clear-cut	6	3	0	web
Linyphantes pualla Chamberlin & Ivie	Forest = Clear-cut	6	9	0	web
Linyphantes sp. 1	Clear-cut > Forest	18	5	16	web
Linyphantes sp. 2	Forest >> Clear-cut	47	13	0	web
Linyphantes sp. 3	Forest = Clear-cut	2	17	0	web
Linyphantes sp. 4	Clear-cut	1	0	0	web
Linyphantes sp. 5	Clear-cut	1	0	0	web
Meioneta sp. 1	Forest = Clear-cut	1	4	0	web
Meioneta sp. 2	Forest > Clear-cut	6	0	0	web
Meioneta sp. 3	Forest	2	0	0	web
Mermessus trilobatus (Emerton)	Forest = Clear-cut	0	4	0	web
Microlinyphia dana (Chamberlin & Ivie)	Forest = Clear-cut	24	13	22	web
Microneta viaria (Blackwall)	Forest	1	0	0	web
Mythoplastoides erectus (Emerton)	Forest > Clear-cut	2	4	0	web
Neriene digna (Keyserling)	Forest > Clear-cut	5	18	13	web
Oreonetides filicatus (Crosby)	Forest	1	0	0	web
Oreonetides sp. 1	Forest	0	25	0	web
Pacifiphantes magnificus (Chamberlin & Ivie)	Forest	1	0	0	web
Pelecopsis sculpta (Emerton)	Forest	6	5	0	web
Pityohyphantes rubrofasciatus (Keyserling)	Clear-cut	0	2	0	web
Pityohyphantes sp. 1	Forest	17	11	0	web
Pocadicnemis pumila (Blackwall)	Clear-cut	60	19	19	web
Porrhomma convexum (Westring)	Forest	2	0	0	web
Saaristoa sammamish (Levi & Levi)	Forest	1	0	0	web
Scotinotylus columbia Chamberlin	Clear-cut	2	0	0	web
Scotinotylus patellatus (Emerton)	Forest	12	7	0	web
Scotinotylus sp. 1	Clear-cut	0	2	0	web
Sisicottus nesides (Chamberlin)	Forest	11	3	0	web
Spirembolus vasingtonus Chamberlin	Forest >> Clear-cut	3	6	0	web
Symmigma minimum (Emerton)	Forest	1	1	0	web
Tachygyna ursina (Bishop & Crosby)	Forest > Clear-cut	41	41	13	web
Tapinocyba dietrichi Crosby & Bishop	Forest	5	0	0	web
Tapinocyba sp. 1	Clear-cut	0	1	0	web
Tenuiphantes zelatus (Zorsch)	Forest	2	2	0	web
Tenuiphantes zibus (Zorsch)	Forest > Clear-cut	7	6	0	web

Table 2.1 (*continued*)

Spider Species	**Habitat Collected**	**Number**			**Guild**
		♀	♂	**Imm.**	
Walckenaeria cornuella (Chamberlin & Ivie)	Forest = Clear-cut	0	2	0	web
Wubana pacifica (Banks)	Clear-cut >> Forest	7	2	0	web
Wubana suprema Chamberlin & Ivie	Forest > Clear-cut	14	5	0	web
TETRAGNATHIDAE					
Metellina curtisi (McCook)	Forest	53	58	22	web
Tetragnatha laboriosa Hentz	Clear-cut	17	45	5	web
Tetragnatha versicolor Walckenaer	Clear-cut > Forest	44	37	17	web
ARANEIDAE					
Araneus nordmanni (Thorell)	Forest	0	0	1	web
Araneus saevus (L.Koch)	Forest	5	2	4	web
Araneus trifolium (Hentz)	Clear-cut	1	4	1	web
Araniella displicata (Hentz)	Clear-cut	1	0	3	web
Larinioides sp.	Clear-cut	0	0	1	web
LYCOSIDAE					
Pardosa dorsuncata Lowrie & Dondale	Clear-cut	39	19	282	cursorial
OXYOPIDAE					
Oxyopes scalaris Hentz	Clear-cut	0	3	0	cursorial
CYBAEIDAE					
Cybaeus eutypus Chamberlin & Ivie	Clear-cut > Forest	11	58	0	web
Cybaeus reticulatus Simon	Forest > Clear-cut	37	154	0	web
Cybaeus signifer Simon	Forest	1	6	0	web
HAHNIIDAE					
Calymmaria emertoni (Simon)	Clear-cut	1	3	0	web
Cryphoeca exlineae Roth	Clear-cut > Forest	1	5	0	web
Dirksia cinctipes (Banks)	Forest	42	39	52	web
Ethobuella tuonops Chambelin & Ivie	Forest	33	33	13	web
DICTYNIDAE					
Emblyna peragrata (Bishop & Ruderman)	Clear-cut > Forest	1	8	6	web
AMAUROBIIDAE					
Callobius pictus (Simon)	Forest >> Clear-cut	31	43	144	web
ANYPHAENIDAE					
Anyphaena aperta (Banks)	Forest > Clear-cut	5	4	0	cursorial
Anyphaena pacifica (Banks)	Clear-cut	0	2	0	cursorial
CLUBIONIDAE					
Clubiona pacifica Banks	Clear-cut > Forest	25	41	0	cursorial

Table 2.1 (*continued*)

Spider Species	Habitat Collected	Number			Guild
		♀	♂	Imm.	
Clubiona trivialis C.L.Koch	Clear-cut	284	321	0	cursorial
CORINNIDAE					
Castianeira longipalpa (Hentz)	Clear-cut	0	1	1	cursorial
GNAPHOSIDAE					
Micaria pulicaria (Sundevall)	Clear-cut	3	0	2	cursorial
Sergiolus montanus (Emerton)	Clear-cut >> Forest	3	4	0	cursorial
Zelotes puritanus Chamberlin	Clear-cut	0	1	2	cursorial
PHILODROMIDAE					
Apollophanes margareta Lowrie & Gertsch	Clear-cut	0	0	1	cursorial
Philodromus rufus pacificus Banks	Clear-cut >> Forest	13	12	5	cursorial
Tibellus oblongus (Walckenaer)	Clear-cut	11	9	20	cursorial
THOMISIDAE					
Misumena vatia (Clerck)	Clear-cut	2	1	1	cursorial
Ozyptila pacifica Banks	Clear-cut	0	0	1	cursorial
Xysticus locuples Keyserling	Clear-cut	4	3	0	cursorial
Xysticus montanensis Keyserling	Clear-cut	3	7	0	cursorial
Xysticus pretiosus Gertsch	Clear-cut	22	64	0	cursorial
SALTICIDAE					
Evarcha proszynskii Marusik & Logunov	Clear-cut	4	20	35	cursorial
Habronattus hirsutus (Peckham & Peckham)	Clear-cut	0	1	0	cursorial
Habronottus oregonensis (Peckham & Peckham)	Clear-cut	0	2	0	cursorial
Pelegrina aeneola (Curtis)	Clear-cut > Forest	3	3	2	cursorial
Phanias albeolus (Chamberlin & Ivie)	Forest > Clear-cut	2	1	0	cursorial
Phidippus johnsoni (Peckham & Peckham)	Clear-cut	4	8	3	cursorial
Salticus scenicus (Clerck)	Clear-cut	0	0	1	cursorial

Table 2.2. A comparison of relative proportions of spider families in each of the two habitats in the Carmanah Valley: a regenerating clear-cut and an ancient forest. Data are based on all trap collections pooled over all time intervals (adult spiders only).

	Regenerating Clear-cut				Ancient Forest			
Spider Family	**# of Species**	**% of total**	**# of Indiv.**	**% of total**	**# of Species**	**% of total**	**# of Indiv.**	**% of total**
Amaurobiidae	1	1.2	8	0.5	1	1.4	66	1.7
Antrodiaetidae	1	1.2	4	0.3	1	1.4	11	0.3
Anyphaenidae	2	2.4	5	0.3	1	1.4	6	0.2
Araneidae	3	3.6	7	0.4	2	2.9	8	0.2
Clubionidae	2	2.4	643	41.3	1	1.4	28	0.7
Corinnidae	1	1.2	1	0.1	0	0	0	0
Cybaeidae	2	2.4	90	5.8	3	4.3	177	4.7
Dictynidae	1	1.2	4	0.3	1	1.4	5	0.1
Gnaphosidae	3	3.6	10	0.6	1	1.4	1	0
Hahniidae	4	2.4	19	1.2	3	4.3	138	3.6
Linyphiidae	43	47	321	20.6	46	64.3	384	10.2
Lycosidae	1	1.2	57	3.7	1	0	1	0
Mecicobothriidae	1	1.2	4	0.3	1	1.4	6	0.2
Mimetidae	1	1.2	1	0.1	0	0	0	0
Oxyopidae	1	1.2	3	0.2	0	0	0	0
Philodromidae	3	3.6	45	2.9	1	1.4	3	0.1
Pimoidae	1	1.2	30	1.9	1	1.4	27	0.7
Salticidae	7	8.4	45	2.9	2	2.9	4	0.1
Telemidae	0	0	0	0	1	1.4	1	0
Tetragnathidae	3	2.4	126	8.1	3	2.9	128	3.4
Theridiidae	5	4.8	30	1.9	2	2.9	1228	32.5
Thomisidae	5	6	103	6.6	1	0	4	0.1
Uloboridae	0	0	0	0	1	1.4	1	0
Total	**91**		**1556**		**74**		**2227**	
Total # families		**21**				**18**		

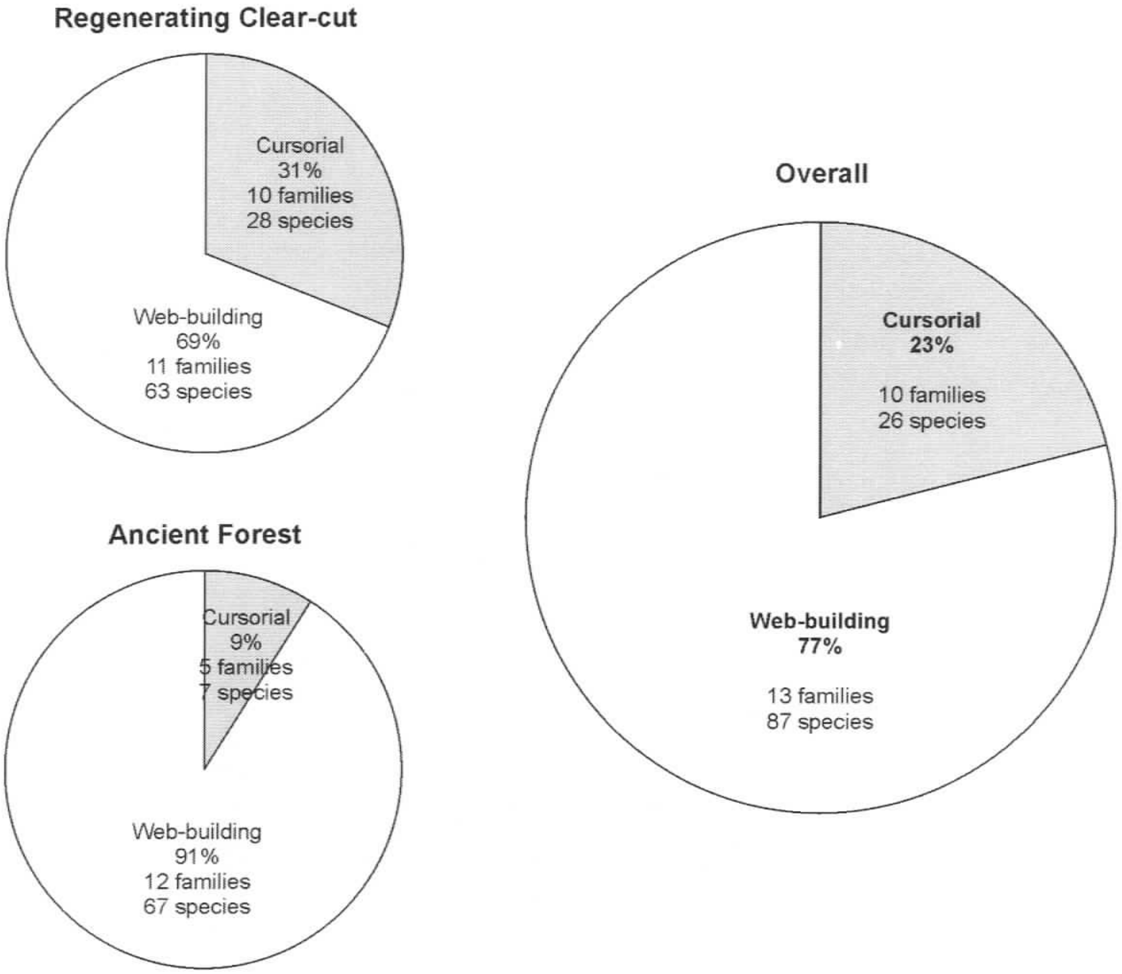


Figure 2.3. Guild structure of the spider species assemblages from the two habitats studied in the Carmanah Valley (a regenerating clear-cut and an ancient forest) and the two habitats combined. Data are based on all trap collections pooled over all time intervals.

The species accumulation curves approach an asymptote, indicating that sufficient sampling was done to make comparisons of spider richness by habitat (Figure 2.4). Rates of increase are similar between habitats, but the ancient forest curve levels off to a greater degree than the regenerating clear-cut curve. The diversity estimates were consistently higher for the regenerating clear-cut. The abundance-based estimators provided the most conservative diversity estimates: ACE in the regenerating clear-cut and Chao 1 in the ancient forest (Table 2.3). The 2^{nd} order Jacknife diversity estimates were the highest values in both treatments (Table 2.3).

Both curves are similar to a log series distribution (Figure 2.5) and are significantly different from each other (Kolmogorov-Smirnov two-sample test: $d_{(74, 91, 0.05)} = 1098.44$; $P < 0.001$). This is considered a conservative test; differences between the habitats must be substantial to generate a significant result (Magurran 2004).

The Bray Curtis percent similarity cluster analysis is presented in Figure 2.6. The two habitats showed less than 25% similarity overall, and within each habitat the fall samples were the least like the others, with a fall regenerating clear-cut sample collected at the creek edge (0 m) nesting in the fall ancient forest samples. The creek edge samples in the regenerating clear-cut were the most dissimilar from the other distances in each season, while in the ancient forest this dissimilarity was seen in the samples collected at 10 m from the creek edge in all seasons. Habitat type (ancient forest versus regenerating clear-cut) and season (spring, summer and fall) both had a significant effect on the spider species assemblage based on the analysis of similarity (habitat: $r=0.82$, $P<0.001$; season: $r=0.378$, $P<0.001$), while distance from the riparian corridor was not significant.

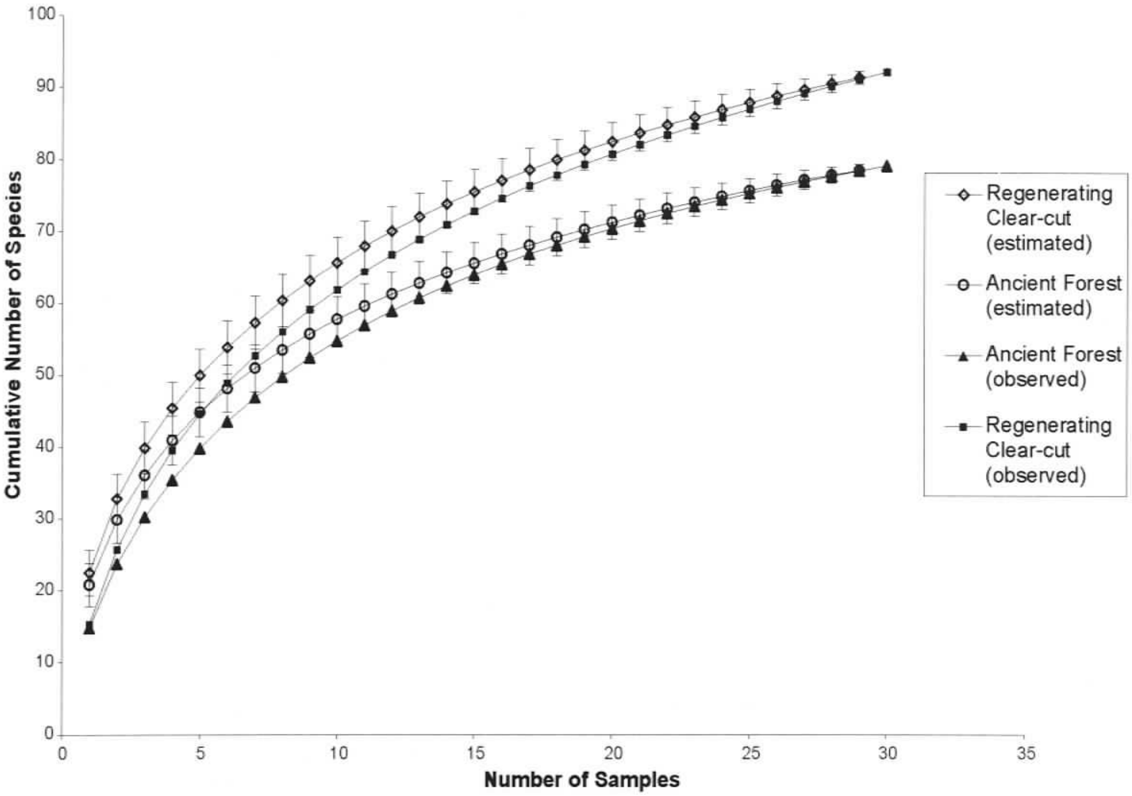


Figure 2.4. Samples-based species accumulation curves (average of 500 randomizations without sample replacement (± SD)) for the two habitats in the Carmanah Valley: a regenerating clear-cut and an ancient forest. Data are based on all trap collections pooled over all time intervals.

Table 2.3. Summary of diversity estimates for each of the two habitats in the Carmanah Valley: a regenerating clear-cut and an ancient forest. Data are based on all trap collections pooled over all time intervals. Values are means ± SD based on 500 randomized permutation tests without sample replacement. Bias-corrected results are shown unless otherwise noted.

Diversity Estimator	**Carmanah Valley Habitats**	
	Regenerating Clear-cut	**Ancient Forest**
Observed	91	74
ACE	110.89	94.08
ICE	120.69	96.6
Chao 1	112.35 ± 11.14 (classic)	89.2 ± 6.42
Chao 2	122.19 ± 15	93.5 ± 8.4
First-order Jackknife	120.03 ± 5.98	99.3 ± 5.23
Second-order Jackknife	136.29	107.19

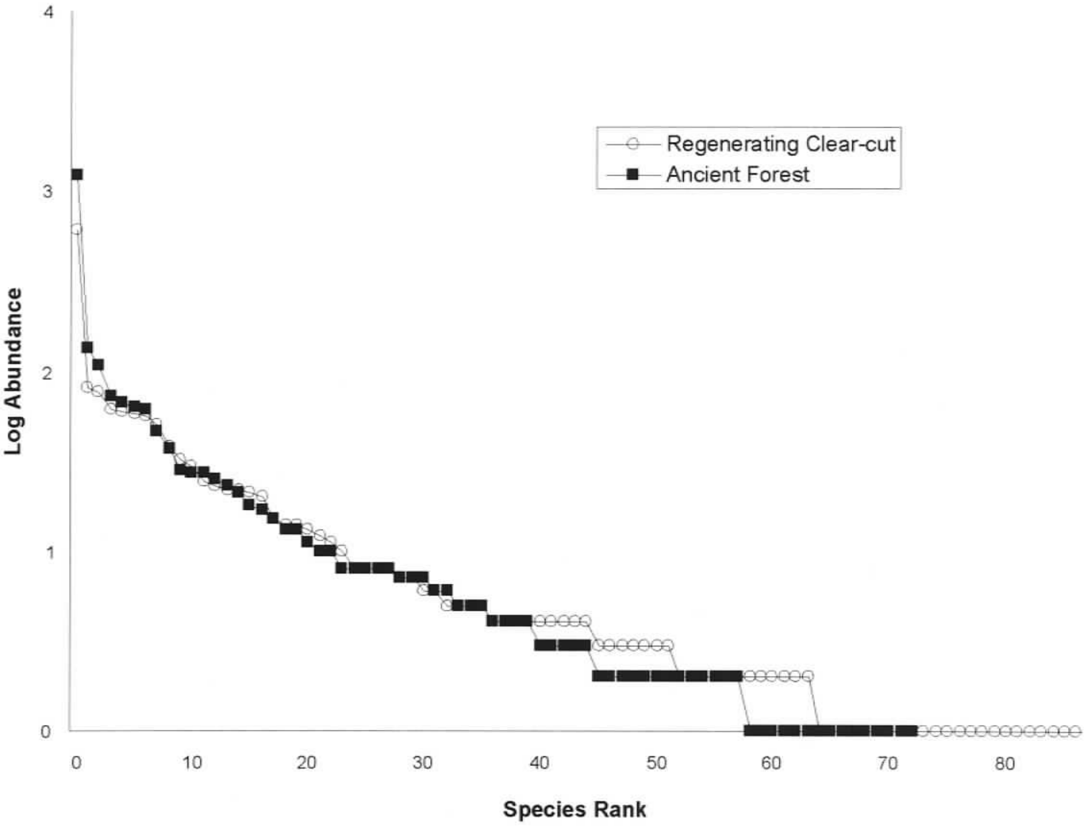


Figure 2.5. Rank/abundance plots for the two habitats in the Carmanah Valley: a regenerating clear-cut and an ancient forest. Data are based on all trap collections pooled over all time intervals.

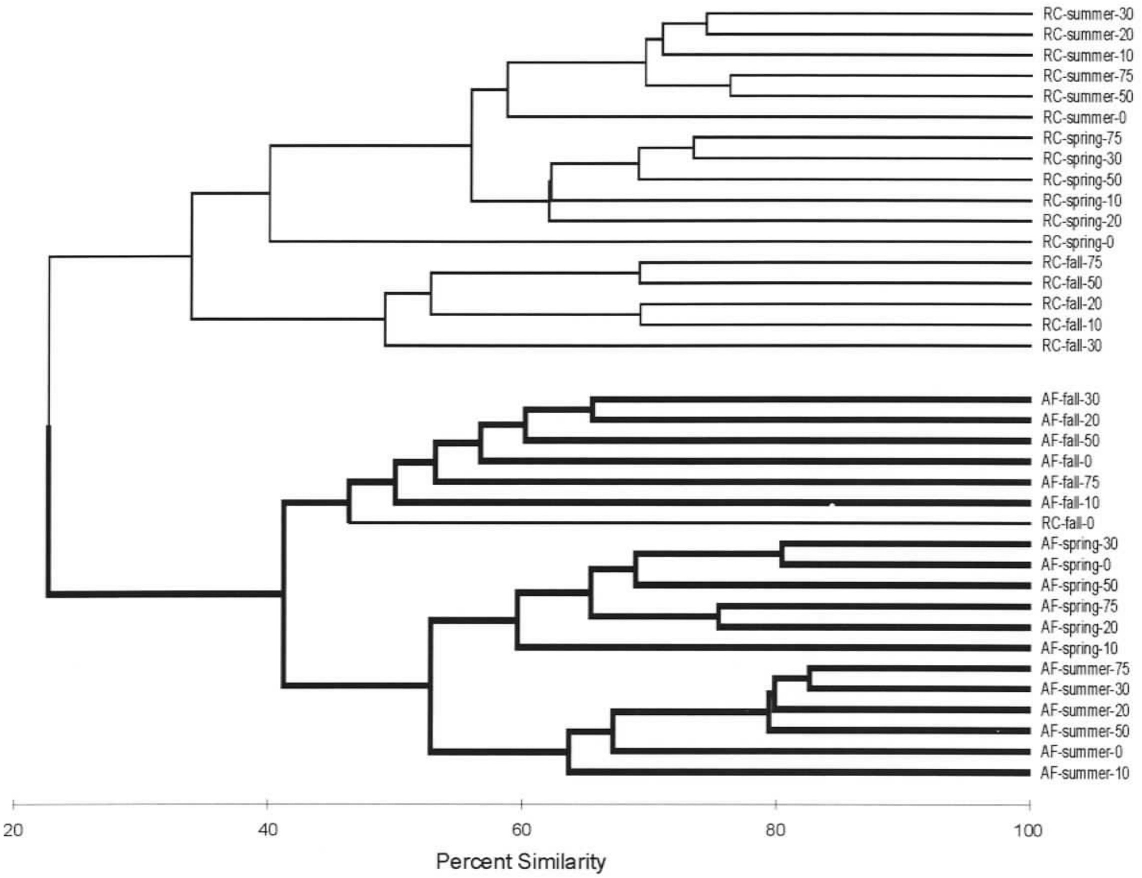


Figure 2.6. Dendrogram showing the percent similarity between the two habitats in the Carmanah Valley: a regenerating clear-cut (RC) and an ancient forest (AF). Samples were further divided by season (spring, summer, and fall) and by distance from the riparian corridor (in metres). Values are based on Bray-Curtis similarity indices of spider species and their abundances.

A similar result was found in the principle components analysis of the 40 most abundant species. Ten principle components (PC) had eigenvalues >1, with the first five components accounting for almost 60% of the variability of the data. Principal component 1 was significantly related to habitat ($F_{1,35}$=65.89, P<0.001). Both principal component 2 and 3 were significantly related to season ($F_{2,35}$=48.06, P<0.001 and ($F_{2,35}$=36.78318, P<0.001 respectively). Distance had a significant effect on principal component 4 ($F_{5,35}$=4.043, P=0.007). The species drivers of principal components 1 (habitat) and 4 (distance) are plotted in Figure 2.7., based on the highest-value species correlations with the principle component coordinates. Figure 2.8 shows species driving PC 2 (season) and PC 3 (season).

The results of the spatial autocorrelation analysis revealed no overall pattern in the species assemblage relative to the riparian corridor. Standardized species abundance and species richness were similar at each distance along pooled transects in both habitats (Figure 2.9). Species represented by 15 or more individuals were examined separately to determine trends relative to distance from the riparian corridor. Of the thirty-eight species examined, eight show abundances that are affected by distance from the creek (*Tetragnatha versicolor*, *Microlinyphia dana*, *Emblyna peragrata*, *Clubiona trivialis*, *Phidippus johnsoni*, *Tetragnatha laboriosa, Pocadicnemis pumila*, and *Dirksia cinctipes*) (Figure 2.10 and 2.11). Three species show no pattern in their predominant habitat, but are only found near Carmanah Creek in the other habitat (sampling point 0 m): *Metellina curtisi, Pardosa dorsuncata* and *Xysticus pretiosus* (Figure 2.12).

Year had a significant effect on spider abundance in the regenerating clear-cut ($T_{10,0.05}$ = 3.23, P= 0.009) but was not a significant factor for species abundance in the ancient

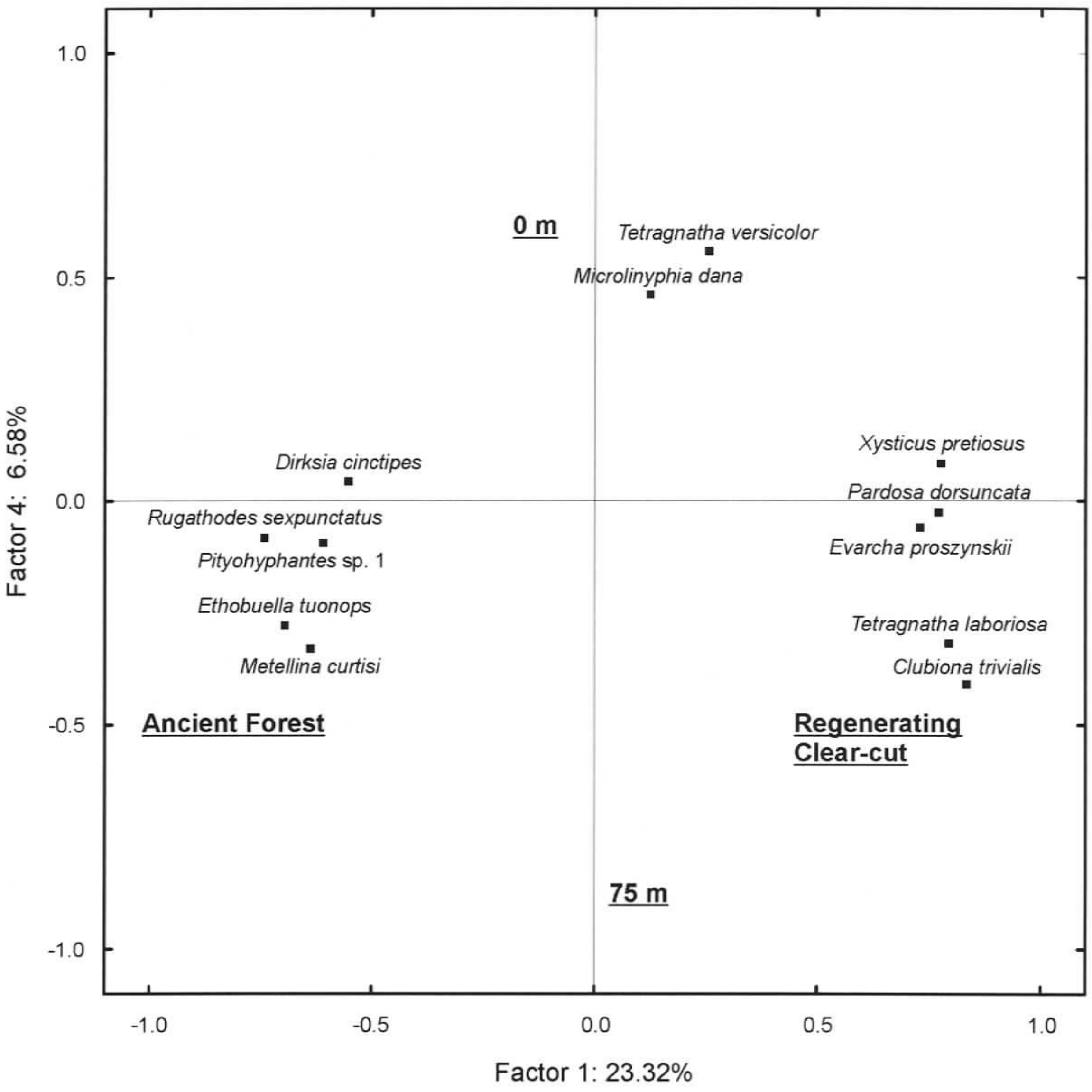


Figure 2.7. Plot of 1^{st} and 4^{th} principal components with percent explained variation for spider assemblages collected in the regenerating clear-cut and ancient forest habitats in the Carmanah Valley at various distances from the riparian corridor. Forty species with adult abundances equal to, or greater than, 10 individuals over all sampling periods were used in the analysis.

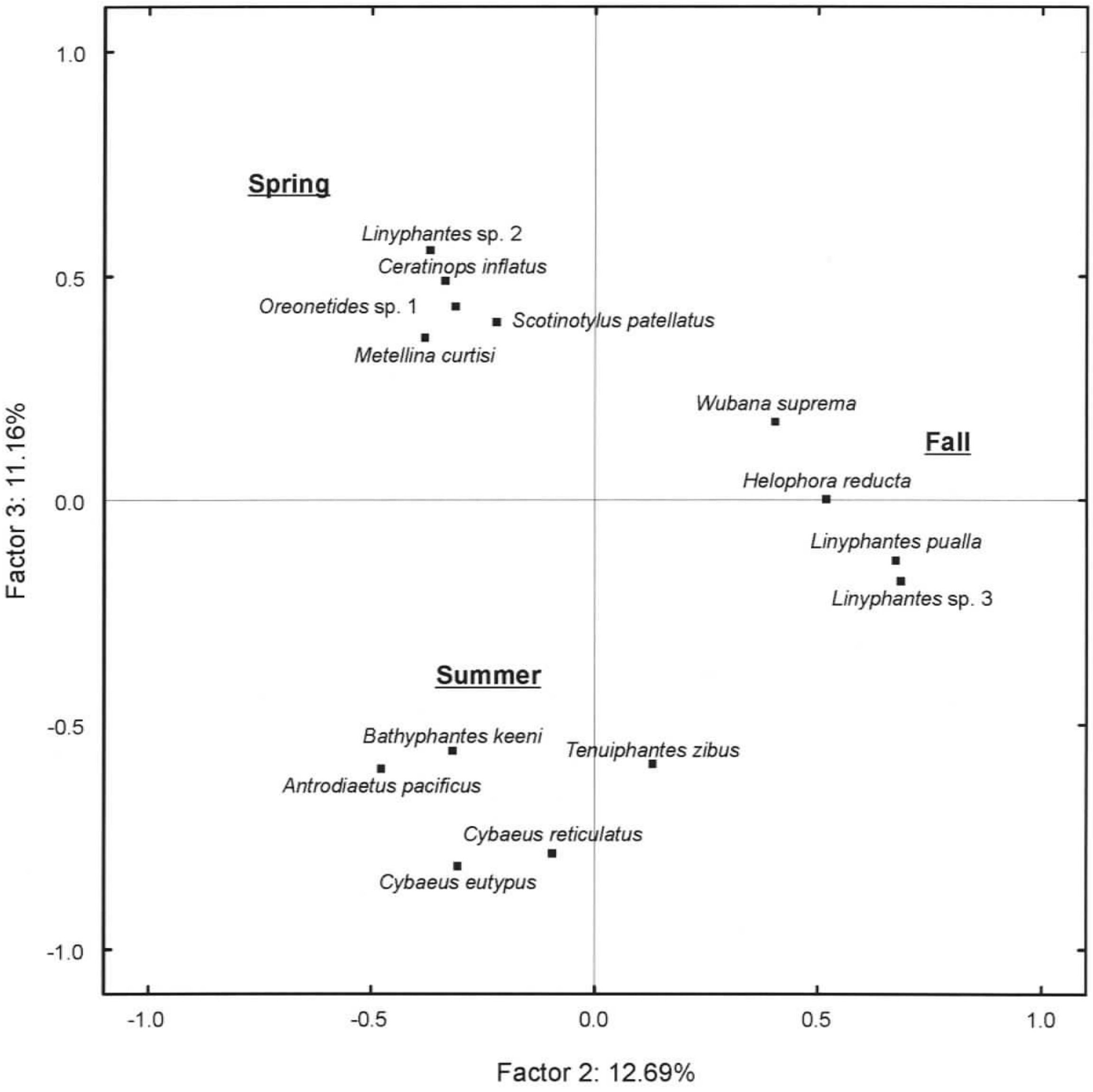
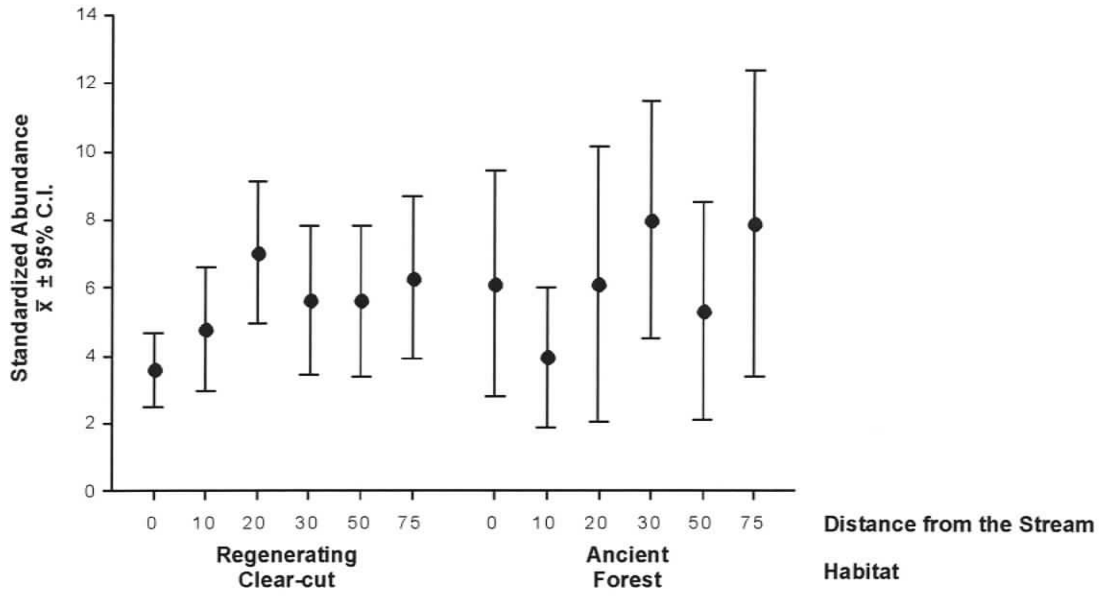


Figure 2.8. Plot of 2nd and 3rd principal components with percent explained variation for spider assemblages collected in different seasons in the Carmanah Valley: spring, summer and fall. Forty species with adult abundances equal to, or greater than, 10 individuals over all sampling periods were used in the analysis.


a) Abundance

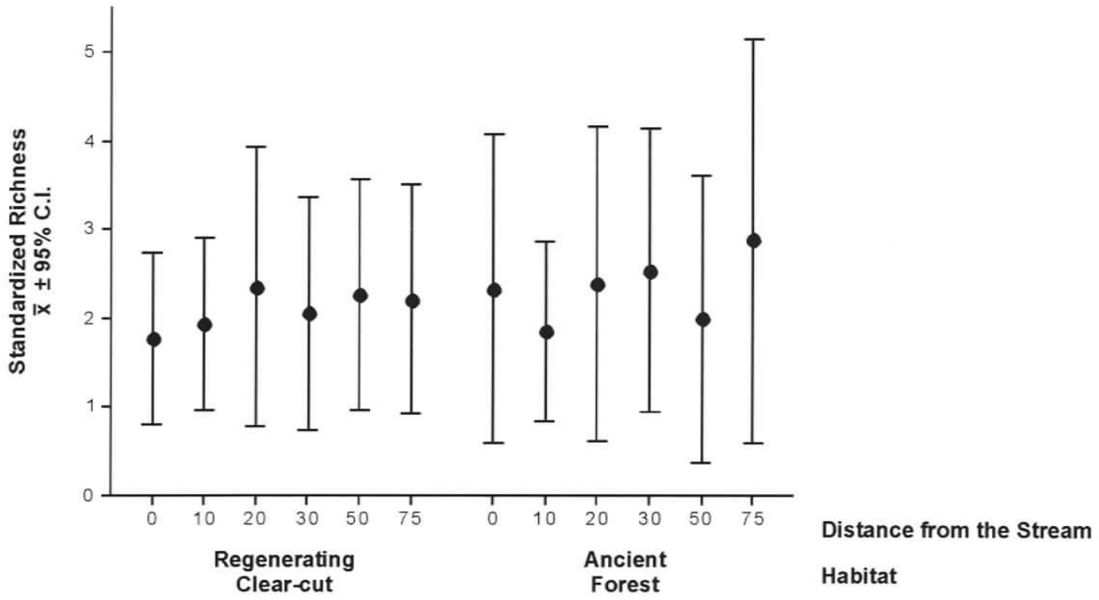
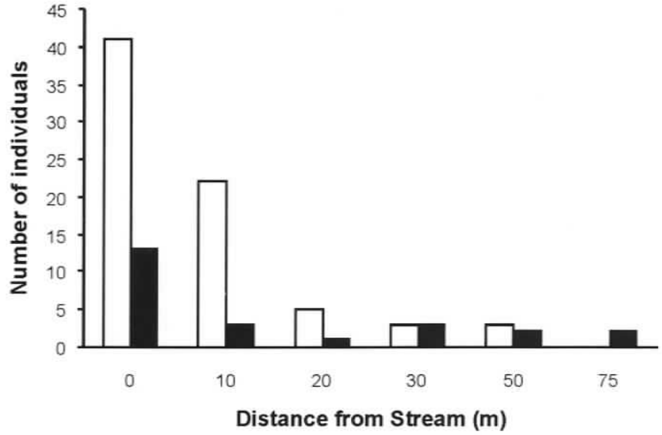
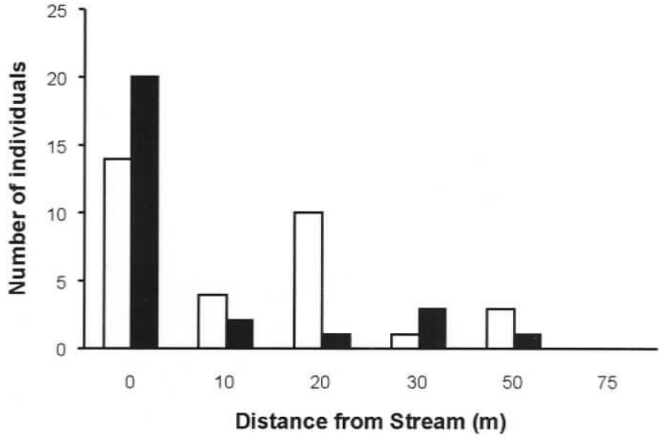

b) Richness

Figure 2.9. Standardized spider species a) abundance and b) richness at each distance (in metres) perpendicular to Carmanah Creek over all sampling intervals and both years. Means and 95% confidence intervals are presented.

a) Tetragnatha versicolor



b) *Microlinyphia dana*



c) *Emblyna peragrata*

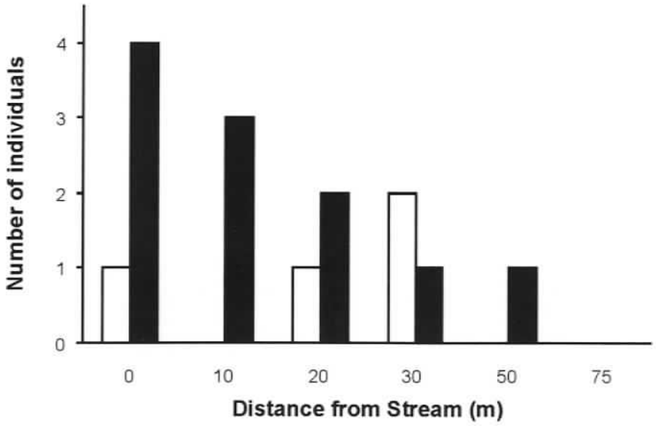
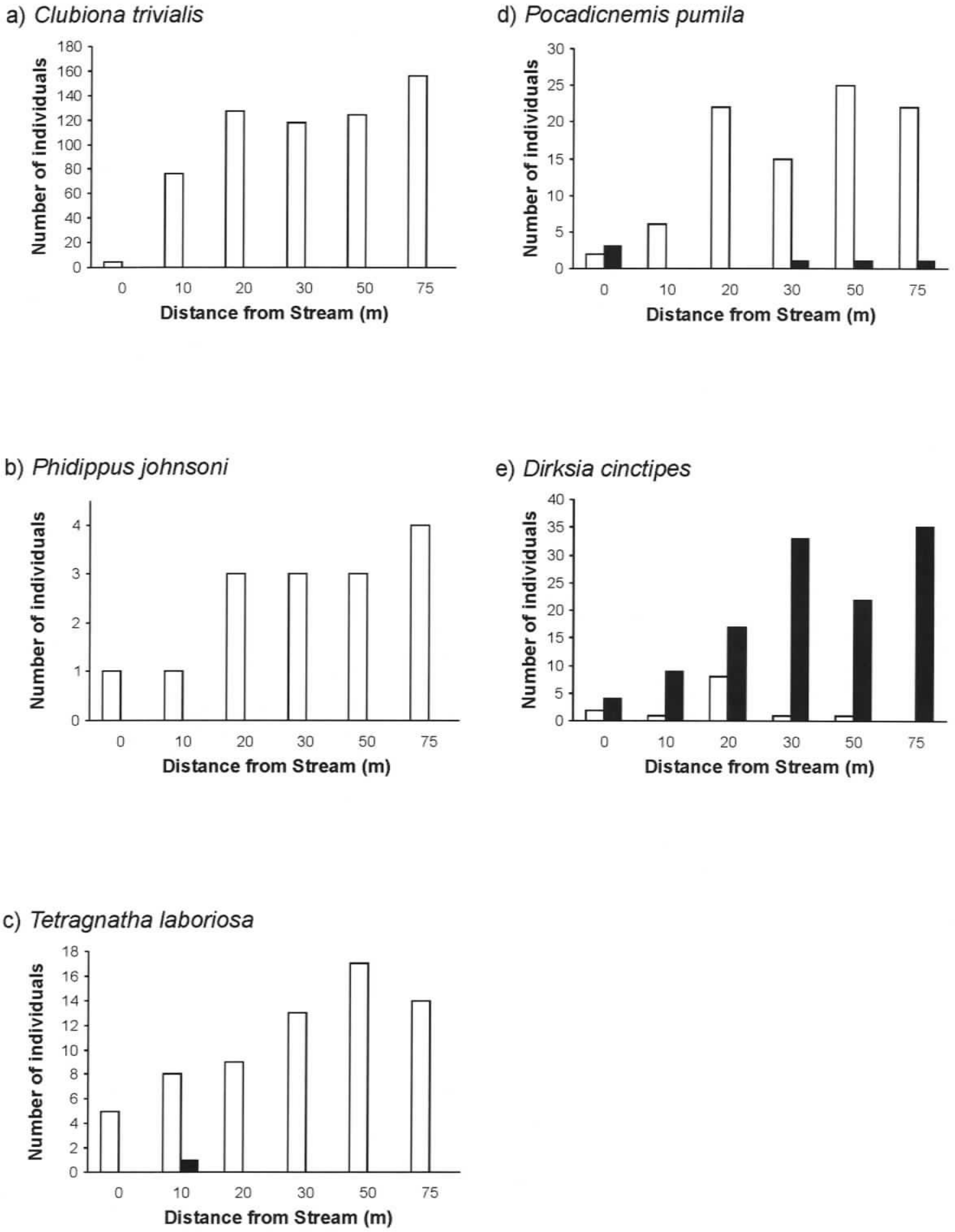


Figure 2.10. Spider species whose abundance decreases with increasing distance from the Carmanah Creek riparian corridor. The ancient forest is indicated by the open bars and the regenerating clear-cut by the shaded bars.



a) *Clubiona trivialis*

d) *Pocadicnemis pumila*

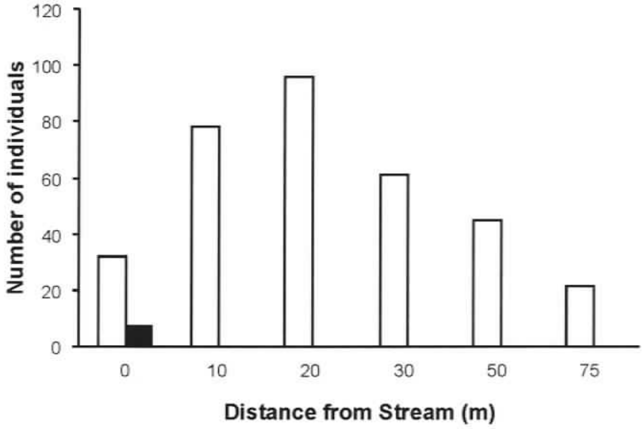
b) *Phidippus johnsoni*

e) *Dirksia cinctipes*

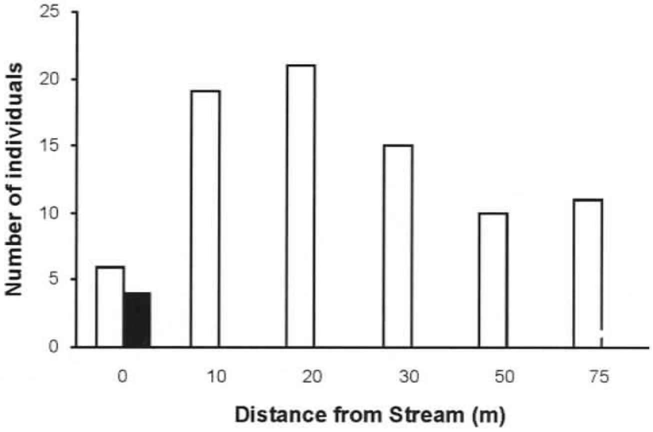
c) *Tetragnatha laboriosa*

Figure 2.11. Spider species whose abundance increases with increasing distance from the Carmanah Creek riparian corridor. The ancient forest is indicated by the open bars and the regenerating clear-cut by the shaded bars.

a) *Pardosa dorsuncata*



b) *Xysticus pretiosus*



c) *Metellina curtisi*

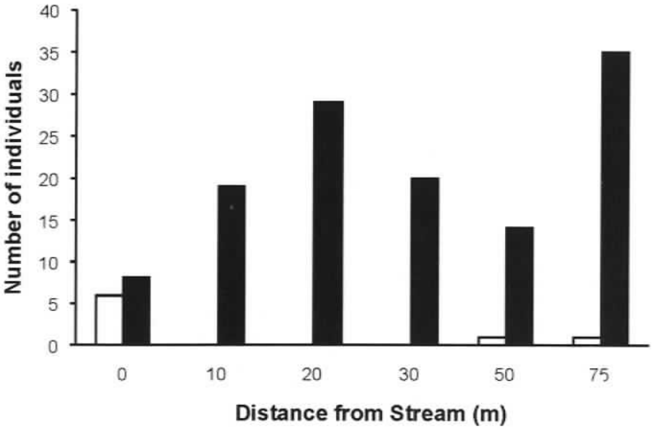


Figure 2.12. Spider species whose abundance pattern is affected by proximity to the Carmanah Creek riparian corridor in only one of the two habitats. The ancient forest is indicated by the open bars and the regenerating clear-cut by the shaded bars.

forest. Average monthly temperatures and average monthly rainfall did not differ significantly between 1996 and 1997 (Figure 2.13).

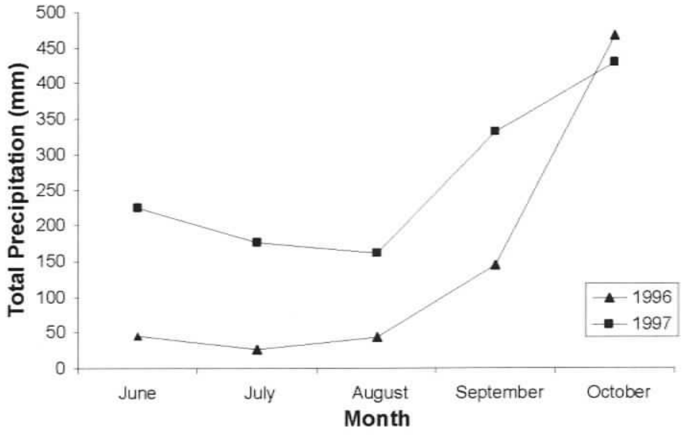
Discussion

Abundance and Diversity

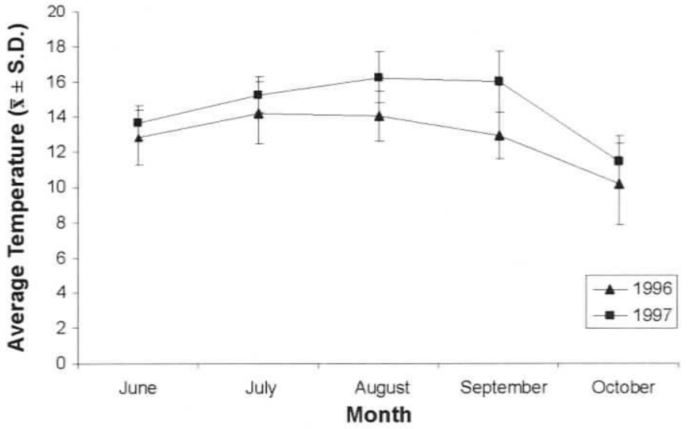
In previous studies of the effect of habitat conversion through logging, spider species diversity is highest in early and mid successional stages (Huhta 1971; Brumwell 1996) compared to that of a climax system, and this has been attributed to a mixing of transitional species. In the Carmanah Valley, the diversity estimates were higher in the regenerating clear-cut and indicate that further sampling is required in both habitats to account for the total diversity. Buddle *et al.* (2000) suggested that some forest-inhabiting spider species survive logging activity, and clear-cuts are rapidly colonized by pioneer species. Huhta (1965) described species that preferred logged areas as photophilous (light-loving), as well as excellent aeronauts. Examples from this study include the lycosid genus *Pardosa* and the thomisid genus *Xysticus* (Crawford and Edwards 1986). When these samples were collected, a decade had passed since logging had occurred, allowing a combination of species preferring characteristics of both habitat types to colonize the area.

The spider assemblages of the two habitats were similar in terms of dominance and evenness, and similar to a log series pattern, suggesting that only a few factors influence the spider assemblages. The log series pattern also suggests that the habitats are somewhat saturated and that the arrival of new species will be random instead of regular (Magurran 2004). Huhta (1965) noted a similar abundance pattern matching that

a) Average monthly rainfall (mm)



b) Average monthly temperature (°C)



c) Average spider abundance (mean ± 95% C.I.)

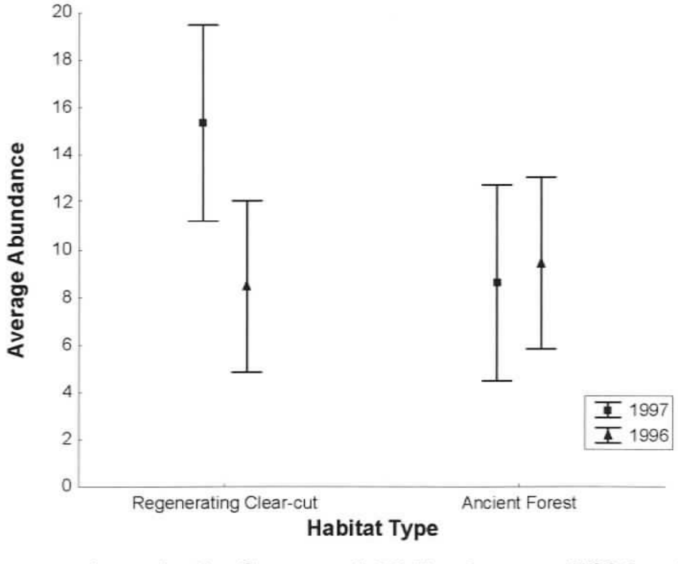


Figure 2.13. Data comparisons in the Carmanah Valley by year (1996 and 1997): a) average monthly rainfall (mm), b) average monthly temperature (°C) and c) average spider abundance by habitat (mean ± 95% CI).

of a log series in his research into the effects of silviculture on soils: one or two species dominate and there is a large proportion of rare species.

Although diversity was higher in the regenerating clear-cut, abundance was slightly higher in the ancient forest, and this has been reported by others (Coyle 1981; Brumwell 1996). Diversity was similar in the same habitat regardless of year, but in 1997 the regenerating clear-cut had significantly higher average abundances than in 1996. This may be attributable to the small differences in rainfall between the two years. The recorded averages for the months in question were higher in 1997 compared to 1996 in every month but October. Turnbull (1973) reported that differences in temperature and humidity in different years resulted in large differences in abundance. In the Carmanah Valley, temperatures differed slightly between the two years, so the change in average abundance is more likely due to increasing moisture. Especially interesting is the lack of effect on abundance in the ancient forest habitat; here deep moss layers and shade provided by the canopy probably have an ameliorating effect and prevent the dramatic shifts in moisture that a regenerating clear-cut would experience (Huhta 1971; Coyle 1981).

The fact that the species accumulation curve of the regenerating clear-cut did not level off to the same degree as that the ancient forest may reflect differences in succession: the ancient forest is a climax system and is stable and self-replacing (Wells *et al.* 1998). The relatively recent conversion of this type of habitat to one in a very early seral stage makes the regenerating clear-cut an extremely dynamic system, more so than at almost any other successional stage (Franklin *et al.* 2002). Studies have demonstrated that these two habitat stages may take many decades to converge in terms of spider species assemblages, even in areas lacking the complexity of the centuries-old forests found in the Carmanah Valley. For example, disturbance-prone systems such as the fire-maintained boreal forests (Buddle *et al.* 2000) and Douglas-fir dominated forests (McIver *et al.* 1992) had convergence of species assemblages after 15 and 30 years, respectively, but Peck and Niwa (2004) reported that a commercially thinned forest that had had as long as 41 years to recover was still different from nearby unthinned stands. Brumwell (1996) found that ground-dwelling species assemblages in logged coastal western hemlock forests were not significantly different from those of an ancient forest after only 25 years. Only 34 species from 13 families were included in the study, so this result may not provide a complete picture of how the spider species assemblage as a whole was affected by clear-cut logging.

Extrapolating the results of this study beyond the region immediately surrounding the Camanah Valley is not valid. To ensure independence, sampling of regenerating clear-cut and ancient forest habitats would, ideally, be from multiple locations. Because all three transects in each habitat were established in the same valley, pseudo-replication is a potential problem. Here, however, as in many other circumstances, it is difficult to find adequately similar but not proximate areas to sample. Even if a neighbouring valley that had equivalent and accessible habitats were, it could have abiotic factors differing from those of the Carmanah Valley. The regenerating clear-cut is a dynamic system undergoing succession, so even a difference in the timing of the original forest removal could manifest differences in the species assemblages. Scale must be taken into account as well: arthropod populations distributed over a four hectare area could be considered independent, whereas a study involving vertebrates would be less appropriate. In many situations where diversity comparisons between two treatments are being made, pseudo-replication is difficult to avoid (Magurran 2004).

Taxonomic and Guild Analysis

Although many species were reported from both habitats, species abundances in the ancient forest and the regenerating clear-cut differed in important ways. The two most frequently collected species, *Clubiona trivialis* and *Rugathodes sexpunctatus,* contributed the greatest amount to differences in the guild structure between the two habitats; each preferred one habitat (regenerating clear-cut and ancient forest, respectively) and each was a member of a different guild (cursorial and web-building, respectively). Huhta's (1971) and Coyle's (1981) studies found cursorial predators to be much more numerous in the regenerating clear-cut and suggested that this shift in the species assemblage was due to microclimate effects, primarily in relation to temperature and humidity. Bultman and Uetz (1982) showed that abundance of the web-building guild is linked to litter depth and that the cursorial guild is unaffected by this habitat characteristic. The guild results for the Carmanah Valley are similar to other studies (see Niemelä *et al.* 1994) and may reflect a typical guild structure in a forested system.

The two habitats share 50% of their species, but the cluster analysis indicates that the ancient forest and the regenerating clear-cut spider assemblages are not similar when species' abundance is considered. The similarity may be explained by the wandering behaviour of male spiders, particularly in the fall, because it is these samples that were most dissimilar in their respective habitats. One fall sample from the regenerating clear-cut even nested in the fall samples of the ancient forest. Female spiders have activity associated predominantly with foraging and egg-laying behaviour (Draney 1997), so their use of a habitat may provide a better measure of habitat suitability than the habitat associations of mate-seeking male spiders.

Characteristic of northern temperate forests (Koponen 1993a; Buddle and Draney 2004), the family Linyphiidae was the dominant family in terms of species, contributing almost ten times more species to the overall assemblage than the next most abundant family. However, the Linyphiidae contributed only 18% of the overall abundance, with many species represented by singletons. Twenty-two of the linyphiids collected are undescribed. Huhta (1971) found reduced diversity and abundance of this taxon in the more open sites, but the two habitats of the Carmanah Valley were similar in terms of diversity and abundances.

Riparian Effect

In the Carmanah Valley, several species showed an affinity for, or an avoidance of, the riparian corridor, but the overall effect of the corridor on species distribution was not significant. However, the cluster analysis revealed that regenerating clear-cut samples adjacent to the stream differed from the samples collected in the same season at the other distances, and the principal components analysis had distance significantly related to the fouth factor, so an effect of the creek was apparent. Except for the presence of open water associated with the creek, it is unlikely that there is a moisture gradient along the sampled transects within each habitat. Moisture levels between the ancient forest and the regenerating clear-cut differ due to the protective canopy, which allows light penetration for epiphytic growth, which in turn retains moisture even during dry periods (Hauge 1976). In contrast, the regenerating clear-cut contains exposed stumps and rocks and a closed canopy of regenerating trees. Few bryophytes survive these conditions due to either excessive exposure or a lack of sufficient light (Shields *et al.* 2007).

Graham *et al.* (2003) included members of the Lycosidae, Linyphiidae and Hahniidae as having an affinity to freshwater, but only some of the lycosids in their study were found to fit into this new definition of "semi-aquatic". This definition applied to species that were most abundant on water surfaces or within 2 metres of shore, and where there was evidence of reproduction on or near the water. Isotopic analysis of lycosids has shown that aquatic invertebrates can make up a significant proportion of their diet (Paetzold *et al.* 2006). Iwata (2007) reported that two spider families, Tetragnathidae and Linyphiidae, showed a distribution pattern along a stream that was directly influenced by the emergence of aquatic insects, while Kato *et al.* (2003) noted a similar pattern, but only in tetragnathids.

The abundances of three species declined with distance from the creek: *Tetragnatha versicolor*, *Microlinyphia dana* and *Emblyna peragrata*. The first two show a similar trend in both habitats, particularly *T. versicolor*. Marczak and Richardson (2007) found that *T. versicolor* and a close relative of *M. dana*, *M. mandibulata,* derive a significant portion of their prey from emerging aquatic insects, so these results agree with those of other studies. In contrast, Aiken and Coyle (2000) describe *T. versicolor* as a habitat generalist that often lives far from aquatic areas. *Emblyna peragrata* did not show the same pattern in the regenerating clear-cut, so it is unclear what factors are influencing its distribution pattern.

Four of the five species that increased in abundance with increasing distance from the creek edge were clear-cut inhabiting species; only *Dirksia cinctipes* was associated with the ancient forest. This species may prefer the forest interior rather than the edge created by the riparian corridor. It is difficult to determine what is driving the distribution patterns of the other species; possibilities include interspecific competition in the case of the orb-weaver *Tetragnatha laboriosa* and the presence of vegetation available for diurnal retreats for *Clubiona trivialis* (Halaj *et al.* 1996). Aiken and Coyle (2000) report *T. laboriosa* as a species of "non-wetland grassy habitats". Salticids such as *Phidippus johnsoni* show a preference for structural attributes in relation to hunting activity (Robinson 1981), and also have an aversion to expanses lacking vegetation (Baker 2007). Perhaps the area closest to the creek edge was unsuitable for these reasons; this might also explain the pattern shown by the linyphiid, *Pocadicnemis pumila,* a member of a family that is vulnerable to desiccation (Hauge 1976).

Three species showed no trend in the habitat they were most commonly reported in (in terms of the riparian corridor), but were found in the area immediately adjacent to the creek in the alternate habitat. The thomisid, *Xysticus pretiosus,* and the lycosid, *Pardosa dorsuncata,* were frequently collected in the clear-cut habitat and showed no pattern relative to the riparian corridor. These species appear linked to exposed habitats rather than a moisture gradient. For example, female lycosids require sunning spots for egg-sac development (Dondale and Redner 1990), and areas immediately adjacent to the creek are boulder-strewn and exposed during the summer, resulting in ideal conditions for this activity. Perhaps these corridors were the typical habitat of some species preferring open habitat before the advent of industrial logging activity, as has been suggested by some authors (Buddle *et al.* 2004).

Metellina curtisi (Family Tetragnathidae) was commonly collected in the ancient forest, but rare in the regenerating clear-cut. Specimens from the clear-cut were collected predominantly at the creek edge, perhaps demonstrating the moisture requirements of this species. Its distribution is linked to the emergence of aquatic insects (Marczak and Richardson 2007).

Conclusion

The spider species assemblages of two habitats studied in the Carmanah Valley differed in terms of diversity, family composition, and guild structure. Species richness was higher in the regenerating clear-cut and habitat preferences were clearly delineated for many species. Animals as vagile as spiders are not limited by their ability to colonize these deforested areas and are instead affected by other attributes of the habitat, such as moisture. Combined with the loss of micro-habitats associated with epiphytic growth, the suite of species preferring the regenerating clear-cut is one of fewer web-builders and fewer habitat specialists.

Previous work has demonstrated that spider species assemblages can take many decades to converge, even in disturbance-adapted systems. The Carmanah Valley and the surrounding areas would have experienced very little natural perturbation before the advent of industrialized logging; nothing functionally equivalent to a clear-cut would have occurred. The impact of the loss of these centuries-old forests on arthropods has only begun to be explored, and only in a limited number of taxa, so the long-term effects remain virtually un-documented. This study provides an exploratory view of the spider species assemblages after they have had more than a decade to recover. The establishment of Carmanah Walbran Provincial Park in 1995 means that this recovery can continue.

Chapter 3. Seasonal activity of spiders in the temperate rainforests of the Carmanah Valley, British Columbia

Abstract

The ancient temperate rainforests of British Columbia's west coast support a rich assemblage of spiders, but information about their life histories remains unknown. My objective is to examine the phenological patterns of the spider species assemblages in terms of reproductive timing, winter activity, and life-history. Spiders collected using Malaise traps over a 15 month period in the Carmanah Valley, Vancouver Island, were examined. Forty of the 113 species were classified as winter-active. The life histories of species inhabiting a regenerating clear-cut and an ancient forest differed in important ways. Winter-maturing species were only found in the ancient forest, and spring/summer stenochrony was seen more often in the species inhabiting the regenerating clear-cut. Species that used both habitats exhibited a range of life-history strategies and did not show a shift in the timing of reproduction, despite differences in abiotic conditions between the two habitats. Species belonging to the same genus also showed no difference in the timing of reproduction. Abundance was not independent of habitat type. Male and female spiders were more numerous in the ancient forest habitat, while immatures were more common in the regenerating clear-cut. This preliminary investigation in the Carmanah Valley shows evidence for inter-taxa similarities in phenology as it relates to habitat.

Introduction

In the Pacific Northwest, rainforests have established with virtually no landscape level disturbance, allowing trees to reach ages in excess of 1000 years (Wells *et al.* 1998; Lertzman *et al.* 2002). These ancient forests contain a multitude of micro-habitats that are suitable for arthropods. For example, in the Carmanah Valley on Vancouver Island, an estimated 10,000 arthropod species have been recorded (Winchester 1997).

Spiders are a major component of these temperate rainforest arthropod communities (Winchester and Ring 1999). In mature stands of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) in the northwestern United States, spiders were found to make up 54-68% of the arthropod predator guild (Schowalter 1995). Although Canadian spiders are relatively well-characterized (Bennett 1999), much of the information about their life-history attributes, including phenological patterns, is lacking (Winchester and Ring 1996a; 1999; Winchester 1997; 2006).

Schaeffer (1977) categorized several life-history patterns for spiders based on over-wintering stages and the timing of reproductive activity. Eurychronous species have adults present in every season and they overwinter in various life stages. These species are able to respond rapidly to habitat changes by reproducing in any season. These taxa also balloon readily (Draney and Crossley 1999). Stenochronous species are those with adults that are present at a particular season; these can be further subdivided into three types: 1) spring/summer reproducers that overwinter as hibernating immatures, 2) autumn reproducers that overwinter in the egg stage and 3) species that mature in the winter. Most spider families fall into the first category, including Salticidae, Lycosidae and

Thomisidae. Some Linyphiidae and most Araneidae overwinter in the egg stage after fall reproductive activity. Linyphiids make up the majority of winter-mature species.

Adult spider abundance is often used to indicate timing of reproductive activity (Buddle and Draney 2004), and for many species timing provides information on over-wintering stages. Researchers often use the timing of male spider peak abundance as the true indication of reproduction; taking into account male mate-seeking activity and the preponderance of pit-fall trap sampling in spider research (Aitchison 1984b; Doane and Dondale 1979). For detailed life histories, both species-level identifications and targeted temporal sampling are required (Dobyns 1997; Cardoso *et al.* 2007).

Some phenological work has been undertaken in the temperate forests in Europe (Hauge 1976; Toft 1976; 1978; 1979; Huhta 1965, 1971; Niemelä *et al.* 1994) and in a variety of habitats in Canada (Dondale 1977; Aitchison 1984b; Doane and Dondale 1979; Buddle and Draney 2004). Seasonal temperature variation can be dramatic and reduces spider activity, but there is also a recognition of the need for year-round sampling, as some species are found to forage subnivially (Toft 1978; Aitchison 1978; 1984a).

Some congeneric species are reported to have different phenological patterns, which may reduce niche overlap and competition between closely related species (Berry 1971; Dondale 1977; Buddle and Draney 2004). Dondale *et al.* (1972) noted differences in the daily activity patterns of ground-inhabiting arthropod assemblages and found that some ecologically similar species were separated by diel activity, potentially reducing competitive interactions. Evidence for interspecific competition among web-building spiders is inconclusive (Wise 1993).

In this chapter I compare reproductive timing and life-history patterns of spider assemblages collected from two habitats in the Carmanah Valley of coastal Vancouver Island. My objective is to determine whether or not there is an effect of habitat on spider phenology.

Methods

Study Site

Carmanah Valley (48° 44' N; 124° 37' W) is within the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991) and is located on the south-west coast of Vancouver Island between the villages of Port Renfrew and Bamfield. A maritime climate prevails, with wet, humid cool summers and mild winters with little snow. The mean annual precipitation is 3000 mm (Winchester 1997).

This 6,731 hectare valley represents an intact watershed dominated by ancient conifers that are approximately 700 years old and commonly exceed 60 meters in height with diameters at breast height in excess of one metre. Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Sitka spruce (*Picea sitchensis* (Bong) Carr.), Pacific silver fir (*Abies amabilis* (Dougl.) Forb.), and western redcedar (*Thuja plicata* Donn ex D. Don.), account for 30, 25, 25 and 10% of the total tree canopy, respectively (Winchester 1997). Salmonberry (*Rubus spectabilis* Pursh), devil's club (*Oplopanax horridus* (Smith) Miq.), Alaskan blueberry (*Vaccinum alaskaense* Howell), false azalea (*Menziezia ferruginea* Sm.), and salal (*Gaultheria shallon* Pursh) are common in the shrub layer.

Approximately four hectares of the Carmanah Valley was clear-cut logged in 1985. Plant species in the regenerating clear-cut were described in Cross *et al.* (1999) as thick scrub and regenerating conifer growth.

Sampling Design

The spider specimens collected for this study were part of a larger project that examined the use of the Carmanah Creek riparian habitat by aquatic insects. On June 24, 1996, six randomly positioned transects, three in a regenerating clear-cut and three in the ancient forest, were established perpendicular to the stream. Ground Malaise flight interception traps (Townes 1962) were erected along each transect and emptied every two weeks until December 1997 (excluding November through February). These traps were positioned at 0, 10, 20, 30, 50, and 75 metres from the stream edge, along each transect, for a total of thirty-six sampling locations. Specimens were collected into a mixture of 75% ethyl alcohol and 5 ml ethylene glycol.

All specimens were sorted into taxonomic groups of interest (Ephemeroptera, Plecoptera, Neuroptera, Coleoptera, Hymenoptera, Lepidoptera, Trichoptera, and Diptera (Asilidae and Tipulidae) and stored in vials containing 75% ethanol. Arachnids were among the initial taxa targeted in this study. Samples that contained both Araneae and Opiliones were stored for future taxonomic work. All 1996 arachnids were identified to species by D.J. Buckle. I identified the 1997 Araneae specimens to genus and species, using the reference collections held at the Royal British Columbia Museum, and various taxonomic keys (Dondale and Redner 1978, 1982, 1990; Bennett 1991; Platnick and Dondale 1992; Paquin and Dupérré 2003; Dondale *et al.* 2003; Ubick *et al.* 2005). Spider species identifications require genitalic characters, so most immatures could only be identified to genus. Determinations were verified by D.J. Buckle and Dr. R.G. Bennett. All specimens collected in 1997 are deposited at the Royal British Columbia Museum. Nomenclature and classification follow Platnick (2008).

Analysis

I compared sample timing and capture bias to examine differences in spider abundance between the regenerating clear-cut and the ancient forest. To determine if abundance was independent of habitat, a chi-square analysis with an alpha level of 0.05 was performed using Minitab 15.1.1.0. (Minitab 2007).

Presence/absence information by month from both years of sampling was used to present phenology patterns of adult spiders of species represented by 15 or more individuals (see Buddle and Draney 2004). Peak male abundances were determined based on 1997 data because trapping in 1996 did not include as many months and the trapping intervals were not identical to those of 1997. Life histories were summarized as relative percents (dates combined) for the regenerating clear-cut and the ancient forest. Species collected 90-100% of the time in a particular habitat were associated with that habitat only, species that were collected in both habitats 40-60% were listed as using both habitats equally.

Species collected in November and December of 1996 and 1997 were defined as winter-active. Species belonging to the same genus were examined to determine if they differed in terms of their reproductive timing. Frequency plots of species with equal abundances in both of the habitats and where more than 15 adults were collected (1997 data only) were compared to determine whether or not there is shift in the timing of reproduction.

Results

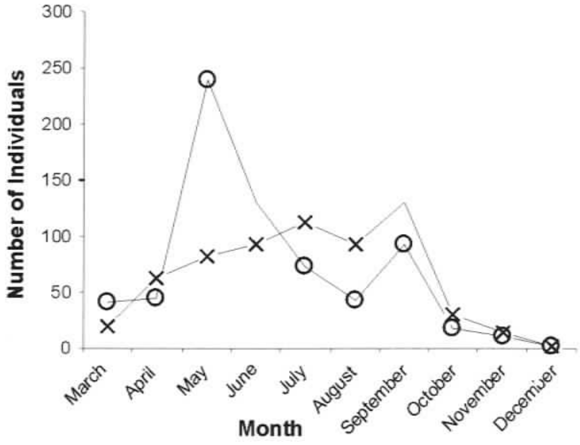
Male and female abundance was highest in the ancient forest habitat but more immatures were found in the regenerating clear-cut ($\chi^2_{2,\,0.05} = 99.9$, $P<0.001$). Peak abundances for males, females, and immatures in the ancient forest habitat occurred in May and June sampling periods (Figure 3.1). Abundances in the regenerating clear-cut varied: male abundances peaked in September, females in May and September, and immatures were numerous from July through September.

Forty of the 113 species (14 families) collected over two years were classified as "winter-active" and 60 % of these were linyphiid species (Table 3.1). Other families with winter-active representatives included: Cybaeidae and Hahniidae, with two species each, and those represented by only one species: Amaurobiidae, Anyphaenidae, Araneidae, Lycosidae, Mecicobothriidae, Philodromidae, Pimoidae, Salticidae, Telemidae, Tetragnathidae, and Theridiidae. These are predominantly web-builders.

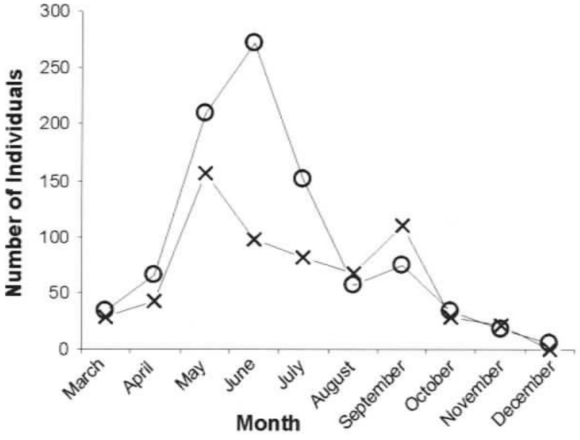
Life histories were summarized for species where 15 or more adults were collected (Figure 3.2). Six of the 12 species in the regenerating clear-cut showed a spring/summer stenochronous life cycle, while four are eurychronous; one, *Helophora reducta,* reproduced in the fall. No *Bathyphantes brevis* males were recorded so reproductive timing is not determined. The ancient forest-inhabiting species had predominantly fall stenochronous and eurychronous life histories. Two winter-mature species occurred in the ancient forest, and two of the thirteen species reproduced in the spring. Species that used both habitats exhibit the range of life-history patterns. The percent contributions for each life history are presented in Table 3.2.

No observable difference in the timing of reproduction is apparent between species of *Tetragnatha, Clubiona,* and *Cybaeus* (Figure 3.2). *Linyphantes* sp. 2 was spring stenochronous and others of this genus had reproductive peaks in the fall. Four species used both the ancient forest and regenerating clear-cut habitats in approximately equal

a) Males



b) Females



c) Immatures

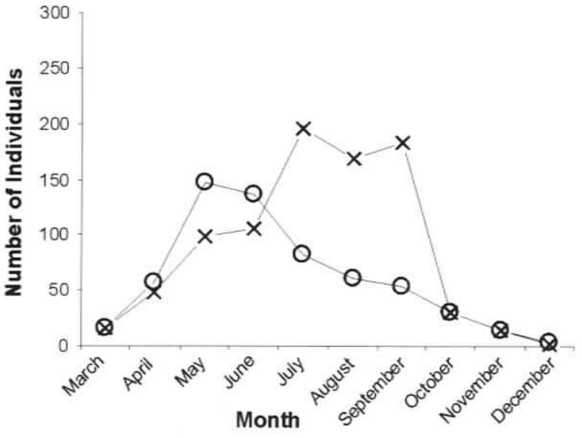


Figure 3.1. Total abundance (all traps pooled over all trapping intervals) of adult and immature spiders collected in the Carmanah Valley in 1997 in two habitats: the regenerating clear-cut (X) and the ancient forest (O).

Table 3.1. Spider species reported from the Carmanah Valley. Species collected in Malaise traps in November and December of 1996 and 1997 are denoted as winter-active. Species represented by 15 or more individuals have their life histories indicated. Nomenclature and classification follow Platnick (2008).

Spider Species	Winter Active	Life History
ANTRODIAETIDAE		
Antrodiaetus pacificus (Simon)		fall stenochronous
MECICOBOTHRIIDAE		
Hexura picea Simon	+	
TELEMIDAE		
Usofila pacifica (Banks)	+	
MIMETIDAE		
Ero canionis Chamberlin & Ivie		
ULOBORIDAE		
Hyptiotes gertschi Chamberlin & Ivie		
THERIDIIDAE		
Achaearanea sp. 1		
Enoplognatha ovata (Clerck)		
Neottiura bimaculata (Linnaeus)		
Rugathodes sexpunctatus (Emerton)	+	eurychronous
Theridion californicum Banks		
Theridion saanichum Chamberlin & Ivie		
PIMOIDAE		
Pimoa altioculata (Keyserling)	+	eurychronous
LINYPHIIDAE		
Agyneta sp. 1		spring/summer stenochronous
Agyneta sp. 2		
Bathyphantes alascensis (Banks)		
Bathyphantes brevis (Emerton)	+	
Bathyphantes keeni (Emerton)	+	winter mature
Bathyphantes orica Ivie	+	
Ceraticelus atriceps (O.P.-Cambridge)		
Ceratinella acerea Chamberlin & Ivie		
Ceratinella alaskae Chamberlin & Ivie		
Ceratinella cf. alaskana		
Ceratinella ornatula (Crosby & Bishop)		
Ceratinops inflatus (Emerton)		

Table 3.1 (*continued*)

Spider Species	Winter Active	Life Cycle
Ceratinopsis nr. *gosibia*		
Disembolus sp. 1		
Erigone aletris Crosby & Bishop	+	
Erigoninae sp. 1	+	
Erigoninae sp. 2		
Erigoninae sp. 3	+	
Erigoninae sp. 4		
Helophora reducta (Keyserling)	+	fall stenochronous
Linyphantes nr. *eureka*	+	
Linyphantes orcinus (Emerton)		
Linyphantes pualla Chamberlin & Ivie	+	fall stenochronous
Linyphantes sp. 1	+	fall stenochronous
Linyphantes sp. 2		spring/summer stenochronous
Linyphantes sp. 3	+	fall stenochronous
Linyphantes sp. 4		
Linyphantes sp. 5		
Meioneta sp. 1		
Meioneta sp. 2	+	
Meioneta sp. 3		
Mermessus trilobatus (Emerton)		
Microlinyphia dana (Chamberlin & Ivie)	+	fall stenochronous
Microneta viaria (Blackwall)		
Mythoplastoides erectus (Emerton)		
Neriene digna (Keyserling)	+	spring/summer stenochronous
Oreonetides filicatus (Crosby)		
Oreonetides sp. 1		spring/summer stenochronous
Pacifiphantes magnificus (Chamberlin &Ivie)		
Pelecopsis sculpta (Emerton)		
Pityohyphantes rubrofasciatus (Keyserling)		
Pityohyphantes sp. 1	+	fall stenochronous
Pocadicnemis pumila (Blackwall)	+	eurychronous
Porrhomma convexum (Westring)		
Saaristoa sammamish (Levi & Levi)		
Scotinotylus columbia Chamberlin	+	
Scotinotylus patellatus (Emerton)		spring/summer stenochronous
Scotinotylus sp. 1	+	
Sisicottus nesides (Chamberlin)		
Spirembolus vasingtonus Chamberlin		
Symmigma minimum (Emerton)		
Tachygyna ursina (Bishop & Crosby)	+	eurychronous
Tapinocyba dietrichi Crosby & Bishop	+	
Tapinocyba sp. 1	+	
Tenuiphantes zelatus (Zorsch)		
Tenuiphantes zibus (Zorsch)	+	
Walckenaeria cornuella (Chamberlin & Ivie)		

Table 3.1 (*continued*)

Spider Species	Winter Active	Life Cycle
Wubana pacifica (Banks)	+	
Wubana suprema Chamberlin & Ivie	+	winter mature
TETRAGNATHIDAE		
Metellina curtisi (McCook)	+	eurychronous
Tetragnatha laboriosa Hentz		spring/summer stenochronous
Tetragnatha versicolor Walckenaer	+	eurychronous
ARANEIDAE		
Araneus nordmanni (Thorell)		
Araneus saevus (L.Koch)	+	
Araneus trifolium (Hentz)		
Araniella displicata (Hentz)		
Larinioides sp.		
LYCOSIDAE		
Pardosa dorsuncata Lowrie & Dondale	+	eurychronous
OXYOPIDAE		
Oxyopes scalaris Hentz		
CYBAEIDAE		
Cybaeus eutypus Chamberlin & Ivie	+	fall stenochronous
Cybaeus reticulatus Simon	+	fall stenochronous
Cybaeus signifer Simon		
HAHNIIDAE		
Calymmaria emertoni (Simon)		
Cryphoeca exlineae Roth		
Dirksia cinctipes (Banks)	+	fall stenochronous
Ethobuella tuonops Chambelin & Ivie	+	eurychronous
DICTYNIDAE		
Emblyna peragrata (Bishop & Ruderman)		
AMAUROBIIDAE		
Callobius pictus (Simon)	+	eurychronous
ANYPHAENIDAE		
Anyphaena aperta (Banks)	+	
Anyphaena pacifica (Banks)		
CLUBIONIDAE		
Clubiona pacifica Banks		spring/summer stenochronous

Table 3.1 (*continued*)

Spider Species	Winter Active	Life Cycle
Clubiona trivialis C.L.Koch		eurychronous
CORINNIDAE		
Castianeira longipalpa (Hentz)		
GNAPHOSIDAE		
Micaria pulicaria (Sundevall)		
Sergiolus montanus (Emerton)		
Zelotes puritanus Chamberlin		
PHILODROMIDAE		
Apollophanes margareta Lowrie & Gertsch		
Philodromus rufus pacificus Banks	+	spring/summer stenochronous
Tibellus oblongus (Walckenaer)		spring/summer stenochronous
THOMISIDAE		
Misumena vatia (Clerck)		
Ozyptila pacifica Banks		
Xysticus locuples Keyserling		
Xysticus montanensis Keyserling		
Xysticus pretiosus Gertsch		spring/summer stenochronous
SALTICIDAE		
Evarcha proszynskii Marusik & Logunov		spring/summer stenochronous
Habronattus hirsutus (Peckham & Peckham)		
Habronottus oregonensis (Peckham & Peckham)		
Pelegrina aeneola (Curtis)		
Phanias albeolus (Chamberlin & Ivie)	+	
Phidippus johnsoni (Peckham & Peckham)		
Salticus scenicus (Clerck)		

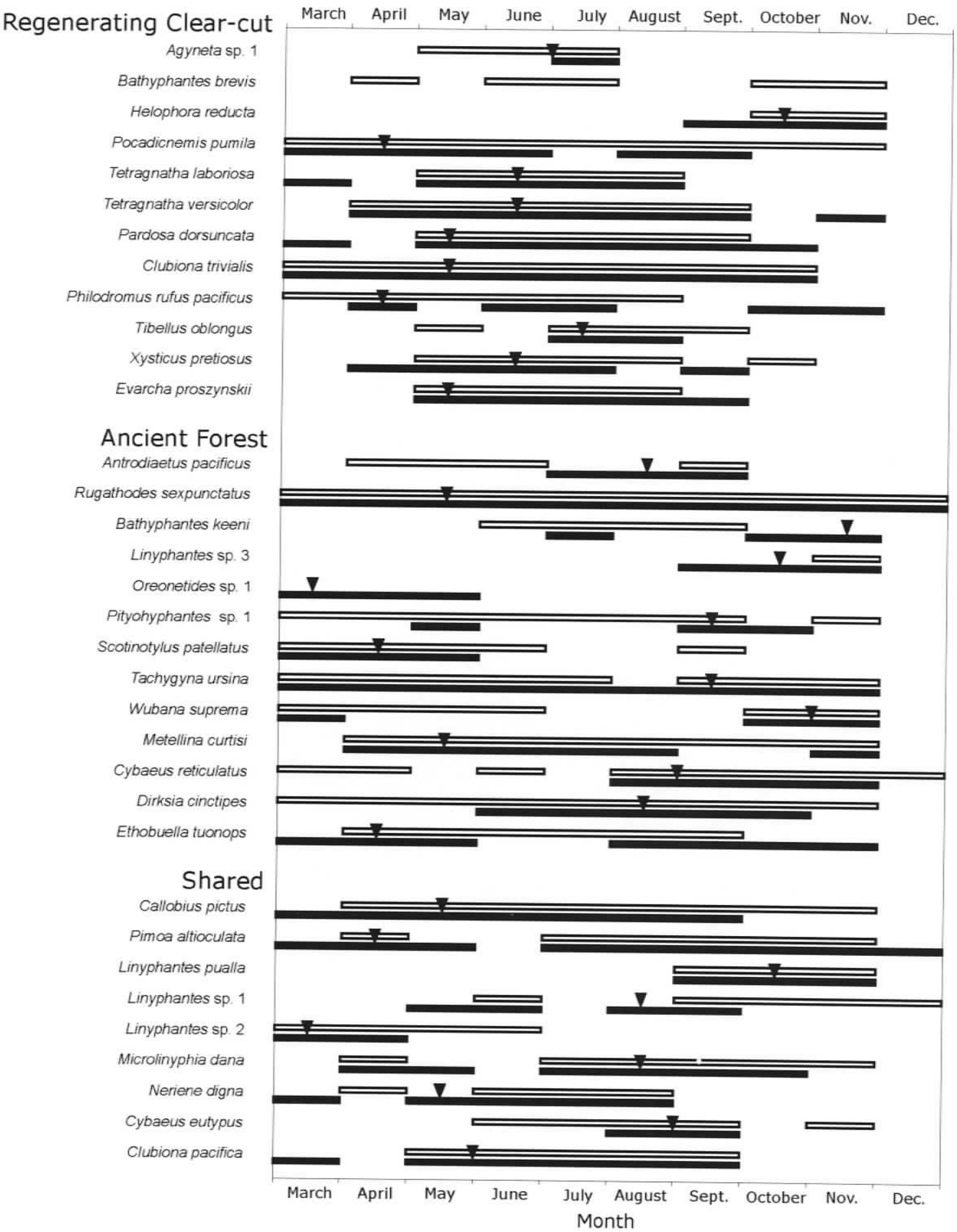


Figure 3.2. Life histories of spider species (males: ■, females: □) in the regenerating clear-cut and an ancient forest in the Carmanah Valley. Species represented by 15 or more individuals were used and presence/absence information is presented monthly from pooled 1996 and 1997 collections. Peak male abundances (▼) were determined based on trapping information from 1997 data. Nomenclature and classification follow Platnick (2008).

Table 3.2. Life histories exhibited by spider species in a regenerating clear-cut and an ancient forest in the Carmanah Valley. Data are based on all trap collections in both 1996 and 1997.

	Habitat Type			
Life history	**Regenerating Clear-cut**	**Ancient Forest**	**Shared**	**Overall**
Eurychronous	4 (36%)	4 (31%)	2 (22%)	10 (30%)
Spring/Summer Stenochronous	6 (55%)	2 (15%)	3 (33%)	11 (33%)
Fall Stenochronous	1 (9%)	5 (38%)	4 (44%)	10 (30%)
Winter Mature	0	2 (15%)	0	2 (6%)
Number of Species	11	13	9	33

abundances (Figure 3.3). There is no apparent shift in the reproductive timing of either sex in these species.

Discussion

Life-History Trends

Species that favour the regenerating clear-cut habitat also tend towards spring/summer stenochronous and eurychronous life histories; none are winter-mature species and only one overwinters as eggs (fall stenochronous). Previous studies have shown that some disturbance-adapted species are capable of withstanding a greater range of temperatures (Huhta 1971) and are eurychronous to ensure that there are always various life stages present (Draney and Crossley 1999). No pattern of increased eurychrony was evident in the Carmanah Valley. Although daily temperature ranges were greater in the regenerating clear-cut and differed by an average of 4°C compared to the ancient forest (Winchester *et al.* 2002), the number of eurychronous species was equivalent in the two habitat types. Winter-mature species only occurred in the ancient forest. These are species that seek mates and reproduce in conditions unfavourable for an ectotherm. Perhaps these species require the moderate conditions of the ancient forest: more stable temperatures (Winchester *et al.* 2002), predictable moisture levels, and moss and duff-layer micro-habitats (Huhta 1965). In contrast, Niemelä *et al.* (1994), working in a 140 year-old boreal forest, did not report any fall stenochronous or winter-mature species and suggested spring or summer stenochrony was a response to the short growing season in the north.

The Carmanah Valley had an even representation of the three most common life-history types compared to a previous study of spiders in northern Germany, where almost

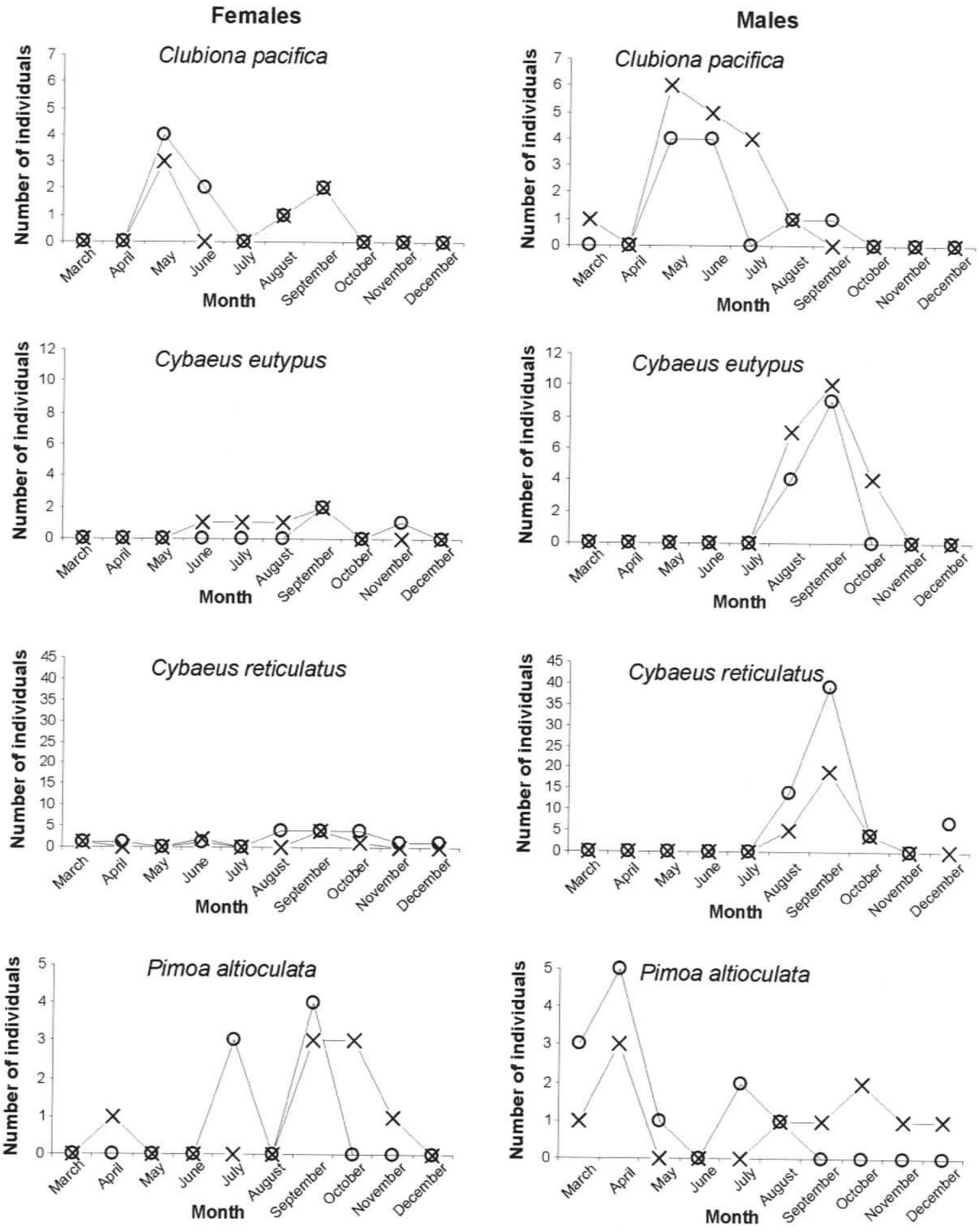


Figure 3.3. Phenological comparison by habitat of spider species that were equally abundant in the regenerating clear-cut (X) and ancient forest (O) and where more than 15 adults of each species were collected (1997 data).

half (45%) were spring/summer stenochronous, with immatures the primary overwintering stage (Schaeffer 1977). Unlike the results of Schaeffer (1977), this preliminary investigation in the Carmanah Valley does show some evidence for inter-taxa similarities in phenology. Toft (1976, 1978, 1979) did report patterns of life histories in species inhabiting the same general region and attributed these findings to the scale of the study; species inhabiting the same strata in a beech forest (litter, shrub layer, and canopy) tended to exhibit similar life-history patterns.

Effect of Forest Succession on Spider Phenology

Species using both habitats did not show a shift in reproductive timing despite the reported temperature difference between the two habitats (Winchester *et al.* 2002). Adult spiders were more abundant in the ancient forest compared to the regenerating clear-cut during the late spring and early summer. In contrast, the regenerating clear-cut had more immature spiders present during July, August and September, but otherwise numbers in both habitats were similar.

A possible reason for the increase in immatures relates to ballooning, a behaviour seen most frequently in young spiders (Dean and Sterling 1985; Bishop 1990). The clear-cut habitat had greater wind speeds reported than those of the ancient forest (Winchester *et al.* 2002), facilitating more frequent dispersal through ballooning (Bishop 1990). Many families that have a tendency to balloon (Linyphiidae, Lycosidae, Theridiidae, Salticidae and Thomisidae) are disturbance-adapted, and would inhabit the regenerating clear-cut (Meijer 1977; Southwood 1962; Crawford *et al.* 1995). The trapping technique used for this study may also be biased towards ballooning spiders, helping to explain the pattern observed for immatures.

Although ballooning can explain the increased number of immatures in the clear-cut, the abundance pattern of adult spiders is only partially explained by this phenomenon. Adult spiders also balloon and both sexes use this dispersal mechanism in the fall (Dean and Sterling 1985). Females of the Linyphiidae, the most aeronautical spider family, balloon significantly more than males (Meijer 1977; Southwood 1962) and in the Carmanah Valley many more female spiders were captured than males, perhaps reflecting this phenomenon.

It is not clear why there is a spring/summer peak in overall adult abundance in the ancient forest compared to the regenerating clear-cut. A greater degree of overwintering success due to the reduced extremes of temperature and the presence of more micro-habitats may be a contributing factor. However, the difference in the abundance peaks evident in the ancient forest may be accounted for by different activities. For instance, male spider activity has been linked to mate-seeking behaviour and female spider activity is associated with looking for oviposition sites (Draney 1997).

Winter-Active

Thirty-five percent of species are winter active, supporting the results of Aitchison (1984b; 1989). The overwintering stage in more extreme climates is often the immatures (Aitchison 1984b; Gunnarsson 1987), although 95% of the winter-active species in the Carmanah Valley were represented by at least one adult. The families that overwintered in the Carmanah Valley included the eleven reported to be winter-active by Aitchison (1984b) in Manitoba and six by Gunnarsson (1987) in Sweden.

Aitchison's (1989) study involved pitfall trapping November to mid-April, as well as soil and leaf litter sampling. I used November and December to accommodate the earlier spring on Vancouver Island compared to that of Manitoba, and the Malaise trapping technique in the Carmanah captured species several feet from the ground. For these reasons the number of winter-active species found in the Carmanah Valley must be considered an underestimate in terms of the number of taxa. Two species that were previously shown to be winter-active (Aitchison 1984a) were collected in this study but were not collected in the winter. This suggests there is life history flexibility within species (Dondale 1977; Duffey 1978; Draney 1997; Buddle and Draney 2004).

Reproductive Timing of Closely-related Species

Previous studies suggest that competitive interactions between closely related species may drive shifts in reproductive timing (Berry 1971; Dondale 1977; Buddle and Draney 2004). This study did not support this pattern, although there are differences in the habitats preferred by closely related species. The species that overlap to the greatest extent are *Tetragnatha laboriosa* and *T. versicolor*; both preferred the regenerating clear-cut habitat and had peak male abundances in June. These species may be partitioning the available habitat. *Tetragnatha versicolor* was found near the creek edge 77% of the time, compared to *T. laboriosa*, 17%. The overlap of the reproductive timing of related species in the Carmanah is a result similar to that of Toft (1979), Niemelä *et al.* (1994), and Draney (1997).

Timing and Methodology

Phenological information can be used to determine sampling time for particular species, ensuring the species are present as adults - the life stage used to reliably identify spider species (Dobyns 1997; Cardoso *et al.* 2007). Sampling effort and timing are difficult to reduce without a loss of information (Dobyns 1997). For example, if the

Carmanah sampling had been restricted to May through September, the typical timeframe of arthropod surveys in northern regions, 20 species would not have been collected. Five additional species would have been missed if sampling had only occurred in 1997. Spiders use a range of life-history strategies and some are long-lived and can occur at relatively low densities; thus inventories can be improved if sampling is conducted over a year or more (Dobyns 1997). For example, in a study designed to test sampling methodology, Scharff *et al.* (2003) reported that 31 species occurred as only one or two specimens, even though the area was intensively collected. In the Carmanah Valley many species were rarely collected.

Ecological studies involving spiders typically use pitfall trapping. This results in two major biases. First, males are reported far more frequently than females due to their wandering behaviour associated with mate-seeking (Muma and Muma 1949). Second, ground-inhabiting spiders dominate these collections (Adis 1979). Active collecting (Miyashita 1969) or extracting specimens from entire sections of soils (Muma and Muma 1949; Hauge 1976) acquires spiders in a more balanced manner and shows a pattern similar to this Malaise trapping study: females generally significantly outnumber males. Interestingly, Malaise traps neither appear to be biased against ground-inhabiting spiders nor towards actively ballooning immature specimens. For example, *Pardosa dorsuncata,* a ground-inhabiting species, was the seventh most commonly collected species in the regenerating clear-cut. Also, *Antrodiaetus pacificus*, a species that rarely balloons (Crawford and Edwards 1986) was collected. Immature specimens did not dominate the collections as one would expect if traps were catching predominantly ballooning spiders; they were outnumbered by adults of both sexes.

Sample sizes in this study are relatively small, so although Malaise trapping potentially provides a more balanced view of the species assemblage, more thorough sampling is required to clarify species' phenologies. Malaise trapping is a measure of activity level rather than density and many authors have shown that year-to-year weather variation has a significant influence on phenological and abundance patterns (Duffey 1962; Huhta 1971).

Conclusion

Information about spider habitat preferences often comes from taxonomic work, and life-history and habitat requirements in general still need to be elucidated (Varady-Szabo and Buddle 2006). In the Carmanah Valley, several spider taxa showed winter activity, and 30% of the species exhibited a eurychronous life cycle, likely a reflection of the overall moderate climate. Reproductive timing was not impacted by habitat, but species abundances and other life-history trends did show an effect of habitat. Species in the regenerating clear-cut tended towards spring and summer reproduction, in comparison to the ancient forest which had more species that reproduced in the fall plus two winter-maturing species.

Chapter 4. Summary

The spider fauna of the Carmanah Valley, Vancouver Island, British Columbia was examined to determine differences in species assemblages in a regenerating clear-cut and an ancient forest, and to characterize the life histories of the spiders. Twenty-three families (113 species from 76 genera) were collected using Malaise traps set perpendicular to the riparian corridor formed by Carmanah Creek.

Richness and evenness were similar in the two habitats, but diversity, both observed and estimated, was higher in the regenerating clear-cut compared to the ancient forest. Higher diversity in the regenerating clear-cut is attributed to the effects of succession and the presence of transitional species. When richness and abundance were incorporated into a comparison of the spider species assemblages, they differed significantly. Based on previous studies, it may take decades for the composition of the spider species assemblages in these two habitats to converge (McIver *et al.* 1992; Buddle *et al.* 2000; Peck and Niwa 2004).

Although many species were reported from both habitats, the distinct habitat preferences of some species were reflected in the guild analysis - web-building species were more common in the ancient forest compared to the regenerating clear-cut. The presence of web-building species has been linked to temperature, humidity, and litter depth (Huhta 1971; Coyle 1981; Bultman and Uetz 1982), characteristics that differ between ancient forests and recently logged habitats (Huhta 1971).

Eight species had a non-random distribution pattern relative to the riparian corridor, and two species that declined in abundance are known to derive a significant portion of their prey from emerging aquatic insects (Marczak and Richardson 2007). Some disturbance-adapted species were only associated with the creek edge in the ancient forest, and riparian corridors may be the typical habitat of these species in these forests (Buddle *et al.* 2004).

Spiders that preferred the regenerating clear-cut often had spring/summer stenochronous life histories, and no winter-maturing species were reported. Species that used both habitats did not show a shift in the timing of reproduction, despite differences in abiotic conditions between the ancient forest and the regenerating clear-cut (Winchester *et al.* 2002). Congeneric species had similar phenologies, but may be partitioning the habitat in other ways. Several spider taxa showed winter activity, while 30% of the species in the Carmanah Valley exhibited a eurychronous life cycle, likely a reflection of the overall moderate climate.

The trapping technique used in this study is not typical of ecological studies involving spiders, where pitfall trapping is the standard. The expected biases in Malaise trapping against ground-inhabiting spiders and towards actively ballooning immature specimens were not seen. In terms of sex ratios, the collections matched the more balanced results of litter extractions, where females outnumber males (see Muma and Muma 1949; Hauge 1976).

Because the Carmanah Valley would have experienced very little in the way of natural perturbation before the advent of industrialized logging (Lertzman *et al.* 2002), there is nothing functionally equivalent in nature to this form of disturbance. How the conversion of these ancient forests to second-growth habitats affects arthropod assemblages has been documented in only a small number of taxa. This study provides a summary of the spider species assemblages in these two habitats a decade after logging.

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