DIVERSITY OF LITTER SPIDERS (ARANEAE)
IN A SUCCESSIONAL DOUGLAS-FIR FOREST IN BRITISH COLUMBIA

by

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to the required standard

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ABSTRACT

Litter spiders were collected at two locations by pitfall trapping: Victoria Watershed South, and Koksilah, located on south-eastern Vancouver Island, British Columbia. Sites were in Douglas-fir forest (in the Coastal Western Hemlock region) and contained four forest successional stages: Regeneration (3-8 years), Immature (25-45 years), Mature (65-85 years), and Old-Growth (>200 years). Thirty-two species were collected in families selected to represent litter spiders. Several of the collected species are listed as potentially rare and endangered in British Columbia. The collection of *Zora hespera* is the first record of the family Zoridae in Canada. Intraspecific comparisons revealed three distinct distribution patterns: generalists, regeneration specialists, and intermediate forest specialists (spiders prefering the Immature and Mature successional stages). These patterns can be related to biological information regarding individual species. Species richness measures and diversity indices indicated that the regeneration sites have the greatest species richness. There was no significant difference between the remaining three successional stages. Factors affecting the distribution of spider species in the forest litter are discussed.

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INTRODUCTION

Since the 1992 Earth Summit in Brazil, biodiversity and its potential loss have received extensive media and scientific attention (Heywood 1995). Awareness regarding international and local environmental issues has motivated conservation research and political action. In Canada, there are numerous threats to biodiversity preservation including agriculture, atmospheric changes, deforestation, environmental stresses, exotic introductions, and urbanization (Biodiversity Science Assessment Team 1994).

The consequences of habitat loss impact all phyla, but the impact on arthropods is exceptional. This phylum possesses the greatest biomass, diversity, and abundance of all animals on earth. Arthropods participate in all trophic levels, except primary production, and contribute to numerous ecological services such as pollination, decomposition, and biological control. Arthropods inhabit all ecosystems from the Arctic Circle to Antarctica, and their presence or absence is important to the distribution, abundance and diversity of both plants and vertebrates (Miller 1993).

Despite this, in western society public perception of most arthropods is negative, excluding those with obvious economic or aesthetic qualities (Kim 1993), and to date, most conservation research has focused primarily on large vertebrates, especially mammals with charismatic features. Amazingly, current conservation management is based upon knowledge of only 15% of extant species (Kim 1993), while species presently unknown are twice as likely to become extinct than to be discovered and described (Stork 1993). Estimates of exact

global species richness remain a contentious issue, but there is little argument that the number of undiscovered arthropod species is in the millions (May 1994).

Knowledge of extirpation and extinction of a species is defined, recognized, measured, and assessed only if the species is identified (Eldredge 1992), and the recognition of described and undescribed species is impossible without taxonomic expertise. In North America there are only a few hundred taxonomists able to identify insects and arachnids, and these numbers are dwindling. The University of Alberta's world renowned systematic entomology program is currently being phased out. Canadian federal taxonomist positions have decreased by 50% in the last 20 years; and in academia, only seven faculty systematist positions remain (Idema 1993). Ironically, taxonomic needs are currently increasing with the accumulation of new information. Owing to the complexity of taxonomy, direct transfer of information between a mentor and student is essential, as taxonomic information (essential for species identification) is not easily interpreted from the literature. Taxonomic research may assist in recognition of endangered species, endemism, and species richness, thereby assisting in the establishment of conservation priorities for different habitats (Novacek 1992, Cotterill *et al.* 1994).

Fortunately, this preclusive vertebrate bias is changing. Scudder's (1994) list of potentially rare and endangered invertebrates in British Columbia brings much needed recognition to this group of organisms and there is increasing interest in the use of arthropods as indicators of ecological health (Danks 1996).

In British Columbia the ecological health of the forest is a prominent issue because of forestry and silvicultural practices. Conversion of forests from old-growth to secondary growth has caused deep public polarization over logging in British Columbia. Approximately 50% of the Canadian and 20% of the North American total standing softwood is located in B.C. (MacKinnon *et al.* 1991), the harvesting of which contributes substantially to the British Columbian economy. The British Columbian Coastal Western Hemlock (CWH) region is the most productive forest region in Canada, and the majority of this region is designated for forestry (Pojar *et al.* 1991). Owing to harvesting practices and natural disturbances in the last century, a unique mosaic of successional stages are located in close proximity within this forest region.

To increase ecological understanding of this forest region on southern Vancouver Island, in 1991 the Canadian Forest Service (CFS) under the Forest Ecosystem Dynamics Program, initiated a comprehensive ecological study of coastal forest chronosequences. Intensive field investigations involving ecosystem description, ecosystem processes, and biological diversity of the soil fauna and flora, small vertebrates and plant communities began in 1992. The focal point of this work was at sites on south-eastern Vancouver Island (Figure 1) (Pollard and Trofymow 1993).

Craig (1995) studied the carabid beetle fauna of a chronosequence at two of these sites. This investigation assessed the influence of current forestry practices on the carabid beetle fauna; specifically, it evaluated the variation in the ground-beetle fauna in four forest

Biogeoclimatic Zones

- ☐ Coastal Western Hemlock
- Coastal Douglas-fir / Dry Coastal Western Hemlock
- Mountain Hemlock
- ■ Alpine Tundra

⊢——⊣ 50 km

Koksilah

Victoria Watershed South
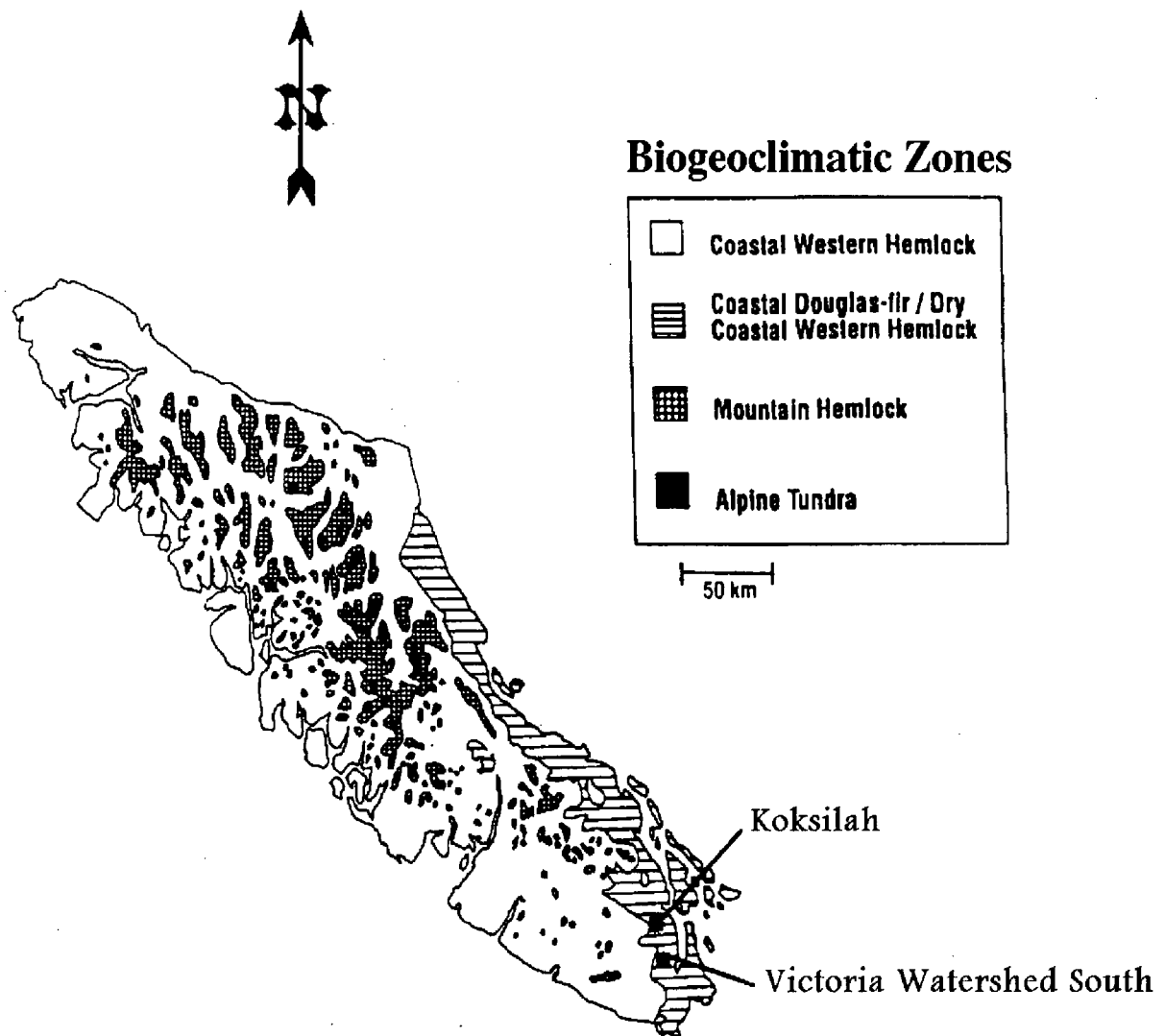
* The western part of the Coastal Douglas-fir zone has recently been transferred to the Dry Coastal Western Hemlock zone (see Meidinger and Pojar 1991)

Figure 1. Locations of forest chronosequences (referred to as Victoria Watershed South and Koksilah) where intensive field investigations (including litter spider collection) took place (From Pollard and Trofymow 1993).

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successional stages, regeneration, immature, mature, and old-growth. Carabids are generalist predators and species have been grouped based on habitat preferences. They are one example of the use of an arthropod as an ecological indicator of forest habitat quality (Niemelä et al. 1993, Craig 1995).

Spiders are also potential ecological indicators (Uetz 1991, Wise 1995, McIver et al. 1992). Spiders are abundant, obligate predators near the top of the invertebrate food chain (Coddington et al. 1991). Examination of soil and litter fauna reveals a dense population of spiders in most terrestrial habitats (Moulder and Reichle 1972). More strictly predaceous than carabid beetles (Wise 1995, Larochelle 1990), spiders, along with carabids and formicids, are the most conspicuous arthropod predators in many western forests (Parsons et al. 1991). In some forests, spiders rank as the most important invertebrate predator of cryptozoans for their numbers and biomass (above both Chilopoda and predaceous Coleoptera) (Moulder and Reichle 1972). They are potentially a regulating influence on prey populations (Clarke and Grant 1968), and contribute high quality detritus to the forest floor (McIver et al. 1992). Spider predation also helps to reduce numbers of certain pest species in coniferous forests (Jennings et al. 1983).

The environmental structure is an important influence on habitat preference for spider species, and on the composition of spider communities, as both web and non-web building species depend primarily on sensory modalities for environmental information (Uetz 1991). Microhabitat selection is dependent on leaf litter composition, landscape features, and canopy

closure, which in turn affects prey abundance, refuge, and microclimatic conditions, all of which are subject to change with the transformation in plant structure that accompanies succession.

Spider species are placed in various guilds based on habitat preference, prey preference and web use (Bultman *et al.* 1982). Diurnal and nocturnal litter spiders are placed in different guilds that reflect their specific utilization of the litter layer (Post and Riechert 1977). Nocturnal and diurnal spiders exhibit specific sensory differences. Nocturnal spiders are more likely to rely on tactile and chemical cues than sight, while vision is more important in the diurnal hunters (Foelix 1982).

The composition of the litter spider community changes in a successional forest (Jennings *et al.* 1988, McIver *et al.* 1992, Huhta 1971). Young regenerative stands are dominated by diurnal pursuit spiders. Immature stands are dominated by both diurnal and nocturnal running spiders, while mature stands are dominated by diurnal salticids (jumping spiders) (McIver *et al.* 1992).

This dependence on environmental structure gives spiders a unique perceptual bias. Foraging and hunting spiders are likely to be highly sensitive to the physical arrangement of objects in space, yet are not influenced by vegetative structures for web supports. This makes them excellent organisms to examine the ecological impacts of habitat structure; which may provide some information which can be generalized to other predaceous taxa (Uetz 1991).

Many spiders are short lived, and exhibit a clear and rapid response to changes in habitat quality (McIver *et al.* 1992). Assays of litter spiders may be useful in areas where, owing to post-cut treatments (shrub removal or prescribed burning), plant species composition no longer reflects habitat quality (McIver *et al.* 1992). Additionally, some groups of spiders are relatively easy to identify, and exist on the forest floor in numbers great enough to allow sufficient material for collection.

Despite this, little is known of species composition, diversity, or abundance of spiders that inhabit individual forest stands, forest-stand types or forest communities in North America (Jennings *et al.* 1988, Halaj *et al.* 1996). An essential prerequisite for any ecological research is a baseline faunal list of the area (Marshall 1993). In British Columbia, there are over 600 known species of spiders (West *et al.* 1984, West *et al.* 1988); and of the approximately 100 species listed as potentially rare and endangered, more than 30 of these are located on Southern Vancouver Island (Scudder 1994). Using collections assembled by Craig (1995), the litter spider fauna of Victoria Watershed South and the Koksilah Watershed are the focus of my ecological study. The specific objectives of this study are as follows:

1. Characterize the litter spider fauna in four successional stages
   (Regeneration/Immature/Mature/Old-Growth)
   and establish baseline faunal information

2. Describe any changes in litter spider fauna after clear-cut logging

3. Relate any faunal changes to biological information and habitat conditions.

MATERIALS AND METHODS

Study Area

The two study locations are located on South-East Vancouver Island (Figure 1). Victoria Watershed South is located at the south end of Shawnigan Lake. Koksilah is located south-west of Duncan (for exact locations and descriptions see Appendix A). These two sites were among several selected by the Canadian Forest Service as part of an extensive ecological study of coastal forest chronosequences.

Koksilah and Victoria Watershed South are located in the Very Dry variant of the Coastal Western Hemlock (CWHxm) biogeoclimatic zone (Pollard and Trofymow 1993). The dominant overstory species is Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), in addition to Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), salal (*Gaultheria shallon* Pursh), and step moss (*Hylocomium splendens* (Hedw.) B.S.G.) (Pojar *et al.* 1991). Blackwell and Trofymow (1993) found that plots equivalent in age contain similar tree species, composition, and stand density.

Each of the selected sites lies within a 5 x 5 km or smaller area, and contains stands of four ages (known as a chronosequence) with similar slope, elevation and aspect (within 200 m, and a midslope below 600 m) (Pollard and Trofymow 1993).

The chronosequence is represented by stands aged in 1990 as follows: Regeneration (3-8 years), Immature (25-45 years), Mature (65-85 years), and Old-growth (> 200 years).

Most of the second-growth stands are of harvest origin, although some of the mature stands are of wildfire or landslide origin. The old-growth stands served as experimental controls for between-site variability and are representative of pre-harvest conditions (Pollard and Trofymow 1993).

There is a considerable difference in the amount of ground cover and litter found in different successional stages. Generally, herb species richness increases with logging (i.e. in the regenerative stage), but cryptogam richness decreases, which modifies the litter layer between stages (Ryan and Fraser 1993). The humus layer also increases with stand age. In many parts of the regenerative stage the topsoil has been removed.

The Canadian Forest Service marked off a 60 m x 60 m plot in each successional stage. Within this plot, eight 10 m x 10 m subplots were allocated for this study (Figure 2) (Blackwell and Trofymow 1993).

Traps and Trap Placement

The following description of traps, trap placement, and trap collection is taken from Craig (1995). Three pitfall traps were randomly placed in each of the eight 10 m x 10 m subplots. Random locations were designated by the hypothetical division of the plots into 100 squares. Using a random number table from Zar (1984), three squares were selected with trap placement in the center of the selected square. If the designated site for the trap was inappropriate due to a rock, tree, or log, the cup was placed in the nearest accessible location.
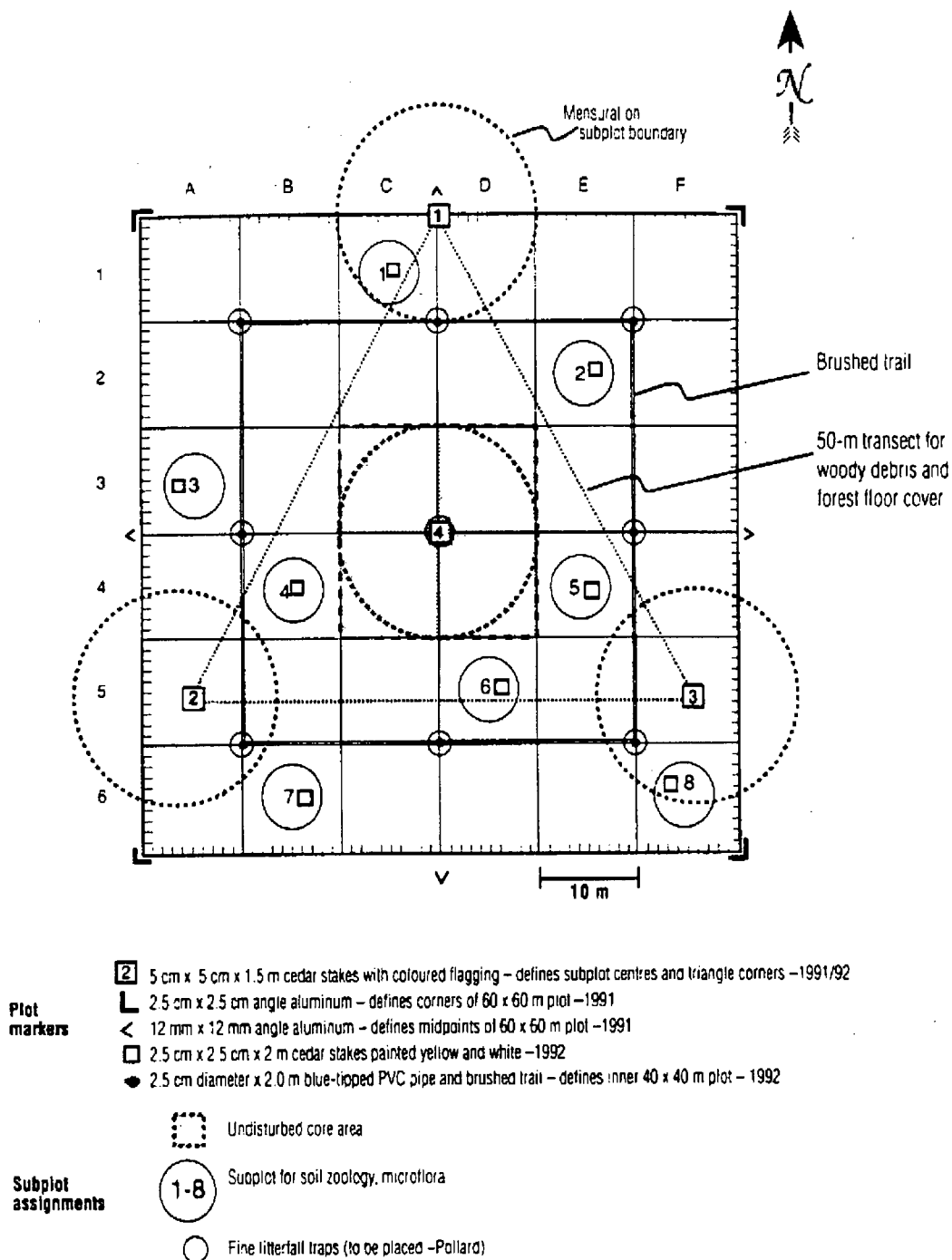
Figure 2. Example of plot layout and subplots assignments provided by the Canadian Forest Service. Circled areas number 1-8 were locations of pitfall traps for litter spider collection (From Blackwell and Trofymow 1993).

The trap consisted of two 450 ml (approximately 9 cm in diameter at the opening and 35 cm in depth) disposable plastic drinking cups nested within each other. The two cups differed slightly in size so that the nested rims were flush. Progress Plastic Disposables Ltd. manufactured the inner cup, and Portion Packaging manufactured the outer cup. The traps were placed in holes in the ground so that the cup rim was flush or slightly below the ground's surface as recommended by Winchester and Scudder (1993).

Each trap was covered by a 19 cm by 19 cm rough-cut cedar roof mounted upon four 4 cm wooden legs to shelter the opening from rain, snow, and debris.

The inner cups were filled with non-toxic 35% propylene-glycol (made for veterinary use). This non-volatile preservative allowed the cups to remain in the field unattended for the length of the collection period. Organisms that fell into the cup would be killed by drowning and preserved. Rapid death also prevented predation of cup occupants.

Trap collection method was as follows: the inner cup was removed (containing the propylene-glycol and trapped organisms) and the propylene-glycol was strained through a fine-mesh, plastic strainer into a new inner cup. This new cup was then placed back into the undisturbed outer cup that remained in the ground. The contents of the strainer were transferred to plastic specimen jars and covered with 70% ethyl alcohol as recommend by Martin (1977). These jars were transferred to the University of British Columbia laboratory for sorting and specimen identification.

During collection, each trap was inspected to ensure that it remained flush to the ground. Additional propylene-glycol was added as necessary. Of the 1440 analyzed traps, only 20 (1.39%) were damaged beyond use. Damaged and missing traps were documented and replaced.

Traps were set at Victoria Watershed South on May 20, 1992, and at Koksilah on May 26, 1992. Trap samples were collected at approximately monthly periods (Table 1) until August 1993, except for the extended collection period from November 1992 to April 1993 as carabid activity was low at this time.

Table 1. Pitfall trap collection dates.

Collection Number	Victoria Watershed South	Koksilah
1	June 17, 1992	June 23, 1992
2	July 15, 1992	July 28, 1993
3	August 12, 1992	September 1, 1992
4	September 9, 1992	October 7, 1992
5	October 6, 1992	November 25, 1992
6	November 24, 1992	April 7, 1993
7	April 6, 1993	May 12, 1993
8	May 11, 1993	June 9, 1993
9	June 8, 1993	July 7, 1993
10	July 6, 1993	August 18, 1993
11	August 17, 1993	

Sorting and Identification

Specimen cups were received with small vertebrates and carabids previously removed and documented (Craig 1995). Spiders from all collection periods were sorted from the specimen cups into dram vials containing 70% ethyl alcohol, and then counted. Families

chosen for analysis (Table 2) are leaf litter inhabitants, several of which belong to the guild of wandering spiders, a distinct group of spiders that run down their prey on the ground rather than relying on webs for prey capture (Uetz and Unzicker 1976). Spiders were identified to species only from collection periods 1 through 8 (Table 1) at the Victoria Watershed, and 1 through 7 (Table 1) at Koksilah to accommodate different species phenologies. Identification of adult spiders was done using the following taxonomic guides: The crab spiders of Canada and Alaska (Araneae: Philodromidae and Thomisidae) (Dondale and Redner 1978), The sac spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae) (Dondale and Redner 1982), The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae) (Dondale and Redner 1990), The ground spiders of Canada and Alaska (Araneae: Gnaphosidae) (Platnick and Dondale 1992), Spider Genera of North America (Roth 1993), A Revision of the Nearctic Amaurobiidae (Arachnida: Araneida), (Leech 1972), American Agelenidae and some misidentified spiders (Clubionidae, Oonopidae and Sparassidae) of E. Simon in the Muséum national d'Histoire naturelle (Roth 1988), New spiders of the family Agelenidae from Western North America (Chamberlin and Ivie 1937), Nearctic genera of the spider family Agelenidae (Arachnida, Araneida) (Roth and Brame 1972), Agelenid spiders of the genus *Cicurina* (Chamberlin and Ivie 1940), and The systematics of the North American cybaeid spiders (Araneae, Dictynoidea, Cybaeidae). (Bennett 1991).

Table 2. List of spider families selected for specimen identification to species.

	Araneae Family	**Common Name**
1	Agelenidae**sensu lato*	Vagrant Web Builders
2	Amaurobiidae	Amaurobiids
3	Anyphaenidae	Sac Spiders
4	Antrodiaetidae	Trap Door Spiders
5	Clubionidae**sensu lato*	Sac Spiders
6	Gnaphosidae	Ground Spiders
7	Lycosidae	Wolf Spiders
8	Thomisidae	Crab Spiders
9	Zoridae*	Zorids

*   A new family record for Canada (Bennett and Brumwell 1996)
** Polyphyletic families - see Appendix B for current systematic status of all species
      (Platnick 1993)

After identification, individuals were placed into separate vials containing 70% ethyl alcohol with collection labels stating the location, successional stage, trap number, latitude, longitude, dates of collection period, and collector's name and identification labels stating the species and identifier's name, as recommended by Winchester and Scudder (1993). Dr. Robert Bennett identified several of the more difficult specimens and confirmed identification of many species. Voucher specimens of all identified species have been placed in the Spencer Entomological Museum, at the University of British Columbia.

METHODS OF DATA ANALYSIS

Species Abundance Plotting

Species abundance was plotted against rank and presented graphically (Excel version 5.0) for each successional stage. Presented in this format, data can be compared to one of our

main distribution models: geometric, log series, log normal and MacArthur (broken stick) (Magurran 1988, Southwood 1978, Pielou 1975).

Intraspecific Comparisons

Species counts for each group of three cups were pooled resulting in eight numbers for each collection period. The data from each trap site were then pooled for all collection periods (e.g. trap site 1 data pooled together for the 8 collection periods at Victoria Watershed). This resulted in eight numbers for each species, one for each trap site. The means and standard errors of these eight numbers were then presented graphically (Systat for Windows, version 5.0) for each watershed .

The Kruskal-Wallis single-factor analysis of variance by rank (herein referred to as the Kruskal-Wallis test) was used to test intersuccessional stage differences (Systat for Windows, version 5.0). This test is applicable when populations are not normal and variances are heterogeneous (Zar 1996), as is the case with the spider data. The Kruskal-Wallis test statistic H and probability, P, were recorded.

A non-parametric multiple comparison test, similar to the Tukey test, was performed on mean numbers of species showing a significant difference between successional stages in an attempt to resolve these differences. These calculations were done by hand following the method outlined in Zar (1996).

Diversity Indices

Number of species and rarefied species richness were used as indicators of species diversity. A standard sample size of 167 was used for rarefaction. Non-parametric diversity indices (Southwood 1978) were calculated for each location and each successional stage individually. The Shannon-Wiener index, a heterogeneous diversity statistic (Peet 1974), was calculated (Ecological Methods computer package by Krebs 1989).

Similarity Coefficients and Cluster Analysis

The Simplified Morisita-Horn index of similarity was calculated to assess intersuccessional stage differences (Ecological Methodology computer program, Krebs 1989) for all species combined. Prior to this calculation, data were transformed by taking the square-root of $x + .375$, where x is the original count, as recommended for count data by Zar (1996).

The resulting Simplified Morisita-Horn index of similarity matrix was used in a single linkage cluster analysis program (Systat for Windows, version 5.0) which grouped similar successional stages and produced a dendrogram.

RESULTS

Number of Species

A total of 2,547 adult spiders, representing 32 species (Table 3, Appendix B) were identified from the selected families of spiders. Seventeen species were uncommon with less than 10 individuals per species trapped (Table 3-Uncommon species). Seven species were represented by three or fewer individuals (Table 3-asterisked). Two species, *Alopecosa kochii* (Keyserling), and *Cybaeus eutypus* Chamberlin & Ivie, accounted for more than 60% of the individuals trapped.

Species Abundance Models

Species rank/abundance patterns in each of the four successional stages in the two watersheds were consistent with the log normal distribution model (Figure 3a, 3b, 3c, & 3d).

Intraspecific Comparisons

Three distinctive patterns emerge from the fifteen species analyzed by the Kruskal-Wallis test and the non-parametric multiple comparison test: generalists, regeneration specialists, and intermediate forest specialists (spiders preferring the immature and mature successional stages). Species that did not exhibit a clear pattern are labeled unresolved species. Uncommon species (those represented by fewer than ten specimens) were not analyzed with this test.

Table 3. Total Species Collected in Victoria Watershed South and Koksilah

Species	Victoria Watershed South					Koksilah					Grand Total
	REG	IMM	MAT	OG	Total	REG	IMM	MAT	OG	Total	
Generalist											
1 *Antrodiaetus pacificus* (Simon)	15	11	11	13	**50**	11	7	9	14	**41**	**91**
2 *Cicurina simplex* Simon	15	5	4	3	**27**	33	8	7	9	**57**	**84**
Regenerational Species											
3 *Alopecosa kochii* (Keyserling)	292	1	0	0	**293**	183	0	0	3	**186**	**479**
4 *Pardosa vancouveri* Emerton	54	0	0	0	**54**	0	0	0	1	**1**	**55**
5 *Pardosa wyuta* Gertsch	52	0	0	0	**52**	153	0	0	0	**153**	**205**
6 *Castianeira longipalpa* (Hentz)	15	0	0	0	**15**	28	0	0	0	**28**	**43**
7 *Drassyllus depressus* (Emerton)	10	0	0	0	**10**	26	0	0	0	**26**	**36**
Intermediate Forest Species											
8 *Cybaeus eutypus* Chamberlin & Ivie	25	187	142	138	**492**	31	288	197	76	**592**	**1084**
Unresolved Species											
9 *Pardosa dorsuncata* Lowrie & Dondale	12	1	1	0	**14**	80	1	2	11	**94**	**108**
10 *Xysticus pretiosus* Gertsch	0	0	0	0	**0**	1	0	2	12	**15**	**15**
11 *Cicurina tersa* Simon	9	7	1	2	**19**	13	2	9	26	**50**	**69**
12 *Zelotes fratris* Chamberlin	40	2	3	0	**45**	34	0	8	6	**48**	**93**
13 *Zelotes puritanus* Chamberlin	7	0	0	0	**7**	11	0	0	0	**11**	**18**
14 *Cryphoeca exlineae* Roth	1	1	1	8	**11**	0	8	13	6	**27**	**38**
15 *Calymmaria nana* (Simon)	7	3	3	4	**17**	37	1	4	3	**45**	**62**
Uncommon Species*											
16 *Anyphaena pacifica* (Banks)	0	1	0	0	**1**	2	1	0	1	**4**	**5**
17 *Calymmaria emertoni* (Simon)	0	0	0	1	**1**	0	1	0	0	**1**	**2**
18 *Callobius pictus* (Simon)	0	1	0	3	**4**	0	2	0	0	**2**	**6**
19 *Callilepis pluto* Banks	2	0	0	0	**2**	6	0	0	0	**6**	**8**
20 *Cybaeus reticulatus* Simon	0	1	1	1	**3**	1	0	1	0	**2**	**5**

Table 3: *Continued*

Species	Victoria Watershed South					Koksilah					Grand Total
	REG	IMM	MAT	OG	Total	REG	IMM	MAT	OG	Total	
Uncommon species: (*cont'd*)											
21 *Callobius severus* (Simon)	0	0	0	0	**0**	0	0	0	3	**3**	**3**
22 *Cybaeus signifer* Simon	0	0	0	0	**0**	1	1	1	2	**5**	**5**
23 *Castianeira walsinghami* (O. Pickard-Cambridge)	2	0	0	0	**2**	0	0	0	0	**0**	**2**
24 *Drassodes neglectus* (Keyserling)	0	0	0	0	**0**	4	0	0	0	**4**	**4**
25 *Micaria pulicaria* (Sundevall)	1	0	0	0	**1**	3	0	0	0	**3**	**4**
26 *Novalena intermedia* (Chamberlin & Gertsch)	0	0	0	0	**0**	0	0	0	2	**2**	**2**
27 *Phrurotimpus borealis* (Emerton)	1	0	0	0	**1**	1	0	0	0	**1**	**2**
28 *Sergiolus columbianus* (Emerton)	1	0	0	0	**1**	4	0	0	0	**4**	**5**
29 *Xysticus cunctator* Thorell	1	0	0	0	**1**	0	0	0	0	**0**	**1**
30 *Xysticus montanensis* Keyserling	3	0	0	0	**3**	2	0	0	0	**2**	**5**
31 *Zelotes hentzi* Barrows	1	0	0	0	**1**	2	0	0	0	**2**	**3**
32 *Zora hespera* Cory and Mott	0	0	0	0	**0**	5	0	0	0	**5**	**5**
	566	**221**	**167**	**173**	**1127**	**672**	**320**	**253**	**175**	**1420**	**2547**

* Species represented by less than ten specimens in the collection.

REG   Regeneration
IMM   Immature
MAT   Mature
OG   Old-Growth

Figure 3a. Species rank/abundance graph of the regeneration stage (REG) of Victoria Watershed (VW) and Koksilah (KOK). Percent abundance of each species is plotted on a logarithmic scale against species rank, ordered from most abundant to least abundant species.
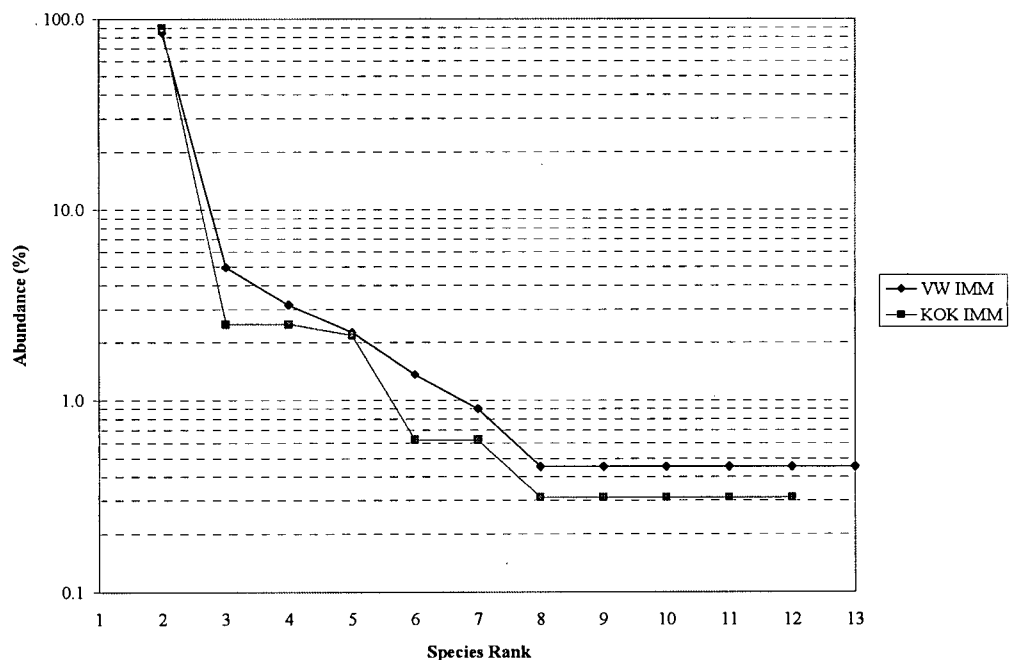
Figure 3b. Species rank/abundance graph of the immature stage (IMM) of Victoria Watershed (VW) and Koksilah (KOK). Percent abundance of each species is plotted on a logarithmic scale against species rank, ordered from most abundant to least abundant species.

20
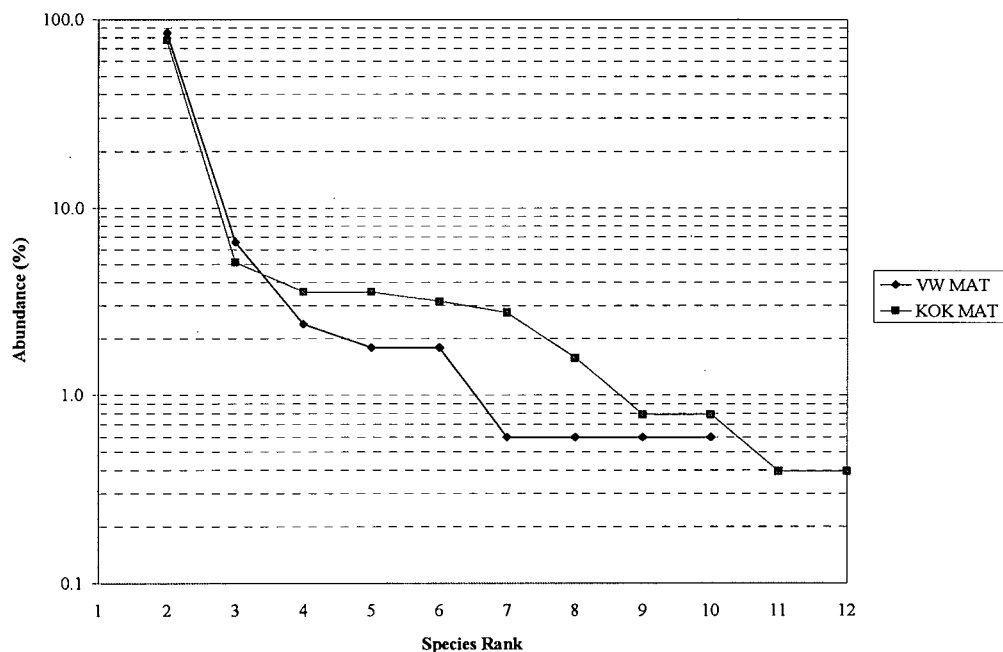
Figure 3c. Species rank/abundance graph of the mature stage (MAT) of Victoria Watershed (VW) and Koksilah (KOK). Percent abundance of each species is plotted on a logarithmic scale against species rank, ordered from most abundant to least abundant species.
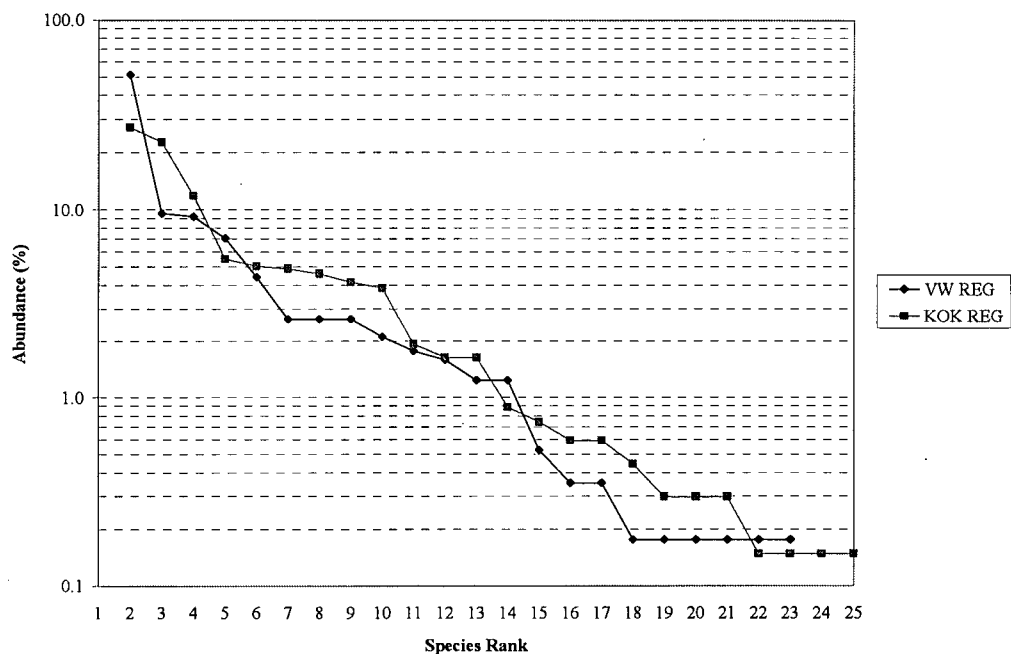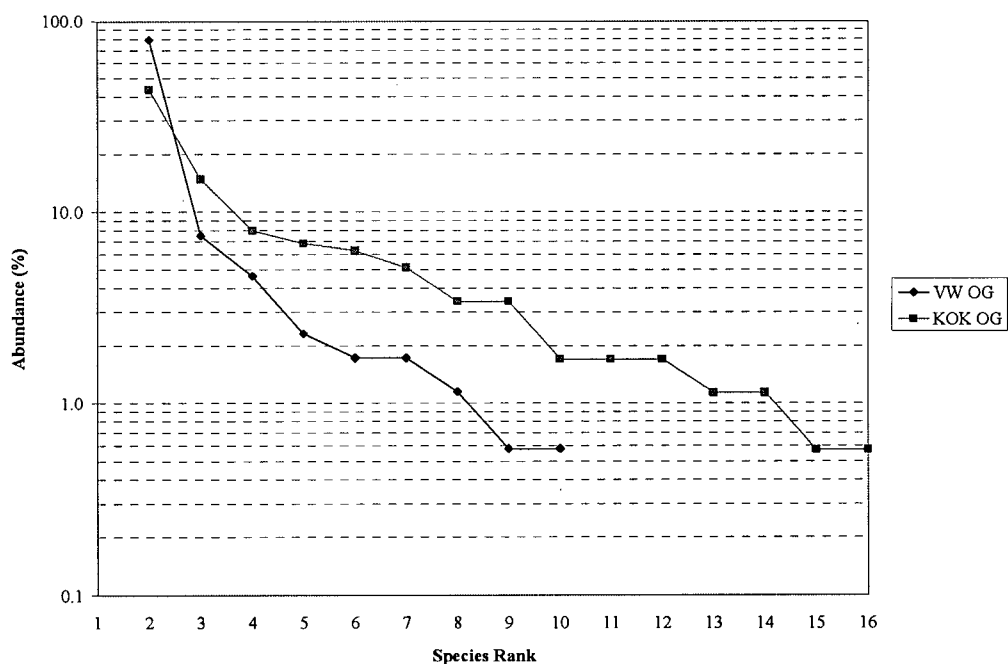

Figure 3d. Species rank/abundance graph of the old-growth stage (OG) of Victoria Watershed (VW) and Koksilah (KOK). Percent abundance of each species is plotted on a logarithmic scale against species rank, ordered from most abundant to least abundant species.

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Generalists

  Species that lack an affinity for a specific succession zone, confirmed by the Kruskal-Wallis test, are termed generalists. Two species, *Antrodiaetus pacificus* (Simon), and *Cicurina simplex* Simon, may be described in this manner. The trend is best exhibited by *A. pacificus* at the Victoria Watershed site, followed by *A. pacificus* at Koksilah (Figure 4a & 4b). The pattern for *C. simplex* is also more distinct at the Victoria Watershed site (Figure 5a), than at Koksilah (Figure 5b).

Regeneration Specialists

  Species with a special affinity for the regenerative forest are grouped in this category. Two species, *A. kochii* (Figure 6a & 6b) and *Pardosa wyuta* Gertsch (Figure 7a & 7b) are strongly associated with this stage. Both species exhibited high capture rates. Another species, *Pardosa vancouveri* Emerton was also found exclusively in the regeneration forest, but only at the Victoria Watershed site. Although the Kruskal-Wallis test found a significant difference (Figure 8), the multiple comparison test could not resolve this species as a regenerative specialist. It is interesting that in the Victoria Watershed site where *P. vancouveri* was captured, the capture rate of *P. wyuta* was approximately one third the capture rate at the Koksilah site (Table 3) where no *P. vancouveri* were captured.

  Two other species may be loosely designated by this category. The Kruskal-Wallis test found significant differences for *Castianeira longipalpa* (Hentz) (Figure 9a & 9b), and *Drassyllus depressus* (Emerton) (Figure 10a & 10b), but the non-parametric multiple
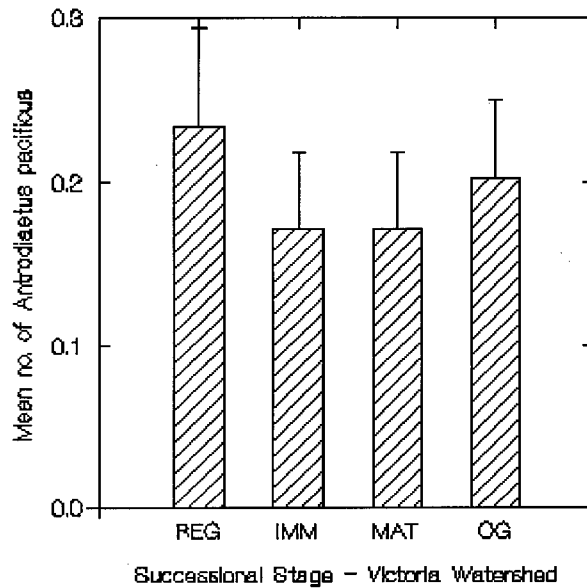
Figure 4a. Mean number of individuals (with standard error) of *Antrodiaetus pacificus* (Simon) trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
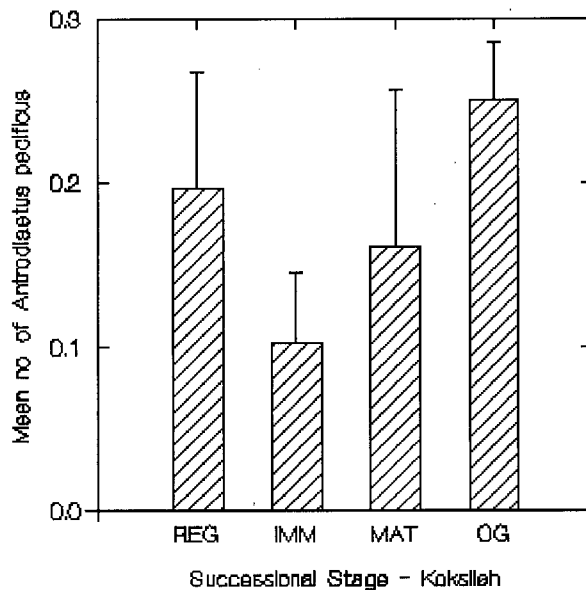
Figure 4b. Mean number of individuals (with standard error) of *Antrodiaetus pacificus* (Simon) trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

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H = 5.665

P = .129

OG	MAT	IMM	REG

Figure 5a. Mean number of individuals (with standard error) of *Cicurina simplex* Simon trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

H = 6.429

P = .092

OG	MAT	IMM	REG

Figure 5b. Mean number of individuals (with standard error) of *Cicurina simplex* Simon trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

Figure 6a. Mean number of individuals (with standard error) of *Alopecosa kochii* Keyserling trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

Figure 6b. Mean number of individuals (with standard error) of *Alopecosa kochii* Keyserling trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

Figure 7a. Mean number of individuals (with standard error) of *Pardosa wyuta* Gertsch trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

Figure 7b. Mean number of individuals (with standard error) of *Pardosa wyuta* Gertsch trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

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Figure 8. Mean number of individuals (with standard error) of *Pardosa vancouveri* Emerton trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
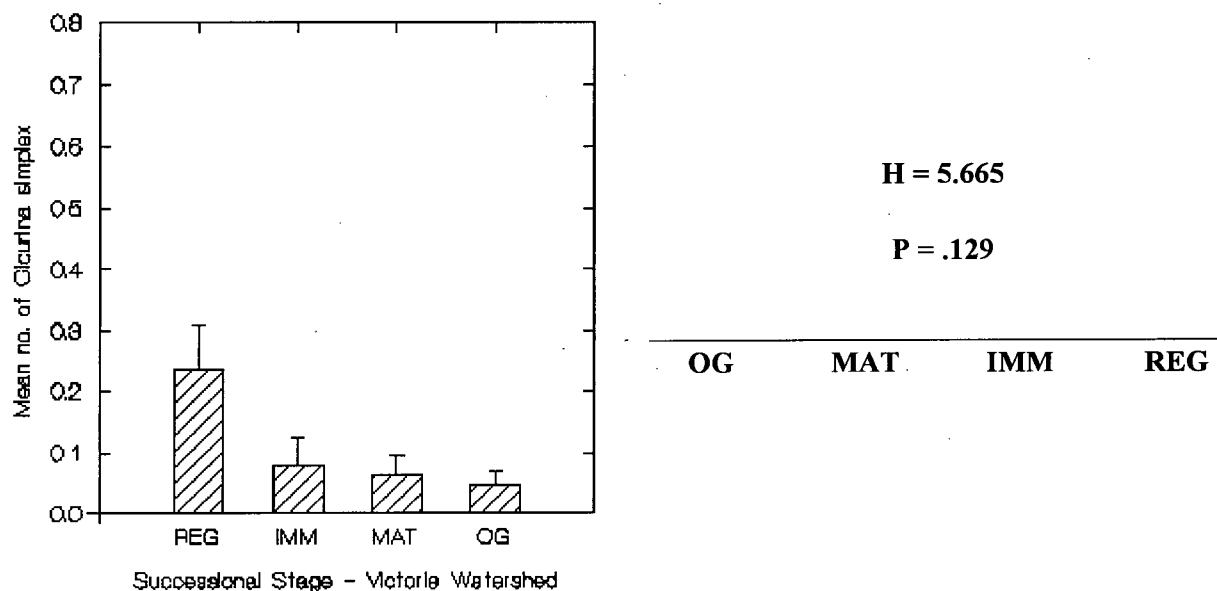
Figure 9a. Mean number of individuals (with standard error) of *Castianeira longipalpa* (Hentz) trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
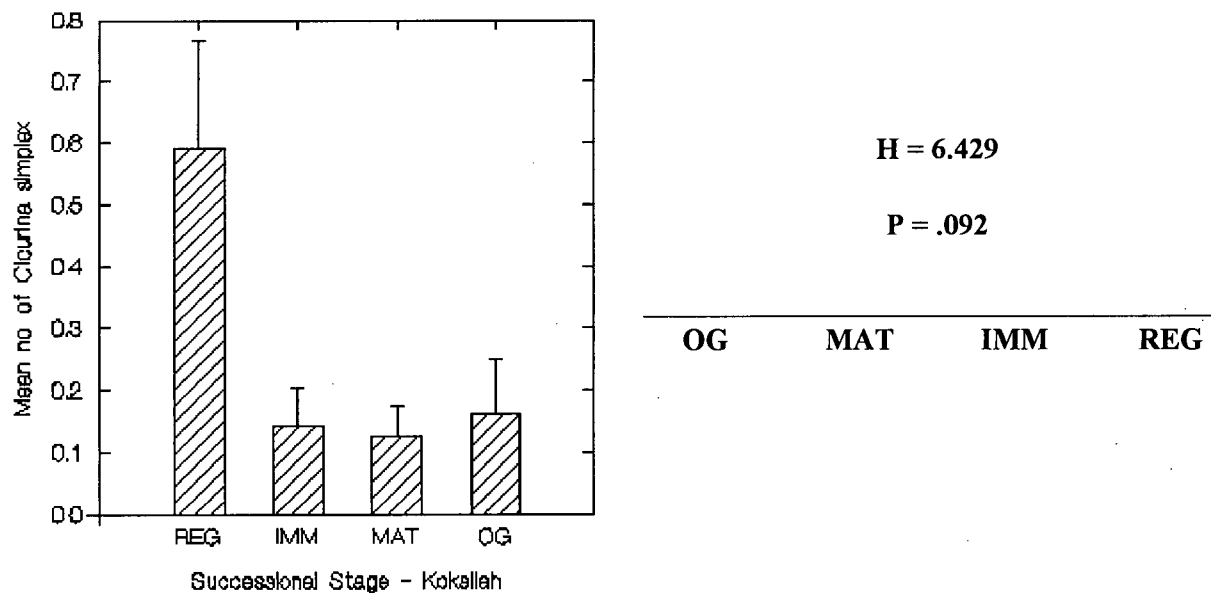

Figure 9b. Mean number of individuals (with standard error) of *Castianeira longipalpa* (Hentz trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
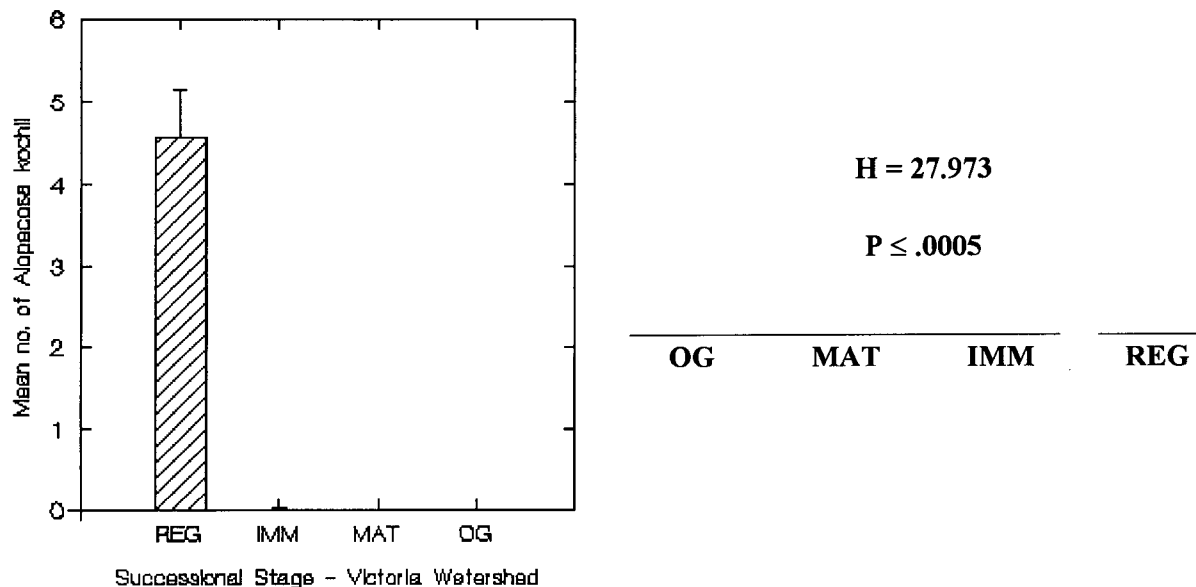
28

Figure 10a. Mean number of individuals (with standard error) of *Drassyllus depressus* (Emerton) trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
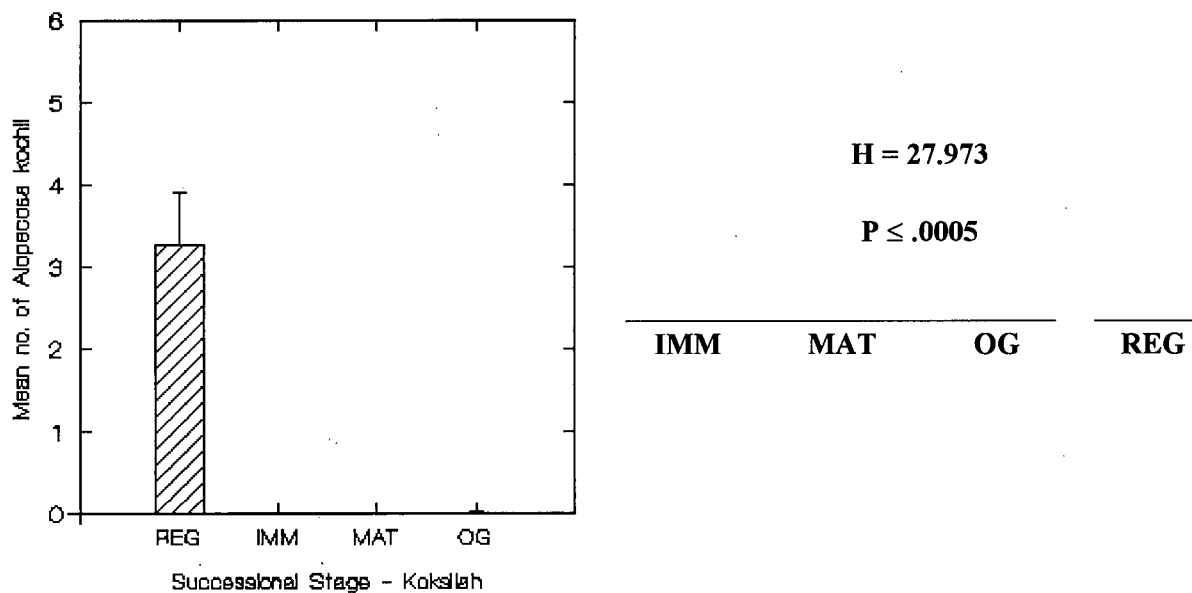

Figure 10b. Mean number of individuals (with standard error) of *Drassyllus depressus* (Emerton) trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
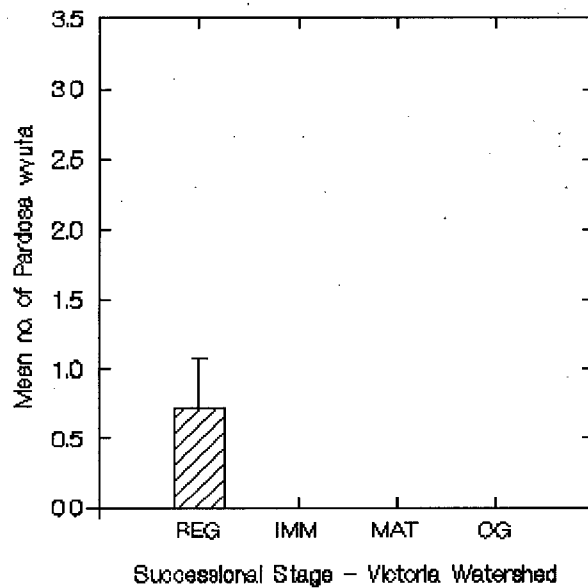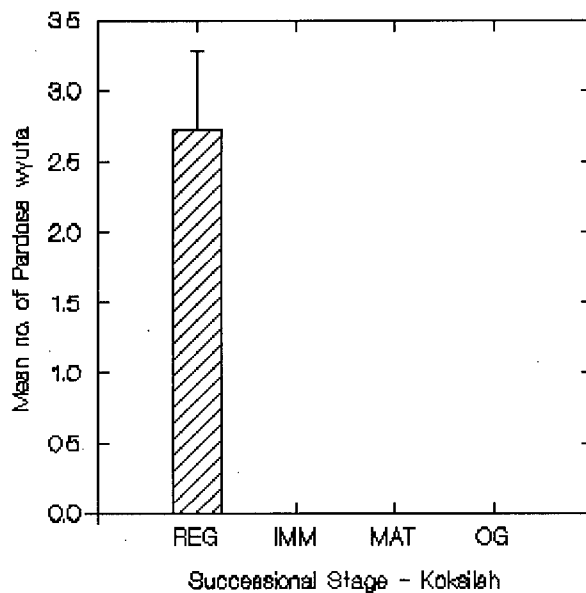
comparison could only resolve a difference at Koksilah. As both species were only found in the regeneration forest, I believe their placement in this category is warranted.

Intermediate Forest Specialists

Cybaeus eutypus Lowrie and Dondale, the most abundant of the spiders identified, was captured in all stages at both watersheds (Table 3), but is the one species that exhibits a distinctive aversion for the regenerative zone. Results of the multiple comparison test at the Victoria Watershed site found a significant difference between the regenerative stage and the immature and mature stages (Figure 11a). The non-parametric multiple comparison could not resolve a difference between the regenerative stage and the old growth stage. At the Koksilah site, the pattern was similar although not quite as clear (Figure 11b). The regenerative zone differed significantly from the immature and mature, but the old growth capture rate was much lower at this site and the multiple comparison test also found a difference between the immature zone and old-growth zone. As at the Victoria Watershed site, the multiple comparison test was unable to resolve a difference between the regeneration stage and the old-growth stage.

Unresolved

The pattern for *Cicurina tersa* Simon is ambiguous, but may be tentatively described as a generalist. Although there was a significant difference in the Kruskal-Wallis test, the multiple comparison test was unable to resolve this difference at the Victoria

Figure 11a. Mean number of individuals (with standard error) of *Cybaeus eutypus* Chamberlin & Ivie trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
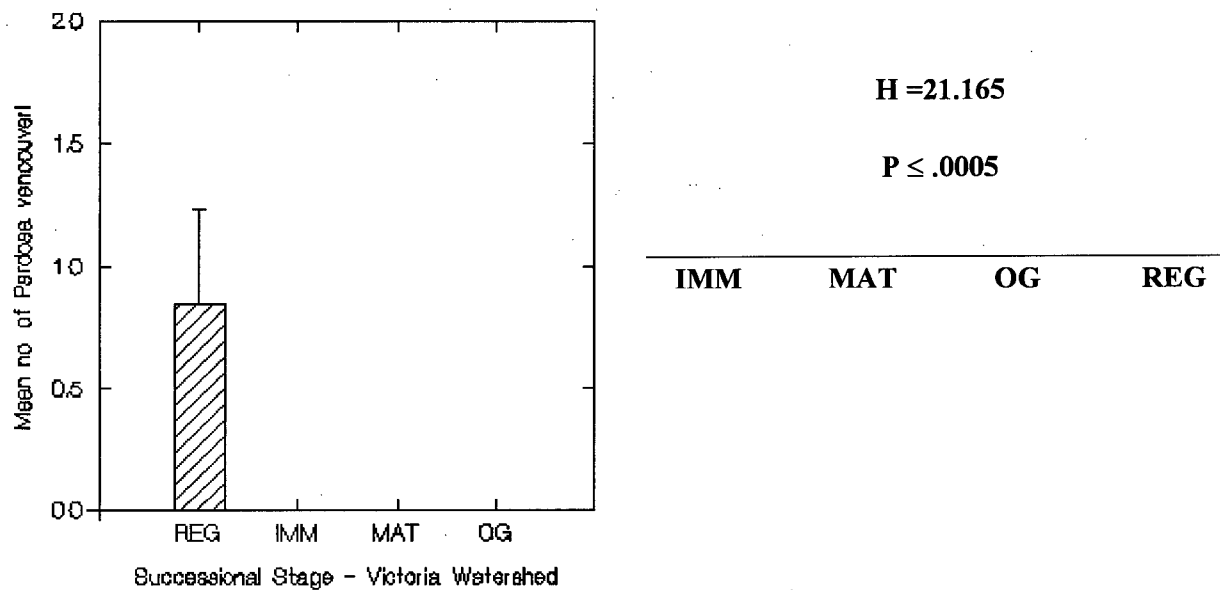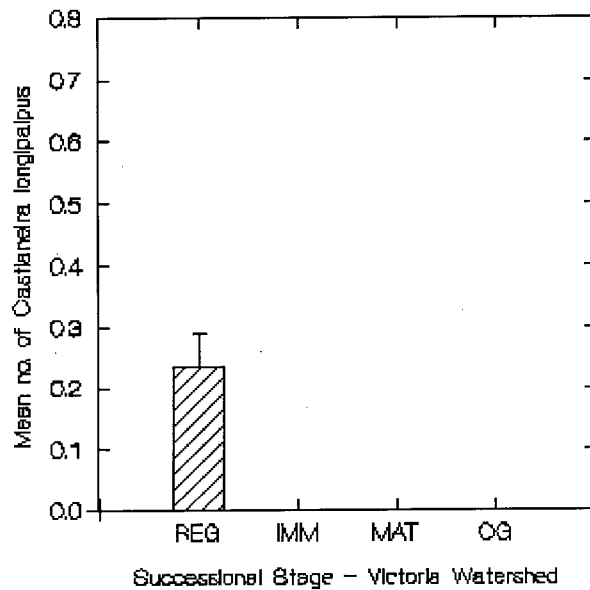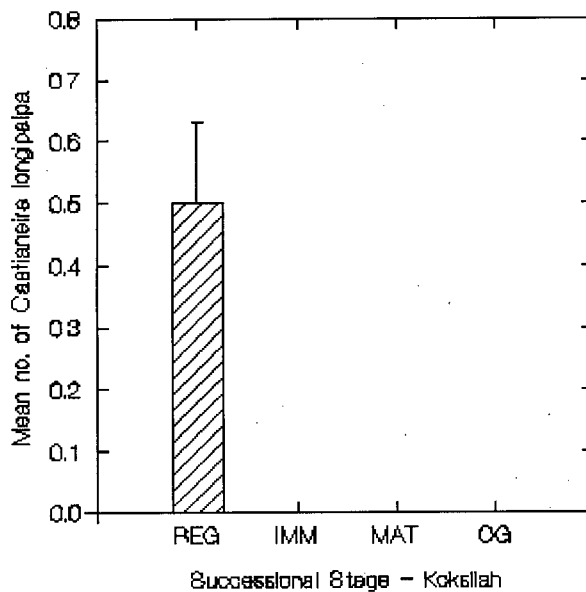

Figure 11b. Mean number of individuals (with standard error) of *Cybaeus eutypus* Chamberlin & Ivie trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
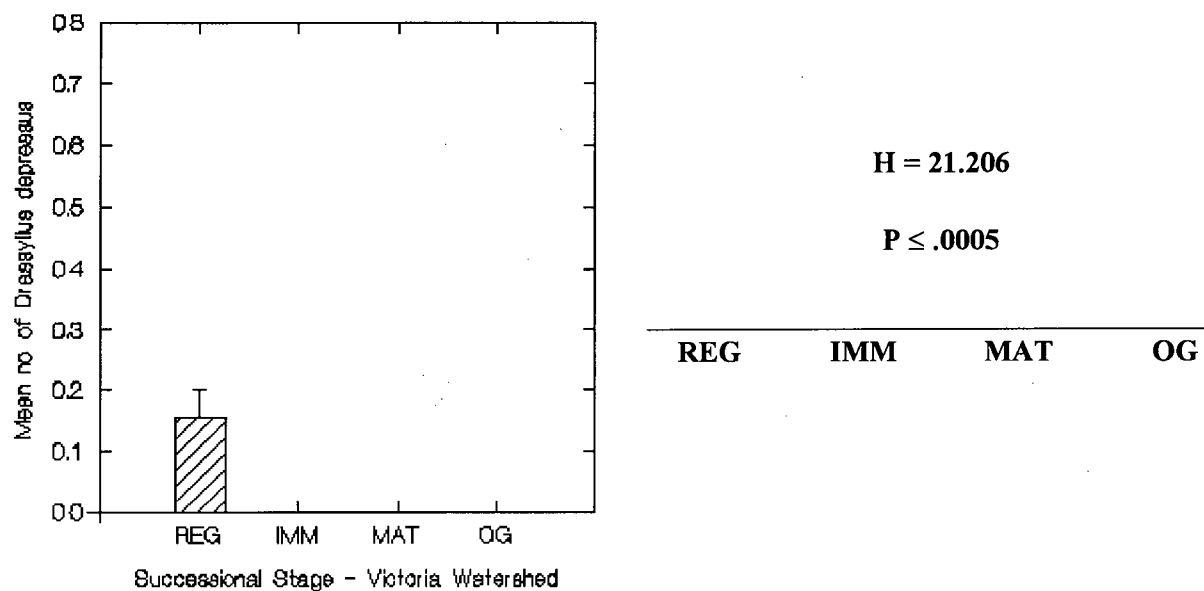
31

Watershed site (Figure 12a). At the Koksilah site, the multiple comparison test found a difference only between the old-growth and immature (Figure 12b).

Unlike *P. wyuta* and *P. vancouveri*, *P. dorsuncata* was not found exclusively in the regenerative stages. At the Victoria Watershed, capture rate was low (Table 3), but the Kruskal-Wallis test found a significant difference, resolved by the multiple comparison test, between the regeneration stage and the mature and old-growth stages. At Koksilah the capture rate was higher and the multiple comparison test found a significant difference between the regeneration zone and the immature and mature zones (Table 3).

Xysticus pretiosus Gertsch was the only thomisid captured in numbers adequate for analysis. Unfortunately the numbers were still quite low (Table 3), and restricted to the Koksilah site; but this spider does appear to trend towards old growth specialization (Figure 13). The non-parametric multiple comparison test found a significant difference between the old growth and immature, but was unable to resolve any other differences.

Like *X. pretiosus*, *Zelotes puritanus* Chamberlin was found to have a significant probability of difference at both watersheds (Figure 14a & 14b), but this difference was not resolved by the multiple comparison test. Despite this, *Z. puritanus* is likely a specialist in regenerating forests as all specimens were captured in this particular stage.

Figure 12a. Mean number of individuals (with standard error) of *Cicurina tersa* Simon trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
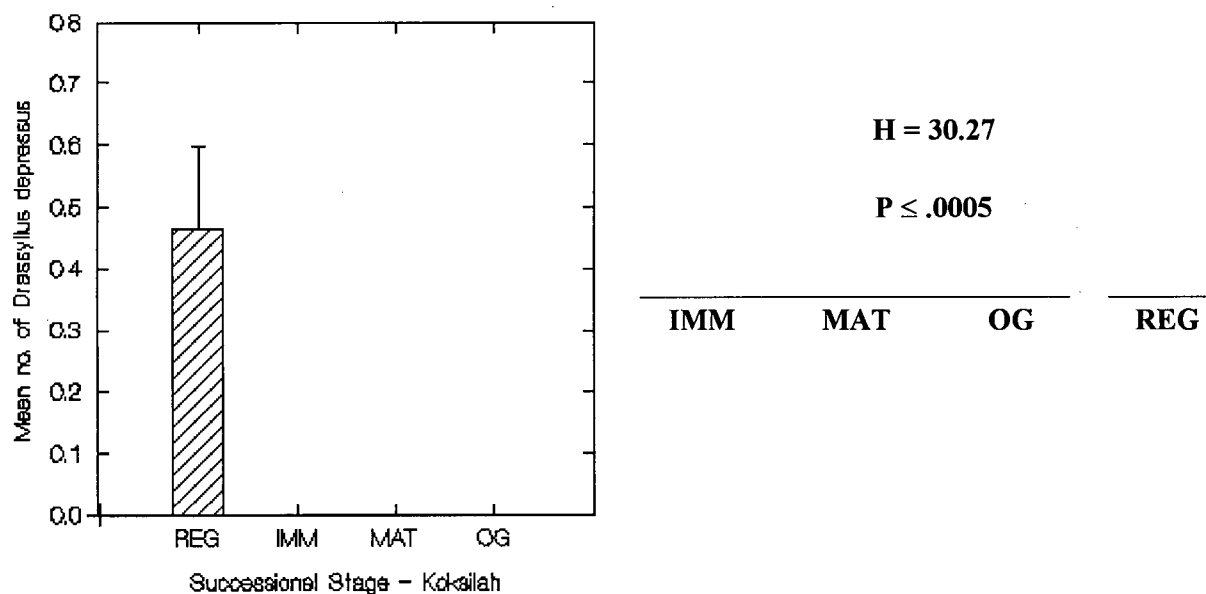

Figure12b. Mean number of individuals (with standard error) of *Cicurina tersa* Simon trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

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Figure 13. Mean number of individuals (with standard error) of *Xysticus pretiosus* Gertsch trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

Figure 14a. Mean number of individuals (with standard error) of *Zelotes puritanus* Chamberlin trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
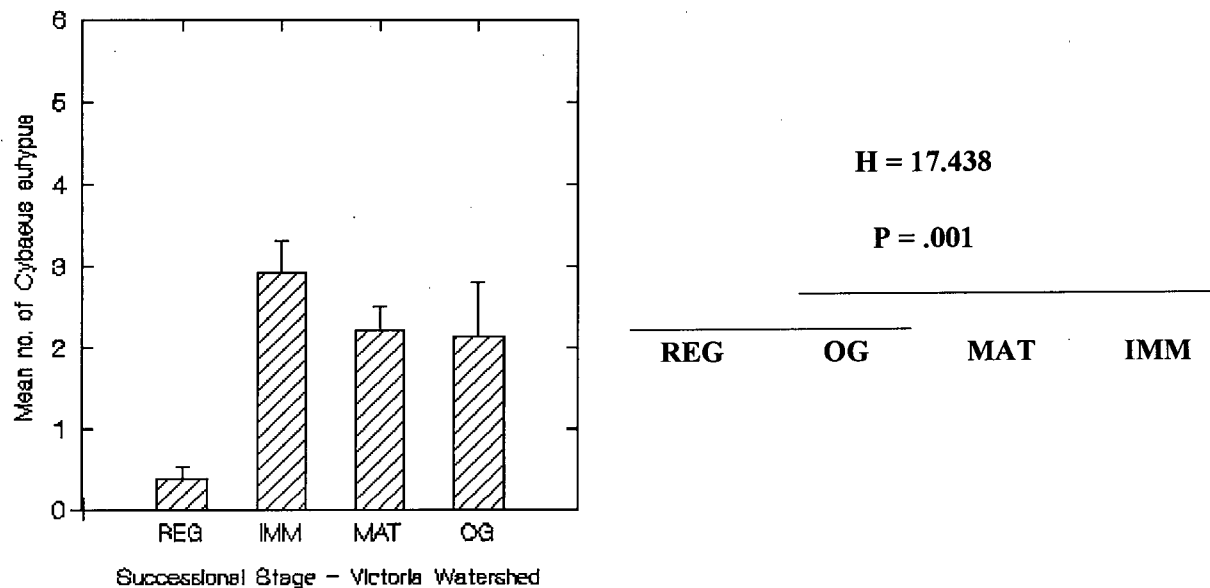

Figure 14b. Mean number of individuals (with standard error) of *Zelotes puritanus* Chamberlin trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
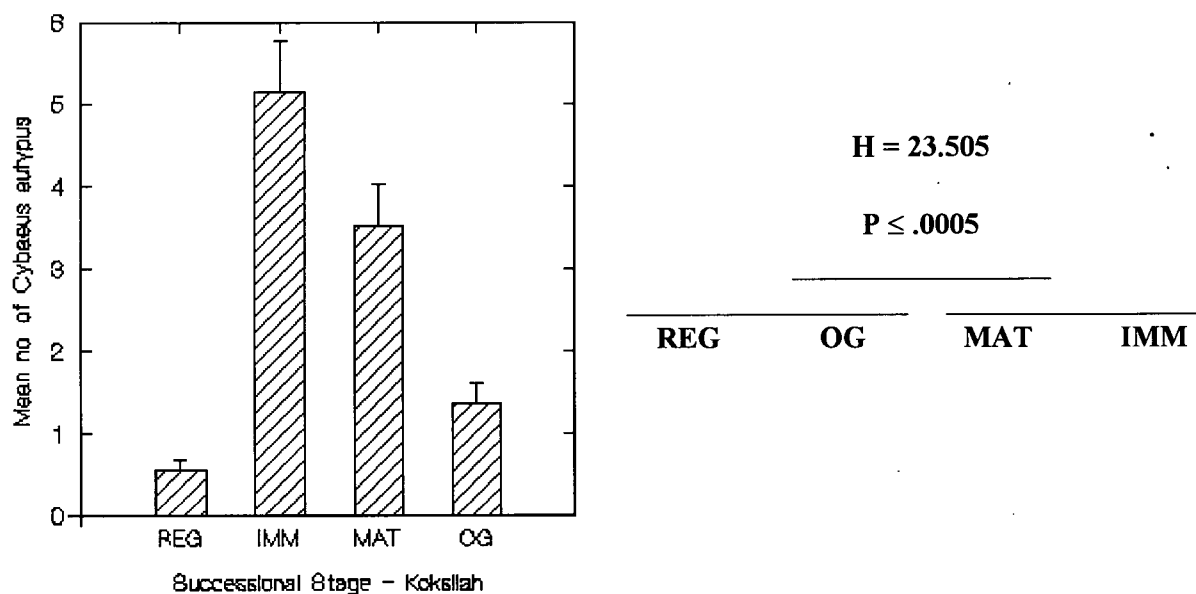
Zelotes fratris Chamberlin also appears to possibly be a regeneration specialist. At the Victoria Watershed, the multiple comparison test determines this spider to be a regeneration forest specialist (Figure 15a), but this trend is not replicated at the Koksilah where significant captures occurred in both the mature and old-growth stages (Figure 15b).

Of the seventeen species considered to be uncommon, ten of these were found exclusively in the regeneration zone, and two exclusively in the old growth forest (Table 3). Low numbers prevent intraspecific analysis using the Kruskal-Wallis test.

Forest Successional Stage Comparisons

Diversity Indices

In both watersheds, the regeneration stage contained the highest number of species before and after rarefaction (Table 4). The next most diverse environment based on these methods is the Koksilah old growth. This was not true at the Victoria Watershed. In general, Koksilah had more species than did the Victoria Watershed (Table 4).

At the two watersheds, the Shannon-Wiener index indicated the regeneration sites as the most diverse followed by the old growth sites (Table 4). At Koksilah, the mature site was next, differing from the Victoria Watershed where the immature site followed the old growth site in diversity. Over-all site diversity indicated that the Koksilah site is richer than the Victoria Watershed site (Table 5).
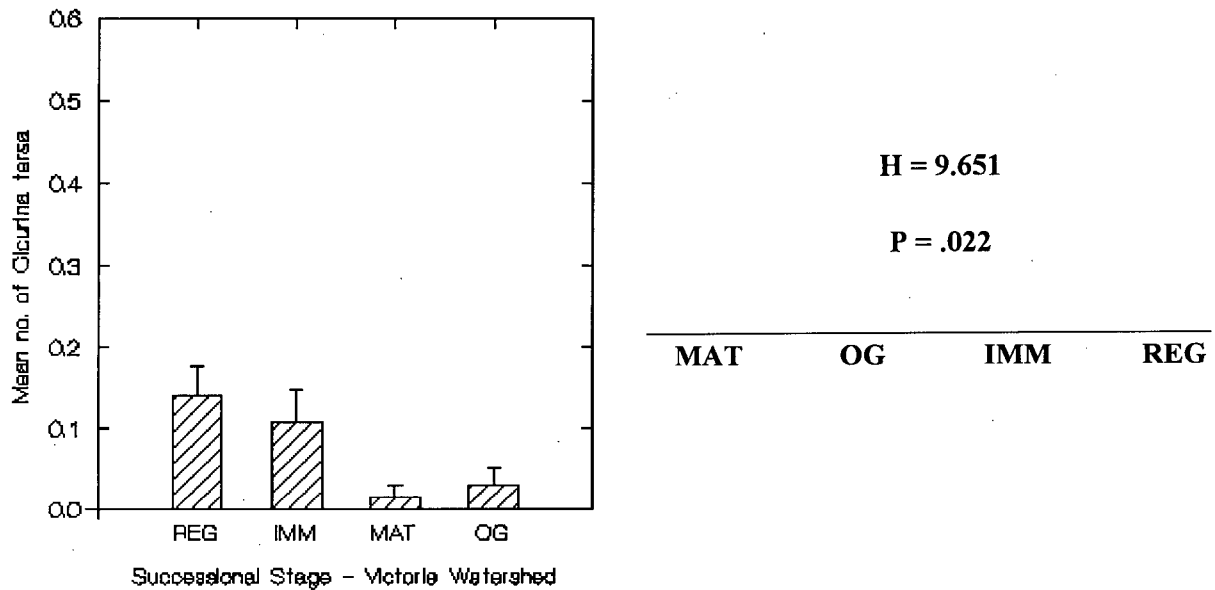
36

Figure 15a. Mean number of individuals (with standard error) of *Zelotes fratris* Chamberlin trapped in each successional stage at the Victoria Watershed site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.

Figure 15b. Mean number of individuals (with standard error) of *Zelotes fratris* Chamberlin trapped in each successional stage at the Koksilah site. The Kruskal-Wallis test statistic, H, and the statistical probability, P, are the result of intersuccessional stage comparisons. Stages which did not differ from one another are joined with a line, as determined by a non-parametric multiple comparison test.
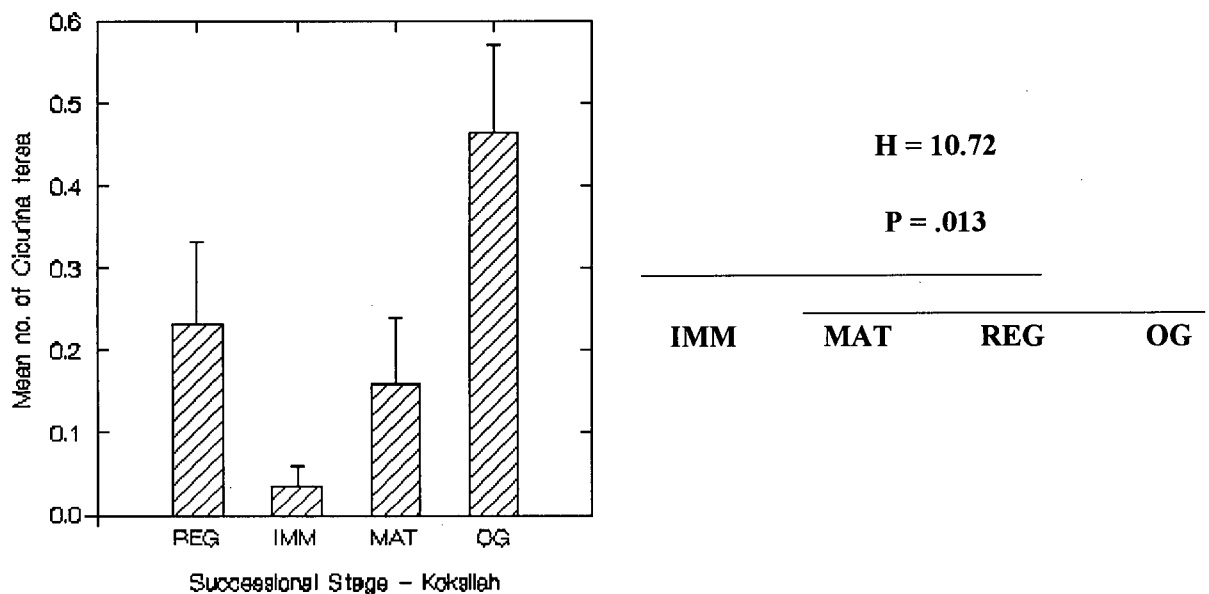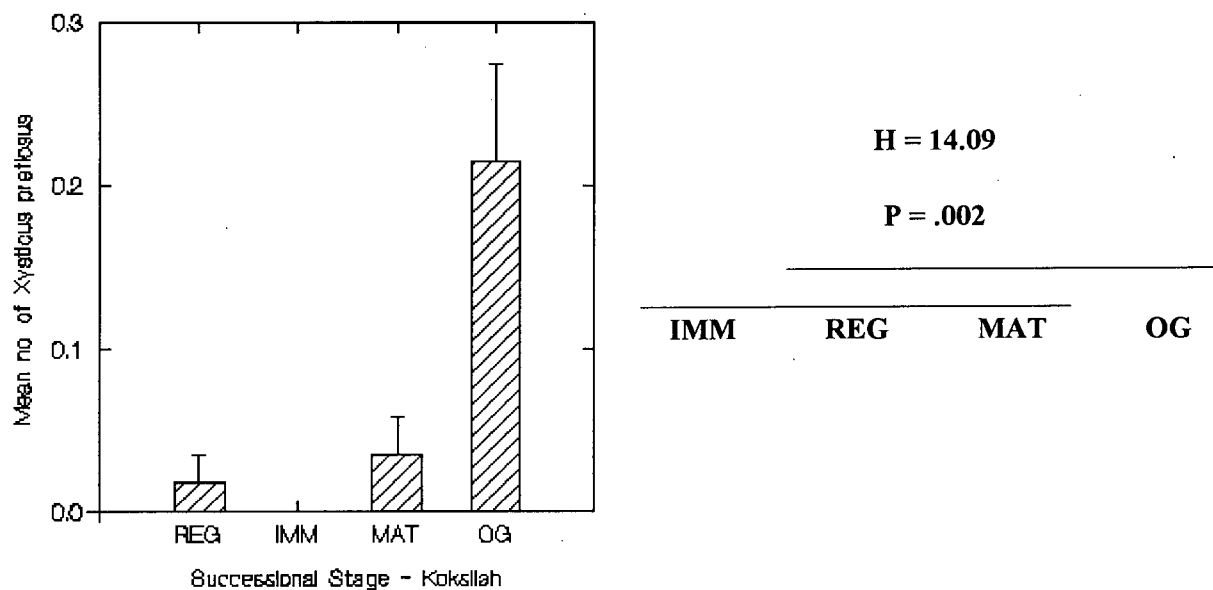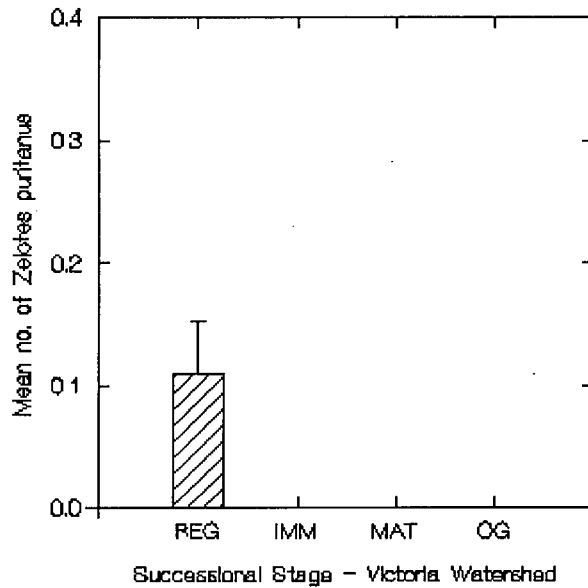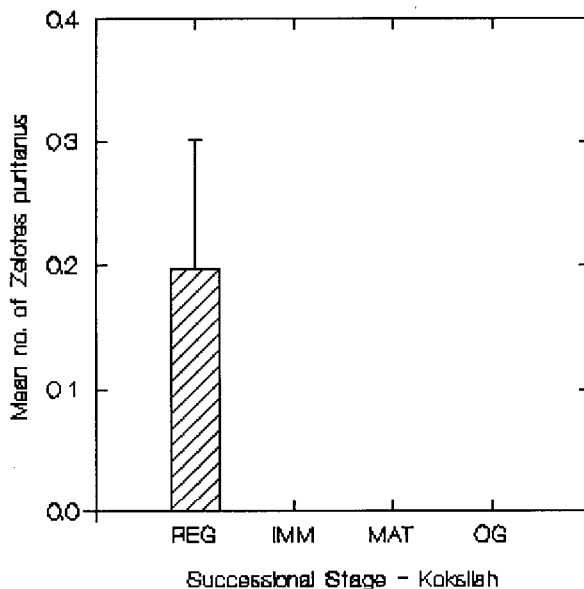
37

Table 4. Number of species (S), corrected number of species $(E(S)_{167})$, and the Shannon-Wiener index (H'), for the Victoria Watershed and Koksilah at all successional stages.

	VICTORIA WATERSHED				KOKSILAH			
	REG	IMM	MAT	OG	REG	IMM	MAT	OG
S **E(S)₁₆₇** **SD**	22 16.16 1.47	12 10.46 1.07	9 9.00 0.00	9 8.93 .26	24 17.72 1.58	11 8.14 1.26	11 10.08 .81	15 14.90 .30
H'	2.685	1.058	.972	1.235	3.273	.745	1.412	2.827

Table 5. Number of species, and the Shannon-Wiener index (H') comparing Victoria Watershed and Koksilah.

	VICTORIA WATERSHED	KOKSILAH
No. Species	26	30
H'	2.649	2.976

Similarity Coefficients and Cluster Analysis

Results of the Simplified Morisita-Horn similarity coefficients (Table 6) and the resulting dendrogram (Figure 16) indicate that the regeneration stages cluster together (indicative of their similarity to each other) and are recognizably different from the other sites. The differences in the remaining data are less dramatic. There is no difference between the Victoria Watershed immature, mature, old-growth, and Koksilah mature stages and only a minor difference between these four stages and the Koksilah immature site. The Koksilah old-growth site is more similar to the Koksilah immature than to the Victoria old-growth site.

Table 6. Matrix of Simplified Morisita-Horn Similarity Coefficients for Victoria Watershed (VW) and Koksilah (KOK) at all successional stages.

	VW REG	VW IMM	VW MAT	VW OG	KOK REG	KOK IMM	KOK MAT	KOK OG
VW REG	1.00	.44	.43	.42	.88	.35	.43	.58
VW IMM		1.00	.99	.98	.46	.97	.98	.87
VW MAT			1.00	.98	.46	.97	.98	.85
VW OG				1.00	.44	.96	.97	.86
KOK REG					1.00	.37	.46	.62
KOK IMM						1.00	.96	.78
KOK MAT							1.00	.89
KOK OG								1.00

SIMILARITIES


```
          1.000                                                    .500

VW REG    ---------
                  |--------------------------------------------------
                  | -
KOK REG   ---------                                          |
                                                             |
KOK OG    ----------------                                   |
                               |                             |
KOK MAT   --                   |---------------------------------
                               |                  -
              |                |
VW IMM    - + |                |
              |                |
VW MAT    - + |                |
              |-----           |
VW OG     --      |            |
                  +---------
              -
KOK IMM   ------- |
```
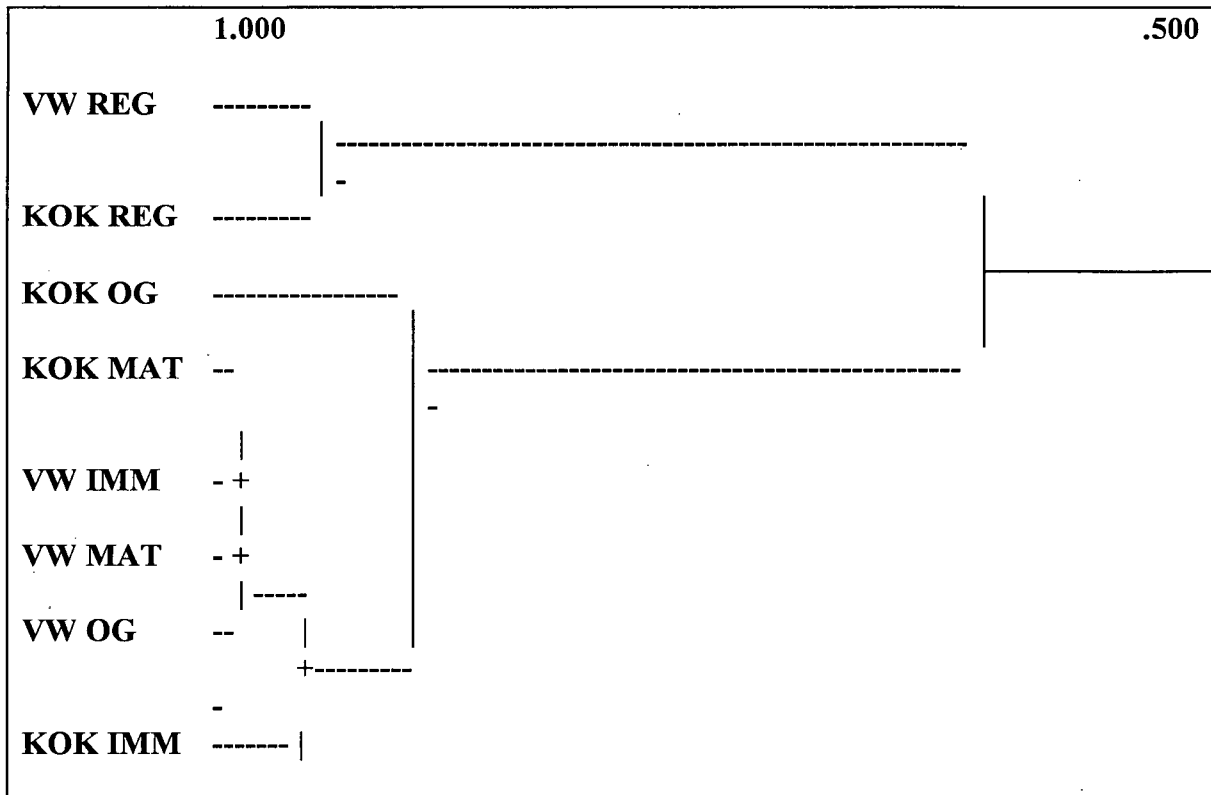
VW - Victoria Watershed
KOK - Koksilah

REG - Regeneration
IMM - Immature
MAT - Mature
OG - Old-Growth

Figure 16. Resulting dendrogram from a single linkage cluster analysis of the Simplified Morisita-Horn similarity coefficients.

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DISCUSSION

Pitfall Trapping Methodology

Pitfall trapping is used extensively to measure the abundance and activity of surface-active arthropods such as spiders (McIver *et al.* 1992, Bultman and Uetz 1982, Jennings *et al.* 1988, Uetz 1979, Niemelä *et al.* 1994). Traps are inexpensive, require little set-up effort, trap sufficient specimens, sample continuously, thus avoiding certain temporal and spot sampling problems (Topping and Sunderland 1992). For these reasons it remains a favoured sampling method for many researchers. However, research on pitfall trapping carabids has demonstrated certain disadvantages of this sampling method (Greenslade 1964, Halsall and Wratten 1988, Luff 1975). Additionally, pitfall trapping may differentially trap male spiders over female spiders (R. Bennett pers. comm.). Adult male spiders wander extensively in search of a mate and often cease feeding (Foelix 1982) thereby increasing their risk of capture. As their wanderings are random, there is a possibility they may be captured in an area that lacks an established community of that particular species.

Litter spiders may be sampled by pitfall or quadrat sampling, and there are trapping methodology problems with each method (Uetz and Unzicker 1976, Curtis 1980). Uetz and Unzicker (1976) examined each method and gave qualified support for the use of pitfall traps for cursorial spiders. Neither method can provide an absolute density measure, but pitfall traps provide a more complete species list than quadrat sampling as they remove any temporal stratification due to continued sampling. Pitfall traps also allow repeat sampling in the same area without disturbance (G. Scudder, pers. comm.). Although pitfall trap data are an

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estimate of activity not density, and species vary in their capture tendency, McIver *et al.* (1992) found that distribution patterns were unaffected by this bias. Therefore, the data collected should accurately represent between-site differences in the species captured as collection effort was equal and concurrent at all sites. Until new sampling methodologies are devised, pitfall traps are the best method available for sampling wandering spiders (Uetz and Unzicker 1976, Curtis 1980, Huhta 1971) and may be used cautiously if the following conditions listed in Uetz and Unzicker (1976) are met:

1. Analysis of data must be restricted to known cursorial forms
2. Collection should be made over a long period of time
3. Community comparisons should be made from samples taken in the same seasons and same general climatic regime.
4. Community comparisons should account for impedance of movement by various habitat factors.
5. Pitfall trapping should be backed by a second method
6. Efforts should be made to reduce known sources of error (i.e., trap placement design, trap numbers, attractant or repellent qualities of preservative).

Species Abundance Models

Species abundance models compare data to one of four main distribution models. The equability of each species will be reflected by the underlying distribution. These models are ordered from (uneven) geometric, log series, log normal, to broken-stick (even). Southwood (1978) states that species abundance models "...may be an excellent manner of presenting the data for publication".

Geometric series are generally found in harsh environments such as an early successional stage, and as conditions stabilize, a log series pattern develops (Magurran 1988). Therefore the exhibited log normal distribution pattern of the regeneration stage was surprising, although not completely without support, as log normal distributions may apply to both opportunistic and equilibrium communities (Southwood 1978). The log normal distribution of the data in the remaining successional stages is possibly reflecting the relative stability of the populations in these three successional stages.

Intraspecific Comparisons

Consistent with Craig (1995), intraspecific comparisons were examined. Three distinctive patterns emerged.

Generalists

Antrodiaetidae

The nocturnal species *Antrodiaetus pacificus* has the most northerly range of any mygalomorph spider (Coyle 1971), and is one of the largest spiders identified in this study. *Antrodiaetus pacificus* possesses a distinct cheliceral rake that aids the spider in digging a well-hidden burrow which may descend a foot or more into the soil (Gertsch 1979). Females and sub-adult males remain in their burrows during the day with the collar (or trap-door) closed. Hunting occurs primarily after nightfall in response to tactile stimuli (Coyle 1971). Sexually mature adult males wander extensively at night in search of a mate (Coyle 1971) which likely explains why the majority of specimens trapped in this study were adult males.

It is surprising that this spider was found in the regeneration forest stage as *A. pacificus* prefers humid, cool, densely forested habitats (Coyle 1971). As all successional stages were confined to a 5 km square area, it is possible that the captured males wandered into the regenerating forest stage in search of a mate. If this is true, this spider would no longer qualify as a generalist species.

Conversely, it is possible that there is a successful community of *A. pacificus* living in the regeneration stage. This spider is also found in the regeneration stage of the H.J. Andrews Forest in Oregon (McIver *et al.* 1992). In the same Oregon forest, numerous diurnal foraging ant species inhabit the litter of the regenerating forest. McIver *et al.* (1992) report that their great abundance may exclude other arthropods that cannot avoid them or compete against them. The secretive habits and large size of *A. pacificus* may minimize its risk of predation by ants and other predators. Ants are known to predate upon wandering spiders, including other mygalomorph species, but it is unknown whether ants and wandering spiders affect each others population (de Vosjoli 1991, Wise 1994). *Antrodiaetus pacificus* is known to feed on ants and carabids (Coyle 1971), both of which were common at my study sites. Utilization of this abundant food source in the regeneration stage may allow *A. pacificus* to survive in a marginal habitat that is dominated by an abundant lycosid fauna. The presence of this spider in the other successional stages is not surprising. Habitat conditions are more favorable here and prey is abundant.

Agelenidae

Cicurina simplex and *C. tersa* are two of the smallest of the spiders identified. There is little specific information known about these species. Both are listed as potentially rare and endangered terrestrial invertebrates (Scudder 1994), and are found only on Vancouver Island (West *et al.* 1984). Also considered shy spiders, *Cicurina* species have been associated with moist habitats under stones and ground debris (Gertsch 1979) where they build small, relatively featureless webs (R. Bennett pers. comm.). Their location of capture in both watersheds was not confined to any specific trap site, but most were trapped during the extended winter trapping period from November to April.

Regeneration Specialists

Three of the five species designated regeneration specialists are lycosids (*Alopecosa kochii, Pardosa vancouveri*, and *P. wyuta*). Lycosids account for 33% of spiders identified in this study, 66% of all spiders identified in this forest stage, and 90% of the spiders designated regenerative stage specialists. *A. kochii, P. vancouveri* and *P. wyuta* are known to be diurnally active (McIver *et al.* 1992, Holmberg and Turnbull 1982). There is little information regarding the remaining two species found in the regeneration stage (*Castianeira longipalpa*: Clubionidae, and *Drassyllus depressus*: Gnaphosidae). The foraging methods of clubionids and gnaphosids are not well known, but they appear to be active pursuit predators (Gertsch 1979).

Lycosidae

In British Columbian *P. vancouveri* is restricted to the southern areas of the province, including Vancouver Island. It is also found in Washington and Oregon. *Pardosa wyuta* is located predominately in southern British Columbia, but is found north to the Queen Charlotte Islands. The distribution of *A. kochii* extends across southern Canada in the north, and south to Baja California and Texas. It is found extensively in southern British Columbia and northern Washington state. (Dondale and Redner 1990). It is noteworthy that in a family as large as Lycosidae, only two species are found on the list of potentially rare and endangered invertebrates in British Columbia (Scudder 1994), perhaps indicative of the adaptability of this group of spiders.

The habitat preference of lycosid spiders is known. Typical field inhabitants, lycosids are well suited for locomotion in areas of minimal litter accumulation (Bultman *et al.* 1982), such as in the regenerating forest stage. Litter augmentation or removal causes a corresponding change in lycosid abundance (Uetz 1979).

The distinctive arrangement of lycosid eyes gives these spiders four-way vision (Gertsch 1979), and the secondary eyes (those other than the posterior median eyes) possess a highly specialized grated tapetum (crystalline deposits) which is assumed to increase visual acuity (Foelix 1982). In *Pardosa*, the posterior median eyes contain approximately 30 times more rhabdomeres, the light sensitive cells in the retina, than the anterior lateral eyes of spiders of the orb-weaving genus *Araneus* (Foelix 1982). Superior visual adaptations make

these diurnal species excellent hunters, a benefit that may be mitigated in areas of lower light and increased leaf litter.

Pardosa species, and other lycosids, also show brood care. After spinning the egg sac, the mother attaches it to her spinnerets and carries it until hatching time when she bites the sac open (Gertsch 1979). Several specimens in the samples had egg sacs attached. The newly hatched spiderlings crawl onto their mother's back where they reside for approximately one to three weeks. It is believed that they derive some additional protection from predation and adverse climatic conditions while they are under her care (Foelix 1982). This maternal care may give lycosid spiderlings a competitive edge over other regeneration specialists furthering lycosid numerical dominance in this stage.

First and second instar lycosids readily balloon (dispersal via air currents using silk strands) (Gertsch 1979), which may in part explain their appearance in early successional habitats (McIver *et al.* 1992). Although other spiders also balloon (Greenstone *et al.* 1987), spiderlings of other species landing in the regenerating areas may be unable to survive the climatic conditions of this stage.

Other studies have found similar levels of lycosid dominance in clear-cut areas (Jennings *et al.* 1988, McIver *et al.* 1992, Huhta 1971). Although these spiders readily dominate this stage, lycosids are still confined to certain environmental conditions. Extreme temperatures found in exposed leaf litter caused stress and mortality in *A. kochii* (Hagstrum

1970). The adaptations and characteristics of lycosids discussed above are likely to contribute to the success of this group in the regeneration stage.

Clubionidae

Castianeira longipalpa is the most widespread species of the North American *Castianeira*. It is distributed across Canada, although confined to the lower latitudes (Dondale and Redner 1982). Most commonly found in shady deciduous forest litter, it has also been collected under logs and stones in open habitats (Dondale and Redner 1982), under leaves in dry places, and on the American prairies (Reiskind 1969).

Like the three lycosid species, *C. longipalpa* is diurnally active and is presumed to disperse by ballooning (Reiskind 1969) thereby explaining its ability for rapid expansion into a disturbed area. Cocoons of this species are reported to have fewer than 10 eggs per egg sac (Reiskind 1969), unlike *Alopecosa kochii* with a reported fecundity of 60 eggs per female (Hagstrum 1970). Lower fecundity in this species may partially explain the lower capture rate of *C. longipalpa*.

Ant mimicry is common in the Castianeirinae, and ranges from general to specific. One Central American *Castianeira* exhibits multiple mimicry. In this case adult male, female and nymphal spiders mimic different ant species (Foelix 1982). North American *Castianeira* species have a more generalized body form without strong constrictions or expansions (Reiskind 1969). Most species, including *C. longipalpa*, are considered familial ant mimics

which resemble moderate to large brown or black ants (Reiskind 1969). They move in an erratic fashion and hold their front legs up somewhat like antennae. *C. longipalpa* is thought to resemble a large unidentified mound-building ant species (Reiskind 1969).

The benefits these species derive from this association are unknown. Although spiders are polyphagous and readily cannibalistic, most avoid ants, beetles, wasps, and caterpillars (Foelix 1982), although there are exceptions such as *Antrodiaetus pacificus* as mentioned previously. Birds also avoid eating ants (Foelix 1982), yet are major predators of spiders. Therefore, it is reasonable to believe that the ant-like habits and appearance of *C. longipalpa* may reduce its risk of predation by both birds and other spiders.

Gnaphosidae

Drassyllus depressus is a small spider previously trapped in a variety of habitats (Platnick and Dondale 1992). It is distributed evenly across southern Canada south to Arizona and Virginia (Platnick and Dondale 1992). Most gnaphosids are nocturnal (Turnbull 1973), although specific information regarding this species is unknown. As the other spiders designated regeneration specialists are diurnal, it is surprising that there is only one nocturnal wandering species captured in numbers sufficient for analysis.

Zelotes puritanus and *Z. fratris* are tentatively classified as regeneration specialists. Both spiders have broad distributions across Canada. *Z. puritanus* is considered an uncommon spider while *Z. fratris* is considered common (Parsons *et al.* 1991). Both have

been trapped in a variety of forested and non-forested habitats including beach litter, meadows prairies, and marshes (Platnick and Dondale 1992).

Intermediate Forest Specialist

Agelenidae

Cybaeus eutypus is a common spider with relatively indiscriminate habitat preferences. It is found where there are reasonably established coniferous woodlands. It spins webs underneath bark or rotting logs, and generally avoids open areas (R. Bennett pers. comm.). McIver *et al.* (1992) found similar depressed levels of abundance of *Cybaeus reticulatus* Simon in the 3-7 year old clear-cuts, with a marked increase in abundance at the 16-19 year old sites. Lack of suitable habitat is likely the primary explanation for this spider's relative absence from the early regeneration stages. Another possible explanation is that this spider is unable to compete with the numerous lycosids in this successional stage. *C. eutypus* is approximately the same size as the three *Pardosa* species. As lycosids actively pursue their prey, the required food supply for spiders in this size class may be depressed enough that *C. eutypus* is unable to firmly establish itself in the regeneration stage. Although *Antrodiaetus pacificus* is larger, *C. eutypus* is the only spider of this size in the immature and mature habitats. Its successful utilization of this habitat has likely excluded other species in a manner similar to the lycosid dominance of the regeneration stage.

Unresolved Species

Four of the species that are unresolved regarding habitat preference have already been discussed in their tentative category placement.

Twelve of the fifteen *Xysticus pretiosus* captured were in old-growth forest. This spider is categorized as a forest litter inhabitant in the H.J. Andrews forest. It is not a common spider (Parsons *et al.* 1991), and its absence from the traps may be explained by its rarity, not its total absence from the area. Thomisids are less active foragers, and more common in deeper, more complex litter (Uetz 1991). The tentative placement of this spider as an old-growth specialist must be viewed with some caution. The capture rate was very low, the Koksilah old-growth was not a large patch of forest and there was a path for off-road motorcycles cut through the trees.

Uncommon Species

Habitat preference may explain the low capture rates of several of these uncommon species. *Anyphaena pacifica* (Banks) is a canopy dweller and *Callobius pictus* (Simon), and *Callobius severus* (Simon) live on tree trunks (R. Bennett, pers. comm.). *Novalena intermedia* (Chamberlin & Gertsch), *Xysticus cunctator* Thorell, and *Xysticus montanensis* Keyserling reside in the herb layer (R. Bennett, pers. comm.). The remaining uncommon species (Table 3), are ground inhabitants, and may potentially be considered rare in the sample area.

Forest Successional Stage Comparisons

Diversity Indices

Despite ever-shifting foci in ecology, diversity has remained a central ecological theme (Magurran 1988). Diversity encompasses two main concepts. The first, species richness, measures the number of species in the defined sampling unit. As the sampling units in this study (the successional stages) are delimited in space (by disjunct habitat), and time, this is considered a useful measure of diversity (Magurran 1988). Rarefaction is another effective method to describe species richness (Curtis 1980). As the samples collected were of unequal size, and species richness increases with sample size, the rarefaction technique calculates the expected number of species in the samples if all samples were a standard size (Magurran 1988).

Although a count of species numbers and indices of such are informative, communities are composed of both common and uncommon species. Therefore species evenness, the second concept of diversity, must also be considered. Differences in diversity indices are based on the weighting of species richness and species evenness (Magurran 1988), and are termed heterogeneous indices by Peet (1974). As these indices do not make assumptions regarding the underlying distribution, Southwood (1979) has labeled them to be non-parametric. The validity of some of these indices has been questioned (Southwood 1979, Peet 1974, Magurran 1988), but their use in ecological studies continues. The Shannon-Wiener index is commonly used for pitfall samples of ground spiders (Coyle 1981, Bultman and Uetz 1982, Bultman *et al.* 1982, Haskins and Shaddy1986).

Both measures of species richness and the Shannon-Wiener index indicate the forest regeneration stage to contain the highest diversity. Contrary to popular beliefs, old-growth stands are not necessarily the most diverse regions (Middleton 1994). Population patterns of species inhabiting a successional stage following disturbances such as fire or logging exhibit different population patterns than those in primary stage succession (Johnston and Odum 1956). These findings of increased diversity in a clear-cut agree with other studies of spiders (Coyle 1981, McIver et al. 1992, Huhta 1971), and carabids (Craig 1995, Niemelä et al. 1993). During early succession, plant and arthropod diversity are strongly associated (Southwood et al. 1979). Increased herbaceous productivity supports a large community of invertebrate herbivores, which in turn supports a greater diversity of predators (Halme and Niemelä 1993). This effect is not restricted to early successional areas, and may also be apparent in fragmented habitat (Halme and Niemelä 1993). These factors may partly explain the higher diversity of the Koksilah old-growth. As mentioned, this patch although long, was not particularly wide, and there was an off-road motorcycle path cut through the trees.

It is important to realize that contrary to general belief, increased diversity is not always the ideal. Currently increased diversity as an ideal is the accepted tenet, exemplified by by this quote in Heywood (1995) stating "... an area with higher diversity may be deemed more important than one with lower diversity." Although not specifically evident in these data, increased diversity in regeneration zones occurs often to the detriment of old-growth specialists, a trend apparent in other arthropod studies (Craig 1995, Niemelä et al. 1993, McIver et al. 1992).

Similarity Coefficients and Cluster Analysis

The Morisita Index of similarity was chosen for its robustness and suitability for ecological count data (Krebs 1989). Wolda (1981) found this to be the only index independent of sample size and diversity. The distinctness of the regeneration stage at these sites is similarly found in the Collembola and Carabidae (Setälä and Marshall 1994, Craig 1995). Again, it is likely that the fragmented nature of the Koksilah old-growth may explain why this stage does not cluster with the other forested zones.

RARE AND ENDANGERED SPECIES

There has already been mention of the potentially rare and endangered spiders in British Columbia. In this research several species from Scudder's (1994) list were trapped and thus worthy of specific mention. The agelenids *Cicurina tersa*, and *C. simplex* are listed as rare in B.C., but are found elsewhere in Canada (West *et al.* 1984). The remaining species are only recorded in British Columbia. *Castianeira walsinghami* (O. Pickard-Cambridge) is found in select locations in British Columbia (West *et al.* 1984). *Antrodiaetus pacificus* and *Cybaeus signifer* Simon are restricted to Vancouver Island, and *Novalena intermedia* (Chamberlin & Gertsch) is recorded only on Vancouver Island and S. Pender Island (West *et al.* 1988, West *et al.* 1984). The remaining species, *Calymmaria emertoni* (Simon), *Calymmaria nana* (Simon), and *Sergiolus columbianus* (Emerton), are recorded only from southern Vancouver Island (West *et al.* 1988, West *et al.* 1984). Special mention must be made of the species *Zora hespera* Cory & Mott. Collection of this species represents the first record of the family Zoridae in Canada (Bennett and Brumwell 1996).

Information regarding habitat preference for these rare species is limited. *Cicurina tersa*, *C. simplex*, and *Cybaeus signifer* appear to prefer older forests, as do *Calymmaria emertoni* and *C. nana* (R. Bennett pers. comm.). *Castianeira walsinghami* specimens have been previously found in conifer forests in Washington State (Dondale and Redner 1982). *Antrodiaetus pacificus* is known to prefer cool, humid, densely forest habitats (Coyle 1971), although significant collections of this species in the regenerational forest conflicts this information. Habitat preferences of *Sergiolus columbianus* appear varied. Specimens have been collected in both coniferous and deciduous forests, in chaparral, sage, grass, under stones, on beaches and in houses (Platnick and Dondale 1992). *Zora hespera* live in shrubs and on the ground, preferring open, sunny areas (Bennett and Brumwell 1996).

GENERAL DISCUSSION

Factors Affecting Litter Spider Distributions

Several factors affect litter spider distribution in a complex manner. If a species is able to immigrate to, or previously resides in a habitat, then litter depth and complexity, spatial heterogeneity, prey abundance, and micro-climatic conditions affect an individual's ability to thrive in a habitat, and both historical and current environmental conditions strongly affect all of these components. The extent of these effects seen on the species in this study are not directly comparable as certain litter families were not examined.

Dispersal Ability

Dispersal and migratory ability varies among species and dictates an individual's access to a habitat. Ballooning is an effective dispersal method for juvenile spiders to cover great distances and is variable among species (Greenstone *et al.* 1987). Lycosids and gnaphosids readily balloon (Gertsch 1979), and McIver *et al.* (1992) believe this may explain the early appearance of these two families in the regeneration stage. Results of Greenstone *et al.* (1987) show that the combined ballooning rate of lycosids, gnaphosids and clubionids is readily surpassed by the aeronautic linyphiids. Linyphiids were not included in this study, but McIver *et al.* (1992) found the numbers of linyphiids to be low in the regeneration stages. It is possible that unsuitable habitat conditions, rather than the inability to disperse to the area prevents their colonization of this area.

Spiders that are unable to balloon may walk from an area if distances to suitable

habitat are not excessive. Barriers to movement can affect dispersal ability. Studies of

lycosids and carabids found that individuals are unlikely to cross roads of various surfaces,

thereby stimulating movements parallel to the road (Mader *et al.* 1990). Logging areas tend

to be criss-crossed with graded roads that may prevent immigration of species that do not

balloon or older individuals unable to balloon.

Habitat Conditions

If a species is able to immigrate, there are numerous factors that affect the individual's

ability to colonize the area. Habitat quality is believed to be the primary determinant of litter

spider distribution in the H.J. Andrews Forest (McIver *et al.* 1992). Aspects of habitat quality

include structural components, climatic components, and nutritional components.

Structural Components

Habitat structure is extremely important to litter spiders. The effect of leaf litter

(presence or absence, depth and complexity) contributes substantially to the species

composition of an area. Several manipulation studies have examined the effects of litter

variation on the spider community (Uetz 1979, Bultman and Uetz 1982, Bultman and Uetz

1984).

The absence of litter, or its removal from an area, causes a profound change in the

species composition of an area. Clear-cut inhabiting species tend not to build webs, or

establish litter based nest sites, and consume different prey species (McIver *et al.* 1992). Uetz (1979) and Bultman and Uetz (1982) document the effects of litter on lycosids. Lycosids are abundant on shallow compressed litter, and removal of litter from an area will increase their dominance. This change in litter habitat from three dimensional to a flatter, uni-dimensional surface may give these spiders a competitive advantage (Uetz 1979) and be imperative for mating. As some lycosids use auditory clues in prey detection, sound attenuation from the ground is important (Uetz 1991). Lycosids have a high rate of intra and interspecific predation (Uetz 1991), and compressed litter may increase the risk of other spiders to lycosid predation (Uetz 1979). Auditory signals employed during mating rituals may be similarly affected by ground structure, and mate recognition is imperative in this potentially cannibalistic group (Uetz 1991).

The addition of litter decreases lycosid dominance and increases the dominance of other leaf litter families such as clubionids, gnaphosids and thomisids (Uetz 1979). Increased litter depth translates to increased complexity, interstitial space, prey abundance and stability of the microclimate. In deeper litter, "within-litter" species have increased habitat resources that are partitioned more effectively, and the relative increase in family abundance is reflective of the increased variety of hunting strategies (Uetz 1991). Certain litter spiders build webs, and the deeper litter layer of more mature forests increases the number of web attachment sites (Huhta 1971). Additionally, deeper litter is insulatory, and thus prolongs prey activity and potentially increases survivorship of species that develop later in the season (Uetz 1979).

These conditions lead to improved survivorship that may increase population size and lower

extinction rates of certain species (Uetz 1979, Bultman and Uetz 1982).

Horizontal and vertical spatial separation are other structural components that affect

litter spider distribution. Habitats with more complex structure support an increased number

of species at greater equability (Uetz 1991). Studies have shown that hunting spiders exhibit a

significant preference for specific structural features and select habitats based on these features

(Robinson 1981, Uetz 1991). Physical structure may affect individual interactions, prey

capture, and reproduction (Uetz 1991). Certain lycosids use "perches" for prey capture, and

perch selection is based on specific habitat features (Uetz 1991). Other litter spiders use

architectural foundations for webs, vibration-conduction and monitoring surfaces in

communication and prey capture (Uetz 1991).

Climatic Components

The microclimate at the forest floor is an important factor in determining the ability of

a species to inhabit an area. Most spiders seek a minimal level of protection from

environmental extremes (Uetz 1991). Canopy closure stabilizes the environmental conditions

at the forest floor by reducing fluctuations of light, humidity, temperature and wind, thereby

benefiting species with reduced tolerance to environmental extremes. Tolerance to

desiccation is variable among species. Nørgaard (1951) found the microclimatic tolerances of

two lycosid species living in close proximity to vary considerably and suggested that this

prevented interspecific competition. McIver *et al.* (1992) found that recovery of spider fauna

in logged areas is correlated with changes in moisture levels. In the regeneration stage, the seedling conifers and leaf litter are not developed enough to reduce such environmental impacts, thereby dictating the species that inhabit the area.

Nutritional Components

Prey availability and competing predaceous arthropods may cause variation in the litter spider community. The leaf litter is inhabited by microarthropods that are a food source for juveniles and small-bodied adults. Clear-cutting and/or burning can remove approximately 90% of the microarthropod food base from a habitat (Moldenke and Fichter 1988). Although a mixed diet is no better than a single prey item (Holmberg and Turnbull 1982), spiders do select prey based on the following factors: size, mobility, integumentary strength, and palatability (Moulder and Reichle 1972).

Larger spiders tend to choose large prey, small spiders choose smaller prey (Moulder and Reichle 1972). Many lycosids are relatively large spiders, and are known to feed on Orthroptera (McIver et al. 1992). Such herbivorous prey fauna is abundant in the H.J. Andrews regeneration forest (7-15 years) (an area dominated by lycosids) owing to the plenitude of edible vegetation. Bultman (1981) found that hunting spiders often congregate in areas of high prey density. As the forest ages, the plant matter, herbivorous insects and diurnal pursuit hunters (such as lycosids) all decrease (McIver et al. 1992). Loss of suitable prey may be one of the deterrents to lycosid colonization of older forests.

Logically then, a lack of sufficient smaller prey may be equally limiting for smaller spiders inhabiting the regeneration zone. Collembola are common spider prey (Clarke and Grant 1968, Moulder and Reichle 1972), yet collembola populations in the Victoria Watershed and Koksilah regeneration stages were significantly lower than in the forested stages (Setälä and Marshall 1994). Suitable prey availability may partially explain the significant increase in the linyphiids (a very small spider) in the old-growth stages in studies conducted by McIver *et al.* (1992) and Huhta (1971).

Moulder and Reichle (1972) also report the following regarding spider prey selection. Spiders are only attracted to moving prey, and reject sedentary forms such as pupae and dipteran or coleopteran larvae. Integumentary strength also determines prey selection as certain arthropods such as Coleoptera, millipedes and isopods are rejected by all but the larger spiders (lycosids/agelenids) with chelicerae strong enough to penetrate the exoskeleton. Species that produce mucous type secretions such as earthworms or slugs are rejected by spiders as prey items and certain hemipterans, coleopterans, and formicids are also avoided because of their repugnatorial scent.

The effect of the above mentioned factors are interdependent, and it is likely that each factor exerts a greater influence on the spider population at different times of the year. Uetz (1979) effectively summarizes the importance of these variables. Early in the season, prey abundance and activity accounts for species richness. During mid-season, when the weather is hot, microhabitats with shelter may be limiting. Therefore litter complexity is of primary

importance. Deeper litter allows for greater refuge from intra and interspecific predation. Late in the season, again litter depth is important as temperature variation increases and environmental conditions become extreme.

However, Bultman and Uetz (1982) report problems with correlations that allow only inferences about causal mechanism. As litter structural complexity increases with litter depth, and most forests with thick litter have structurally complex litter, there is no ability to determine if depth/structural complexity or nutritional quality of litter is responsible for increased spider diversity (Bultman and Uetz 1984). Additionally, Jennings (1988) suspects that the influence of litter development on spider abundance in coniferous forests is less than in deciduous forests, although species diversity does increase with litter depth and studies by Bultman and Uetz (1982) found that hunting spiders showed no clear response to litter structural complexity.

SUMMARY

Litter spiders were collected by pitfall trapping at two sites in Douglas-fir forest on south-eastern Vancouver Island. Both sites (Victoria Watershed South and Koksilah) contained four successional stages (regeneration, immature, mature, old-growth) in close proximity. Trapping was equal and concurrent at all stages, at both sites.

Accurate taxonomic knowledge was an important aspect of this study. Spiders of selected families were identified to species. Of the thirty-two species collected, 17 were considered to be uncommon (less than 10 individuals). Several species are listed as potentially rare and endangered in British Columbia. The species *Zora hespera* represents a new Canadian record for the family Zoridae.

Three distinctive distribution patterns are recognizable: generalists, regeneration specialists, and intermediate forest specialists. Limited biological information regarding several of the species collected made inferences regarding habitat choice difficult. The lycosids are exceptional in this regard. Further studies regarding life history of species are needed.

Unlike findings in other arthropod studies, there are no obvious old-growth specialist species, although increasing collection effort may reveal significant patterns in the less abundant species. There were however several regeneration specialists, making the regeneration stage distinct among the four successional stages. The presence of such

regeneration specialists in an area is also indicative. Spiders, such as lycosids have increased tolerance to marginal environmental conditions, but are excluded as the forest canopy closes.

Diversity indices and species richness measures indicate no significant difference between the three forested regions. The selected litter spiders appear to recover quickly with the closure of the canopy, although information regarding other families of litter spiders may differ. Additional research on litter spiders may help elucidate some of the tentative patterns observed.

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APPENDIX A

SITE LOCATIONS

Victoria Watershed	Latitude	Longitude	UTM System Zone	Easting	Northing
Regeneration	48 33 51.9	123 38 55.4	10	452250	5379000
Immature	48 33 51.9	123 38 55.4	10	452400	5378800
Mature	48 34 15	123 39 45	10	451100	5379700
Old-Growth	48 33 44.6	123 38 53.2	10	452600	5378500
Koksilah Watershed					
Regeneration	48 39 25	123 45 51.4	10	443600	5389400
Immature	48 39 41.2	123 46 10	10	443850	5389850
Mature	48 39 20	123 44 50	10	444500	5389500
Old-Growth	48 39 30	123 45 50	10	444500	5389500

SITE DESCRIPTION

Victoria Watershed	Aspect	Slope	Elevation
Regeneration	50	15%	250 m
Immature	20	40%	305 m
Mature	315	11.4%	240 m
Old-Growth	30	40%	390 m
Koksilah Watershed			
Regeneration	170	15%	595 m
Immature	170	15%	710 m
Mature	210	35%	590 m
Old-Growth	180	15%	630 m

Data provided by the Canadian Forest Service (Craig 1995)

APPENDIX B

Order Araneae

Family Antrodiaetidae
Antrodiaetus pacificus (Simon)

Family Lycosidae
Alopecosa kochii (Keyserling)
Pardosa dorsuncata Lowrie & Dondale
Pardosa vancouveri Emerton
Pardosa wyuta Gertsch

Family Agelenidae
Novalena intermedia (Chamberlin & Gertsch)

Family Cybaeidae
Cybaeus eutypus Chamberlin & Ivie
Cybaeus reticulatis Simon
Cybaeus signifer Simon

Family Hahniidae
Calymmaria emertoni (Simon)
Calymmaria nana Simon
Cryphoeca exlineae Roth

Family Dictynidae
Cicurina tersa Simon
Cicurina simplex Simon

Family Amaurobiidae
Callobius pictus (Simon)
Callobius severus (Simon)

Family Anyphaenidae
Anyphaena pacifica (Banks)

Family Liocranidae
Phrurotimpus borealis (Emerton)

Family Corinnidae
Castianeira longipalpa (Hentz)
Castianeira walsinghami (O. Pickard-Cambridge)

APPENDIX B: *Continued*

Family **Gnaphosidae**
Callilepis pluto Banks
Drassodes neglectus (Keyserling)
Drassyllus depressus (Emerton)
Micaria pulicaria (Sundevall)
Sergiolus columbianus (Emerton)
Zelotes fratris Chamberlin
Zelotes hentzi Barrows
Zelotes puritanus Chamberlin

Family **Zoridae**
Zora hespera Cory & Mott

Family **Thomisidae**
Xysticus cunctator Thorell
Xysticus montanensis Keyserling
Xysticus pretiosus Gertsch