

**FACULTATIVE GROUP LIVING IN THE WESTERN
BLACK WIDOW SPIDER, *LATRODECTUS HESPERUS*: AN
EVOLUTIONARY APPROACH**

by

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ABSTRACT

A major goal of evolutionary research is to elucidate the processes involved in the evolution of group versus solitary living, by examining the selective forces driving or constraining a particular type of social system. Species with intermediate group living tendencies are particularly interesting because they offer insight into evolutionary transitions and, in particular, how different selective environments may modulate group living behaviours. This dissertation explores the different factors that shape the social strategies of the western black widow spider, *Latrodectus hesperus*, a facultatively group-living spider. Over a period of four years, I characterized the social structure of coastal British Columbia populations of *L. hesperus*, and show that individuals live either solitarily or in groups depending on the time of year, their reproductive status, and age. I then used an experimental approach to investigate the dynamics and adaptive value of facultative group-living behaviours, by testing different hypotheses about the decisions involved in social interactions, web building, microhabitat settlement, movement, and foraging. Several factors were manipulated and shown to influence the patterns of group living in *L. hesperus*, including individual nutritional state, prey availability, group size, population density, and neighbour proximity. Spiders adjusted their group living behaviours according to changes in these factors, and responded strategically to the presence and proximity of conspecifics. Based on the results of these experiments, I developed a model of group living in spiders that specifically considers the dynamic and strategic nature of social interactions in the context of frequency-dependent selection. The research presented in this thesis furthers our understanding of the evolution of social behaviour by providing new evidence on the mechanisms that promote and regulate facultative group-living behaviours.

Keywords: aggregation; foraging; group living; social; spiders; web building

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TABLE OF CONTENTS

Approval	ii
Abstract	iii
Acknowledgements	iv
Table of Contents	vi
List of Figures	viii
List of Tables	xii
Chapter 1: General Introduction	1
1.1 General Context of Thesis Research	2
1.2 Focus of Thesis Project and Definitions.....	4
1.3 Overview of Thesis Chapters	5
1.4 References	6
Chapter 2: Microhabitat use by <i>Latrodectus hesperus</i> spiders in coastal British Columbia: evidence of facultative group living *	9
2.1 Abstract.....	10
2.2 Introduction.....	10
2.3 Materials and Methods.....	13
2.4 Results.....	19
2.5 Discussion	27
2.6 Acknowledgements	34
2.7 References.....	34
2.8 Appendices.....	45
Chapter 3: Cohabitation dynamics among web-building spiders as a function of prey availability and population density *	50
3.1 Abstract.....	51
3.2 Introduction.....	51
3.3 Materials and Methods.....	55
3.4 Results.....	63
3.5 Discussion	73
3.6 Acknowledgements	79
3.7 References.....	79
Chapter 4: Combined influence of neighbours and feeding state on movement decisions made by a web-building spider	91
4.1 Abstract.....	92
4.2 Introduction.....	92
4.3 Experiment 1: Microhabitat Tenacity in Established Spiders.....	95

4.4 Experiment 2: Effect of Neighbours on Microhabitat Residence Time	97
4.5 Experiment 3: Effects of Multiple Factors on Microhabitat Residence Time	100
4.6 Discussion	104
4.7 Acknowledgements	109
4.8 References.....	109
Chapter 5: Western black widow spiders express state-dependent web- building strategies tailored to the presence of neighbours *	118
5.1 Abstract.....	119
5.2 Introduction.....	119
5.3 Materials and Methods.....	122
5.4 Results.....	130
5.5 Discussion	133
5.6 Acknowledgments	140
5.7 References.....	141
Chapter 6: Group size influences prey capture success in a facultatively group-living spider *	150
6.1 Abstract.....	151
6.2 Introduction.....	151
6.3 Methods.....	154
6.4 Results.....	160
6.5 Discussion	168
6.6 Acknowledgements	174
6.7 References.....	174
Chapter 7: General Conclusion.....	189
7.1 Summary of Main Findings, Implications and Perspective	190
7.2 Future Directions: Building a Theory of Group Living	193
7.3 References.....	202
7.4 Appendix.....	205

LIST OF FIGURES

<p>Figure 2.1. Natural lifecycle of <i>Latrodectus hesperus</i> in coastal British Columbia, Canada. Changes over time in densities (number per m²) of (a) males and females (adults and subadults); (b) juveniles, egg sacs, and webs; (c) large, medium and small juveniles (aF: adult females; saF: subadult females; aM: adult males; saM: subadult males; Juv: juveniles; Egs: egg sacs)</p>	38
<p>Figure 2.2. Distribution of <i>L. hesperus</i> spider group sizes (number of spiders per occupied web) in natural microhabitats on a monthly basis in 2006. Box plots show medians (centre bold lines), means (filled squares), 25th and 75th percentiles (bottom and top of boxes, respectively), and 10th and 90th percentiles (cap of lower and upper whiskers, respectively)</p>	39
<p>Figure 2.3. Spatial distribution of <i>L. hesperus</i> spiders (all spiders, adult and subadult females (aF+saF), and juveniles (Juv)) in 2006. Values on the y-axis represent the Standardized Morisita Index of dispersion, which ranges from -1 to +1, with 95% confidence intervals at -0.5 and +0.5 (see methods for a detailed explanation of the index). Note that the juvenile (Juv) curve only starts in July, because too few individuals were found from March to June (see Fig. 2.1b) to calculate a meaningful value of this index</p>	40
<p>Figure 2.4. Distribution of <i>L. hesperus</i> spiders in September and June from 2002 to 2005: (a) Changes over time in densities (number per m²) of <i>L. hesperus</i> spiders and webs and <i>Tegenaria</i> spp. spiders (i.e. <i>T. agrestis</i> and <i>T. duellica</i>; aF+saF: adult and subadult <i>L. hesperus</i> females); (b) Distribution of <i>L. hesperus</i> spider group sizes (number of spiders per occupied web; refer to Fig. 2.2 for box plot specifications)</p>	41
<p>Figure 2.5. Changes over time in densities (number per m²) of spiders and webs from 2003-2005 in artificial microhabitats for (a) <i>L. hesperus</i> adult females, subadult females, and adult and subadult males combined; (b) <i>L. hesperus</i> juveniles and egg sacs; (c) <i>T. duellica</i> and <i>T. agrestis</i> adult and subadult spiders, and <i>Tegenaria</i> spp. juveniles; (d) <i>L. hesperus</i> and <i>Tegenaria</i> spp. webs. Each data point represents a month of the year, abbreviated as the first letter of the month on the x-axis (refer to Fig. 2.1 for an explanation of the abbreviations used on the graphs).....</p>	42
<p>Figure 2.6. Distribution of <i>L. hesperus</i> spider group sizes (number of spiders per occupied web) in artificial microhabitats on a monthly basis from</p>	

2003 to 2005 for (a) all spiders; (b) adult and subadult females; (c) juveniles. (Refer to Fig. 2.2 for box plot specifications)	43
Figure 2.7. Prey captured by <i>L. hesperus</i> spiders on a monthly basis in 2005: (a) total number of prey; (b) total prey biomass; (c) prey size (body length) distribution. Also represented in (a) is the total number of <i>L. hesperus</i> spiders (i.e. predators) present under the sheds. In (a) and (b), prey are grouped according to their taxonomic order and the 4 most abundant orders are shown with the rest grouped into a single category, "Other" (i.e. Dermaptera, Orthoptera, Lepidoptera, and Diptera). For (b), only the 2 most abundant orders are shown and the remainder is lumped into "Other". Data for Araneae prey are omitted from (c), since they are not based on body length (see Appendix B). (Refer to Fig. 2.2 for box plot specifications).....	44
Figure 3.1. The circular enclosures used in the experiment contained 6 evenly-spaced wooden sheds that served as spider microhabitats	85
Figure 3.2. Survival rate of <i>L. hesperus</i> spiders kept on two different feeding regimes (well fed vs. poorly fed), and 3 different initial spider densities: (a) 1 <i>L. hesperus</i> spider per microhabitat; (b) 2 <i>L. hesperus</i> spiders per microhabitat; (c) 1 <i>L. hesperus</i> + 1 <i>Tegenaria</i> spp. spider per microhabitat.....	86
Figure 3.3. Final <i>L. hesperus</i> spider density at the end of the experiment (mean number of spiders per microhabitat \pm SD) as a function of feeding regime and initial spider density	87
Figure 3.4. Web-building dynamics of <i>L. hesperus</i> spiders as a function of initial spider density (number per microhabitat): (a) Mean (\pm SE) number of webs per microhabitat; (b) Mean (\pm SE) area per web; (c) Mean (\pm SE) number of spiders per occupied web. The dotted line in (c) corresponds to the total area under a microhabitat available for web building	88
Figure 3.5. Change over time in mean (\pm SE) per capita number of moves by <i>L. hesperus</i> spiders kept at 2 different feeding regimes (well fed vs. poorly fed) and 3 different initial spider densities: (a) 1 <i>L. hesperus</i> spider per microhabitat; (b) 2 <i>L. hesperus</i> spiders per microhabitat; (c) 1 <i>L. hesperus</i> and 1 <i>Tegenaria</i> spp. spider per microhabitat	89
Figure 3.6. Change over time in mean (\pm SE) number of <i>L. hesperus</i> spiders per occupied microhabitat across (a) initial spider density treatments, and (b) feeding regimes	90
Figure 4.1. Mean daily web area (\pm SE) of established <i>L. hesperus</i> females whose webs were either left untouched or manipulated in one of two ways (N = 20 per group). Manipulations were implemented on days 1-4.....	115

Figure 4.2. Rate of microhabitat departure of *L. hesperus* spiders tested in a field experiment. Each line corresponds to a different microhabitat occupancy treatment: alone (N = 22), or with a conspecific spider (N = 22)116

Figure 4.3. Rate of microhabitat departure by *L. hesperus* spiders tested in a laboratory experiment. Spiders were maintained on two different diets (well fed vs. poorly fed) and tested at one of two microhabitat occupancy levels (alone (N = 24), or with a conspecific spider (N = 20)). Each graph corresponds to a different diet group: (a) well fed, (b) poorly fed117

Figure 5.1. Percentage of (a) well-fed (N = 33) and (b) poorly fed (N = 36) *L. hesperus* spiders that had constructed a silken structure (with ≥ 10 threads) within a subdivision at each time step. The different lines correspond to different microhabitat occupancy treatments: alone (broken line, circles), with conspecifics (full line, squares) and with heterospecifics (full line, triangles). The horizon bar below the X axis denotes the duration of each lighting phase: dark and light. The vertical lines indicate the end of the dark phase (the 9th hour), at which time the lights came on and stayed on until the end of the experiment146

Figure 5.2. (a) Mass of silk and (b) density of silk webbing produced by well-fed (\square , N = 33) and poorly fed (\blacksquare , N = 36) *L. hesperus* females housed for 24 h under three different microhabitat occupancy treatments (alone, with conspecifics, or with heterospecifics). Data are represented as box plots, with the mean (square symbols), the median (central lines), the 25th and 75th percentiles (top and bottom of boxes), and the 5th and 95th percentiles (cap of lower and upper whiskers)147

Figure 5.3. Percentage weight loss (least square means + 95% CI) in well-fed (\square) and poorly fed (\blacksquare) *L. hesperus* females, after residing in the experimental units for 24 h at three microhabitat occupancy levels148

Figure 5.4. Least square means (\pm SE) of the ratio between the quantity of silk mass produced (mg) and the associated loss in body weight (mg) in well-fed (\circ) and poorly fed (\bullet) *L. hesperus* females subjected to three different microhabitat occupancy treatments149

Figure 6.1. Wooden sheds (i.e. spider microhabitats) used in both experiments (dimensions: 125 cm L \times 15 cm W \times 8 cm H). The sheds had a removable lid with underneath a sheet of metal meshing (mesh size: 2 mm) that was stapled onto the sides, and under which *L. hesperus* females built their webs. The lid and metal meshing were 1 cm apart to prevent females from attaching silk to the underside of the lid. Both openings were closed off with synthetic meshing (mesh size: 1 mm), and in the centre of each sheet of meshing was glued a circular piece of

plastic with a hole in the middle (hole diameter: 16 mm) that was capped with a rubber cork. These holes were used to introduce prey under the sheds	182
Figure 6.2. Mean (\pm SE) number of prey captured per capita by <i>L. hesperus</i> females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2	183
Figure 6.3. Mean (\pm SE) latency to first prey capture (min) by <i>L. hesperus</i> females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2	184
Figure 6.4. Mean (\pm SE) mass of silk (mg) produced by <i>L. hesperus</i> females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2	185
Figure 6.5. Mean (\pm SE) ratio between the number of prey captured and the mass of silk produced by <i>L. hesperus</i> females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2.....	186
Figure 6.6. Mean (\pm SE) distance moved by <i>L. hesperus</i> females at different group sizes and prey densities over the course of the acclimation period and prey capture (experimental) phase in (a) Experiment 1, and (b) Experiment 2. Distances on the y-axis represent the mean number of microhabitat zones travelled over 2 consecutive census times	187
Figure 6.7. Summary of data from Exp. 1 (prey abundance) and Exp. 2 (prey limitation) for relationships between prey density and (a) the number of prey captured per capita (log-transformed), (b) the latency to first prey capture (log-transformed), (c) the mass of silk produced per capita, and (d) the ratio between the number of prey captured and the mass of silk produced per capita. Results of both experiments are plotted on the same scale for the x-axis (number of prey per microhabitat), and datapoints of each experiment are represented with the same symbol within each spider group size treatment. Each datapoint represents a mean value of a given response variable	188
Figure 7.1. Basic model algorithm: sequence of events taking place within a given lapse of time. Each transitional step is associated with a specific set of probabilities for the occurrence of stochastic events, and each conditional decision is associated with a particular fitness return (see text for details).....	212

LIST OF TABLES

Table A2.1.	List of plant species present at Island View Beach in the open habitat where <i>L. hesperus</i> and <i>Tegenaria</i> spp. spiders co-occur (non-exhaustive list). The status column indicates whether the species is native or introduced in western Canada.....	45
Table A2.2.	List of regression equations used to calculate dry prey biomass (y) in mg based on total body length measurements (x) in mm for different orders of arthropods. For Araneae prey, the regression equations were based on tibia-patella length of leg pair I (tp) and wet prey biomass (w)	48
Table A2.3.	Number and biomass of prey consumed by <i>L. hesperus</i> spiders on a monthly basis in 2005. Each column represents a different order of arthropod prey belonging either to the insects, arachnids or malacostraca. The first row of each cell has the number of prey and the second row has prey biomass (in mg). Data are presented as means \pm SE per microhabitat (N = 30)	49
Table 3.1.	Effect of different predictors on the survival rate of <i>L. hesperus</i> spiders, analyzed using the Cox regression method	83
Table 3.2.	GLMM analyses of the effects of different factors on (a) the daily number of prey captured per capita, and (b) the daily mass of prey captured per capita (log-transformed), by <i>L. hesperus</i> spiders	84
Table 4.1.	Microhabitat tenacity of established <i>L. hesperus</i> females during a 5-day experiment. Manipulations were done on days 1-4. Values represent: number that left / number that stayed (percentage leaving).....	113
Table 4.2.	Number of spiders in each treatment group that left their microhabitats during the first 24 h and over the whole 48 h, in Experiments 2 and 3. Values represent: number that left / number that stayed (percentage leaving).....	114
Table 5.1.	Effect of different predictors on the time to onset of web construction during the 24-h experiment, determined by survival analysis, using the Cox regression method	145

Table 6.1.	GLM analyses of the effects of spider group size and prey density on: (a) the number of prey captured per capita (log-transformed); (b) the latency to first prey capture (log-transformed); (c) the per capita mass of silk produced; and (d) the per capita ratio between the number of prey captured and the mass of silk produced, by <i>L. hesperus</i> spiders.....	179
Table 6.2.	GLM analyses of the effects of spider group size and prey density on (a) per capita weight change (log-transformed final weight), and (b) per capita changes in body condition (log-transformed final condition), among <i>L. hesperus</i> spiders	180
Table 6.3.	GLMM analyses of the effects of different factors on (a) the average per capita distance moved by <i>L. hesperus</i> spiders, and (b) the average nearest-neighbour distances in spider group sizes 2 and 4 (log-transformed)	181
Table 7.1.	List of parameters used in the dynamic game model	210

Chapter 1: **GENERAL INTRODUCTION**

1.1 General Context of Thesis Research

Many animals are gregarious to a certain degree and associate with other conspecific or heterospecific individuals during a specific portion of their life. The distribution of individuals therefore constitutes an important aspect of the environment that influences many ecological factors such as foraging outcome, reproductive output, and mortality risks (i.e. predation pressure, disease transmission, cannibalism), which control the expression and evolution of individual traits. Studies of social behaviour, defined here as an individual's tendency to live within a group versus solitarily, make important contributions to the understanding of the evolution and diversity of species.

Over the last two decades, group living has been studied widely across the animal kingdom using a cost/benefit approach, where experiments and/or observational studies were conducted to determine the influence of different environmental factors on social behaviours and consequently individual fitness (reviewed in Choe & Crespi 1997; Krause & Ruxton 2002). A range of factors have been explored, including ecological ones such as predation pressure (Hass & Valenzuela 2002), parasitism pressure (Hieber & Uetz 1990), climate (Avilés et al. 2007), food availability (Rypstra 1986), habitat structure (Pays et al. 2007), as well as factors that are intrinsic to the individuals involved in a particular grouping association, such as nutritional state (Hensor et al. 2003), the level of relatedness between individuals (Rannala & Brown 1994), group size (Beauchamp 1998), differences in size and stature (Jakob 2004), energetic requirements (Herskin & Steffensen 1998), reproductive behaviour (Salomon & Lubin 2007), and spatial distribution (Brown & Brown 2000). Collectively, the results of these studies show that social behaviours serve different purposes and thus may have evolved through distinct pathways. However, many of these studies have focused on species that express high levels of sociality, while in reality most animals express low or intermediate levels of social behaviour. Therefore, it is important to investigate social dynamics in species that

are mostly solitary and that only live in groups under specific conditions (e.g. high food availability) or at specific times (e.g. during the growth period).

Spiders fit this criterion well as most species are solitary and only a handful of them express group-living tendencies (Riechert 1982; Avilés 1997; Whitehouse & Lubin 2005). This general lack of social behaviour makes them good study organisms to investigate the conditions that favour, maintain or inhibit the evolution of sociality. Spiders have long been the focus of ecological studies, both because they are the dominant invertebrate predators in many terrestrial ecosystems and on account of their diverse modes of habitat use (Uetz 1992; Wise 1993; Foelix 1996). Web-building spiders in particular have evolved very elaborate settlement strategies: they construct an energetically costly web made of silk prior to habitat exploitation. Settling at a microhabitat therefore requires a large energy investment, which favours a sedentary lifestyle and limits habitat sampling. The presence of other individuals at a microhabitat could therefore influence various decision-making processes involved in such activities as foraging and reproduction, and thereby affect group-living strategies. For example, their presence may be correlated with direct benefits or costs (e.g. enhanced prey capture vs. interference competition), and/or their presence may be a source of social information about net microhabitat quality. The latter is dependent on the reliability of social versus private sources of information (King & Cowlshaw 2007).

Spider silk plays an important role in determining social dynamics by influencing the expression of solitary- vs. group-living strategies. It is both a building material for web structures used in foraging and reproduction, and also an important medium of communication. Spiders produce different types of silk that serve various purposes such as anchoring webs, capturing prey, moving, depositing and facilitating the recognition of courtship and territorial signals, and also protecting eggs in silken sacs (Craig 2003). Furthermore, the presence of silk at a particular location may attract spiders ('sericophily'), provided that it is properly recognized (e.g. Sckuck-Paim & Alonso 2001).

1.2 Focus of Thesis Project and Definitions

The main goal of this project was to study the social dynamics of a facultatively group living animal, the western black widow spider, *Latrodectus hesperus* Chamberlin & Ivie (Araneae: Theridiidae). Little is known about the ecology and behaviour of this species in western North America, and there is no comprehensive study to date on the social organization of any species in the genus *Latrodectus*. Anecdotal evidence from a few studies suggests that *L. hesperus* females and females of other *Latrodectus* species are generally solitary (D'Amour et al. 1936; Kaston 1970). However, males and females in various *Latrodectus* species cohabit during the mating season (e.g. Segev et al. 2003; Segoli et al. 2006; pers. obs.).

In this dissertation, I often use the terms “group”, “web sharing”, and “territory” when discussing group- vs. solitary-living behaviours in *L. hesperus* spiders. These terms are relatively subjective and prone to confusion, and need to be properly defined. A “group” of *L. hesperus* spiders is an assemblage of more than one individual that shares either a microhabitat or a web, depending on the level of group living being examined. *Latrodectus hesperus* spiders typically build three-dimensional cobwebs that comprise distinct regions: a main tangle of threads in the centre of the web is anchored to the substrate on various sides with support threads, sticky prey capture threads (‘gumfooted lines’) extend downwards from the tangle sheet, and in some habitats spiders build silken retreats in concealing cracks or crevices in the substrate, usually in the upper section of the web (pers. obs.; see also Benjamin & Zschokke 2003; Blackledge et al. 2005). “Web sharing” occurs when at least two spiders are found on the same cobweb. Webs shared by several spiders are often quite large and consist of a network of interconnected tangle and anchor threads that often contain separate foraging platforms, and spiders freely move between different areas. I sometimes use the word “territory” when referring to a spider web, as it constitutes an extension of the spider which is necessary to perform various activities such as foraging and egg laying. However, spiders inhabiting a given territory in this context are not assumed to be territorial (i.e. to defend this space against intruders for its exclusive use).

1.3 Overview of Thesis Chapters

My dissertation is organized into five research chapters, and a conclusion chapter that combines a general discussion and some theoretical research. Below, I provide a brief summary of the goals and each chapter.

Chapter 2 investigates the social structure of natural populations of western black widow spiders, *Latrodectus hesperus*, from coastal British Columbia by means of field surveys, and provides evidence of their facultative group-living behaviours. It also includes an experiment that examines the mechanisms of group formation among *L. hesperus* spiders, and a study of the ecological interactions between *L. hesperus* spiders and co-occurring web-building spider species *Tegenaria agrestis* and *T. duellica*, to assess their impact on group-living behaviours.

The research presented in the remaining chapters is based on some of the major findings of Chapter 2, namely that most subadult and adult *L. hesperus* females live in groups from late summer to winter. Therefore, in the next chapters I investigate group living dynamics among adult females.

Chapter 3 consists of a field experiment that examines the influence of prey availability and spider density on the dynamics of cohabitation between *L. hesperus* females, and also between *L. hesperus* females and *Tegenaria* spp. females. This study shows how these spiders interact and under what conditions they join together in groups or live individually.

Chapter 4 is a series of three field and laboratory experiments that examine movement decisions of *L. hesperus* females in more detail, and specifically test how (1) individual nutritional state, and (2) the proximity of conspecifics affect these decisions.

Chapter 5 considers the web-building behaviours of *L. hesperus* females, as webs are instrumental in many activities (e.g. prey capture, egg laying). Using an experimental approach, I investigated the role of (1) individual nutritional state and (2) presence/absence of conspecifics and heterospecifics (*Tegenaria* spp. spiders), on several components of their web-building behaviours.

Chapter 6 addresses the relationship between group living and foraging behaviours. Two laboratory experiments were conducted to examine the influence of group size on different aspects of foraging behaviour among *L. hesperus* females, when food is scarce versus abundant.

Finally, I close with a conclusion chapter that (1) outlines and discusses the major findings of this dissertation and their implications, and (2) offers a new perspective by proposing a theoretical model of group living in spiders based on the empirical evidence gathered in this project.

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Chapter 2: **MICROHABITAT USE BY *LATRODECTUS*
HESPERUS SPIDERS IN COASTAL BRITISH COLUMBIA:
EVIDENCE OF FACULTATIVE GROUP LIVING ***

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2.1 Abstract

Animal social systems come in a wide range of forms characterized by different types of group living relationships. Species that express facultative group living behaviours, where individuals associate with each other only under certain conditions or at certain times, are especially interesting for studying how group living may have evolved. We investigated over several years the social structure of the western black widow spider, *Latrodectus hesperus*, in a coastal British Columbia habitat where individuals have been observed to live in groups during part of their life. Here, we show that *L. hesperus* spiders spontaneously associate with conspecifics and form groups at certain times of the year, which leads to an aggregated population distribution; adult and subadult females form groups in the fall and early winter and juveniles associate with each other and adult females in the summer. When living in groups, *L. hesperus* spiders are tolerant of close neighbours and share large webs with one or more conspecifics. We also report on the relationships between different habitat and ecological factors and their group-living behaviours, including their interaction with two other abundant species of introduced spiders (*Tegenaria agrestis* and *T. duellica*). We present the first empirical evidence of facultative group living behaviour in the genus *Latrodectus*, and discuss the implications of our findings in terms of the costs and benefits associated with this behaviour and how these may drive the evolution of higher forms of sociality.

2.2 Introduction

Various animals associate with conspecifics to satisfy specific needs (e.g. prey capture, anti-predator defence), which would either not be met by an individual on its own or not achieved as profitably. These associations often result in the formation of a group, wherein several individuals share a unit of space and engage in at least one common activity. Groups may persist for various lengths of time depending on the nature

of the association, the types of individuals involved in it, and the adaptive value of grouping (Krause & Ruxton 2002). In general, species are categorized as being either solitary or social, which is unfortunate because these categories only represent the two extremes of a social continuum, and most social systems fall somewhere between these two end points. Some animals only behave socially during certain phases of their life (e.g. the juvenile phase), when performing particular activities (e.g. foraging), or under certain conditions (e.g. high predation risks), and live solitarily the rest of the time (Prokopy & Roitberg 2001). For example, in many species of butterflies, larvae live in groups during the early stages of their juvenile life to facilitate their access to food and improve their protection from predators and, once individuals reach later instars, groups usually break up due to a shift in their feeding and protective requirements (Costa & Pierce 1997). It is difficult to categorize group-living behaviours because an animal's tendency to live in a group versus solitarily (i.e. its level of sociality) is usually determined both by the ecological context it is currently experiencing and the one it has evolved in (Strassmann & Queller 1989).

Species that show facultative group-living behaviours are particularly interesting model organisms for the evolution of sociality, because they help us understand factors involved in the transitions between solitary and social modes of living. The potential for group living behaviours may be overlooked in animal taxa considered to be mostly solitary. For example, spiders (order Araneae) are notoriously asocial animals, which are for the most part territorial, cannibalistic, and solitary (Wise 2006). Yet, a few species of spiders are in fact social, and a number of others exhibit sub-social behaviours (Avilés 1997; Whitehouse & Lubin 2005). Furthermore, some spider species, thought of as solitary, will facultatively live in groups, meaning that they are either found alone or in a group depending on environmental conditions, such as prey availability, prey size, habitat topography and microhabitat availability, as well as characteristics of interacting individuals, such as relative body condition and size, and maturity level (Smith 1982, 1983; Lloyd & Elgar 1997; Uetz & Hieber 1997; Jakob 2004). Because spiders' potential for plasticity in social behaviour is generally under appreciated, group living in this taxon may be more common than previously thought.

Many studies have examined the costs and benefits of a particular form of group living in a given species; however, there is a general lack of knowledge about the basic social structure of a species living in a particular habitat, i.e. how and when do individuals associate vs. live individually. One way to address this issue would be to conduct a longitudinal study examining the spatial and temporal distribution of individuals in relation to different resources and demographic factors. Here, we examine the social structure of the western black widow spider, *Latrodectus hesperus* Chamberlin & Ivie (Araneae: Theridiidae), a species found in western North America and considered to be solitary (Kaston 1970). Females and juveniles build cobwebs that are used for foraging, reproduction, and protection, and males travel between webs in search of mates (pers. obs.). Our preliminary field observations of *L. hesperus* populations in coastal British Columbia, Canada, at the northern limit of their range, indicated that females may either build webs individually or share a web with other females or juveniles, suggesting that they exhibit facultative group-living behaviours. This observation is unexpected and thus interesting, because in non-social spider species, group living usually involves associations among juveniles and not adults (e.g. Jones & Parker 2000; Pekár & Král 2001). Furthermore, group living behaviour has been documented primarily in species found in tropical and sub-tropical environments and seldom in species from temperate regions such as in this study (Avilés 1997; but see Furey 1998; Jones et al. 2007). We also observed that *L. hesperus* spiders often share microhabitats with two common non-native web-building species, *Tegenaria agrestis* Walckenaer and *T. duellica* Simon (Araneae: Agelenidae), which have recently been introduced to the Pacific Northwest (Vetter et al. 2003). This raises the question of whether the presence of these heterospecific spiders influences their group-living behaviours.

The main objective of this study was to investigate the social structure of *L. hesperus* spiders in their natural habitat in coastal British Columbia. In particular, we addressed the following questions to characterize their group-living behaviour: Do *L. hesperus* spiders associate and form groups seasonally or year-round? Are certain age classes more prone to form groups? Do they live in groups due to microhabitat shortage?

How prominent is cannibalism among group members, and do conspecifics constitute an important part of their diet? How is the spatial distribution of *L. hesperus* influenced by the presence of *Tegenaria* spp. spiders in their habitat? This study combines population surveys and field manipulations conducted over several years (2002-2006), and is divided into four parts that were conducted separately. In the first part, we document the lifecycle of *L. hesperus*, which has not yet been fully described, and examine the variation in group-living behaviour over one year. In the second part, we compare the spatial distribution of *L. hesperus* over four consecutive years and at two different times of year: in early summer and in late summer. In these first two parts, we also draw correlations between habitat factors and the distribution of *L. hesperus* spiders. In the third part, we manipulate the natural habitat of *L. hesperus* by adding new microhabitats, and examine the colonization pattern of these microhabitats over a period of three years. This allows us to examine how individuals associate and form groups, and explore their social dynamics. In the last part, we characterize the prey captured by *L. hesperus* spiders over one year. Throughout, we also examine the ecological interactions between *L. hesperus* and both *T. agrestis* and *T. duellica*. Together, these different parts provide a complete picture of the group-living behaviour of *L. hesperus*.

2.3 Materials and Methods

2.3.1 Study Area and Species Descriptions

This study was conducted along a coastal beach on the Saanich Peninsula, southern Vancouver Island, British Columbia, Canada (48°34' N, 123°22' W, elevation: 3-5 m). This region is located in the Coastal Douglas-Fir Biogeoclimatic Zone, which enjoys warm dry summers and mild, wet winters. Our research area was located along a c. 300-m section of the beach above the high-tide line in open sandy habitat with sparse low vegetation characterized by grasses, herbs, sedges, dwarf shrubs and mosses (see Appendix A for a list of species), and bordered by a more densely-vegetated habitat (primarily *Cytisus scoparius*, *Malus fusca* and *Pseudotsuga menziesii*). The northern half of this section is on the land of the Tsawout First Nation, where open sand dunes

dominate. The southern half is part of Island View Beach Regional Park, a site that has been diked close to the high-tide line, which has facilitated its colonization by vegetation. This open sandy habitat is very windy and often disturbed by humans and their recreational vehicles, and it is also commonly wave-washed during winter storms.

Latrodectus hesperus, *Tegenaria agrestis*, and *T. duellica* are the dominant web-building spiders in this open habitat, and they build webs underneath logs of driftwood that are found in clusters throughout this area. *Latrodectus hesperus* spiders (i.e. females and juveniles) build 3-dimensional cobwebs on the underside of logs of driftwood, often spanning the entire space between a log and the ground. *Tegenaria* spp. spiders build funnel-sheet webs that are mostly 2-dimensional either on the underside of a log or directly on the ground. None of these spiders and their webs were ever found in the vegetation between the logs (mainly *Polygonum paronychia*), or in the shrubs surrounding the open habitat.

2.3.2 Lifecycle and Natural History Study

We conducted monthly surveys of driftwood logs (i.e. spider microhabitats) in a c. 900-m² area of open sandy habitat located in the northern half of the study area from March to December 2006 to document the lifecycle of *Latrodectus hesperus*. Prolonged snow cover prevented us from surveying the site in January and February. All logs were measured to assess the amount of space available underneath (i.e. total length and average of 3 different widths), and we only turned over and surveyed logs that were bigger than 320 cm² and detached from the substrate (in keeping with the methods of another study reported in this chapter; see 2.3.3). Likewise, we only turned over and surveyed those logs that could be lifted and were free from the ground. This accounted for a total of 68 logs, among which 2 went missing during the study period. In 3 different months, we noticed that some logs were subjected to minor anthropogenic disturbance. Furthermore, on one occasion (in June) the site was heavily disturbed by human activity, causing damage to 11 logs and the disappearance of 1 log. Logs that had been moved were surveyed in their new location, and those that had been disturbed (e.g. turned over) were put back in their original position, unless spiders had successfully adapted to the

new position of the log (i.e. settled on the new underside). The total area available to spiders under the logs ranged from 28.4-28.9 m², depending on the date.

For each log, we recorded the number of *L. hesperus* spiders present underneath, their gender and age class (i.e. juvenile, subadult or adult), the number of unhatched and hatched egg sacs, the number of webs, and the number of individuals per web. We also recorded the number of co-occurring *T. agrestis* and *T. duellica* spiders present under each log and the number of *Tegenaria* webs (*T. agrestis* and *T. duellica* webs were indistinguishable to us). Juveniles were separated into 3 categories on the basis of their size and colour patterns: ‘Small’ juveniles were hatchlings that had recently emerged and were characterized by white abdomens with brown spots or stripes on the dorsum and very lightly-coloured translucent legs with brown spots at the joint regions (post-emergence instars 1-2); ‘Medium’ juveniles resembled hatchlings except that they were larger and had brown, cream and white striping patterns on the dorsum and darker legs (instars 3-5); ‘Large’ juveniles had black and white stripes on the dorsum with various amounts of black and were larger than spiders from the other two categories (instars 5-6). Males generally start maturing in their fourth instar and subadult males occur as instars 3-5, whereas most females start maturing in their seventh instar, and subadult females occur as instars 6-8 (see also Kaston 1970).

We assessed changes over time in the following measures of population distribution: density of individuals (number per m² available under driftwood logs), level of cohabitation (number of individuals per web and per log), and spatial distribution (the standardized Morisita index of dispersion, I_p). The standardized Morisita index ranges from -1 to +1, with values above 0 indicating a clumped distribution, values below 0 a uniform distribution, and 0 a random distribution, with 95% confidence limits at +0.5 and -0.5 (Krebs 1999). We also tested the distribution of spiders under logs against a Poisson distribution using Kolmogorov-Smirnov tests. To determine what factors influenced the distribution of *L. hesperus* spiders, we tested for correlations between log size and the number of *L. hesperus* spiders per log in each month using generalized linear models (GZLM) with a Poisson distribution, a log-link function, and an overdispersion

parameter. We also used GZLMs (without an overdispersion parameter) to analyze the influence of the presence and number of *Tegenaria* spp. spiders on the number of *L. hesperus* spiders per log each month, controlling for log size.

2.3.3 Annual/Biannual Surveys of a Natural Population

The aim of this study was to measure the distribution and level of cohabitation among and between *L. hesperus*, *T. agrestis* and *T. duellica* spiders over several years (2002-2005) and at two different times of year: (1) in mid September, a time when mating generally takes place and adults of all 3 species co-occur, and (2) in mid-June, when *L. hesperus* females lay egg sacs and juveniles start to emerge (see Fig. 2.1). The September surveys were conducted over 4 years (10-11 Sep. 2002; 13-14 Sep. 2003; 10-11 Sep. 2004; 15-16 Sep. 2005), and the June surveys over 2 years (11-13 Jun. 2004; 17-18 Jun. 2005). The study site was located in Island View Beach Regional Park, and consisted of 3 different clusters of driftwood logs inhabited by natural populations of all 3 spider species (total habitat area: 794.3 m²; cluster 1: 177.4 m²; cluster 2: 161.5 m²; cluster 3: 455.4 m²; the amount of microhabitat area under logs varied among surveys). The first year (2002) we surveyed all logs (i.e. logs and log debris) present at the site to determine whether there was a minimum size used by *L. hesperus* spiders as a microhabitat. None of the logs smaller than 36 cm in length or 378 cm² in area were occupied, whereas logs with spider occupants ranged in size from 36-571 cm and 378-21,253 cm². Therefore for that year's survey and all subsequent ones, we only examined logs that were above this size threshold, while giving a generous margin of error (i.e. >30 cm and >320 cm²). The location and occurrence of some of the logs varied from year to year, but the majority of the logs were present each year.

Logs were turned over to record the following parameters: number of spiders present underneath, species, gender and age class (juvenile, subadult or adult), number of egg sacs, number of *L. hesperus* and *Tegenaria* spp. webs, and number of individuals per web. We only surveyed logs that could be lifted and were detached from the ground. In 2004 and 2005, we also measured distances between the centre of each log (to control for log size) and the closest piece of vegetation that was ≥ 1 m in height to the nearest cm (a

value of 0 was assigned to logs with overhanging vegetation). We assessed population distribution in terms of the density of individuals (number per m² of space available under driftwood logs), level of cohabitation (number of individuals per web and per log), and spatial distribution based on individual counts (the standardized Morisita index of dispersion, I_p). We tested for correlations between log size, presence of *Tegenaria* spp. spiders, distance to vegetation (predictors; controlling for log size in the latter two models), and the number of spiders and webs per log using GZLMs with a Poisson distribution, a log-link function, and an overdispersion parameter.

2.3.4 Study of Cohabitation Dynamics in Supplemented Microhabitats

We conducted a three-year study from January 2003 to December 2005 to examine how *L. hesperus* spiders colonize and distribute themselves across new unoccupied microhabitats and how the presence of co-occurring conspecifics and heterospecifics (*Tegenaria agrestis* and *T. duellica*) influence their distribution. The study site was located in Island View Beach Regional Park on the south side of the study area, in a 483.5 m² area of open sandy habitat bordered by sand on one side and shrubs on the other. All 3 spider species naturally co-occur under logs of driftwood clustered in the centre of our study site. To examine their mode of colonization of new microhabitats, we added 30 unoccupied microhabitats (sheds) in and around the cluster of driftwood logs. The sheds were constructed with 2 planks of cedar wood (150 cm long × 14 cm wide × 2 cm thick) nailed together at a 90° angle and with the long edges buried 1-cm deep into the sand, providing a triangular-shaped c. 12'500 cm³ volume underneath for settlement and web construction. The dimensions of these sheds were chosen based on the average size of a log of driftwood available to *L. hesperus* spiders in this habitat (i.e. above the minimum size threshold), measured at the onset of the study in 2002 (Mean ± SD: length = 158.111 ± 92.119 cm, width = 18.967 ± 8.297 cm, N = 152). On January 7, 2003, we placed 10 sheds inside the aggregation of driftwood logs, 10 sheds immediately surrounding the aggregation (within 2 m of the edge), and 10 sheds between 2-6 m of the edge of the aggregation. Spiders were free to move between the supplemented microhabitats (i.e. sheds) and their natural microhabitats (i.e. logs of driftwood).

During the first year of the study, we surveyed half the sheds (5 from each group) every 2 weeks and the other half every 4 weeks to (1) witness colonization events on a biweekly versus monthly basis and (2) determine whether our surveying procedure had any impact on their rate of microhabitat colonization. To survey a shed, we simply turned it over and examined spiders living underneath, which sometimes damaged a spider's web. However, there were no differences in the mean number of spiders and webs per shed each month between the biweekly and monthly treatment groups in 2003 (repeated-measures GLMs with month as within-subject factor and treatment as between-subject factor; statistics for the effect of treatment on the following response variables: number of *L. hesperus* spiders: $F_{1,28} = 0.133$, $P = 0.718$; number of *L. hesperus* webs: $F_{1,28} = 1.819$, $P = 0.188$; number of *Tegenaria* spp. spiders: $F_{1,28} = 0.026$, $P = 0.873$; number of *Tegenaria* spp. webs: $F_{1,28} = 0.940$, $P = 0.341$). Therefore, we are confident that our surveys had no major impact on the distribution of *L. hesperus* spiders, and as such we surveyed sheds on a monthly basis over the next two years (2004-2005), and only present monthly data for the first year of the study (2003).

During each survey, we counted the number of spiders present underneath each shed (alive and dead), and determined their identity by species (*L. hesperus*, *T. duellica* or *T. agrestis*; *Tegenaria* juveniles were not identified to species level), gender, and age class (juvenile, subadult or adult). We also measured the dimensions of *L. hesperus* and *Tegenaria* spp. webs (length and width), and counted hatched and unhatched egg sacs. The site was subject to minor antropogenic disturbances on a few occasions during the summers, when some of the shed were flattened, moved or turned over. However, *L. hesperus* spider are commonly associated with disturbed habitats and these minor disturbances did not have any major effect of their population dynamics.

To examine the colonization rate of new microhabitats by *L. hesperus* and *Tegenaria* spp. spiders, we analyzed changes in spider densities over time for each age class (i.e. the number of individuals per unit area available under a shed and the number of individuals per shed), and changes in group sizes (i.e. the number of spiders per web).

These data also allowed for a description of their lifecycles over several consecutive years.

2.3.5 Prey Capture Rate and Prey Composition

The aim of this study was to examine the diet of *L. hesperus* spiders in their natural habitat over one year (in 2005). The study was conducted in the same setting as the previous one, under microhabitats (i.e. sheds) that had been added in the natural habitat of *L. hesperus*, *T. agrestis* and *T. duellica* spiders at Island View Beach Regional Park (see 2.3.4). By the time that we initiated this study, spiders had established themselves and acclimated to these new microhabitats. In late December 2004, all prey remains were cleared from under the sheds, and from January to December 2005, we collected all the prey that these spiders had consumed. This was done either by carefully picking them off the webs (unless they were still being consumed) or collecting them from the substrate beneath the sheds once they had been discarded. We collected only prey items that were still whole or were broken into only a few recognizable pieces. Prey were identified to taxonomic order and their lengths measured (in mm) to estimate their mass (in mg) based on regression equations specific to each order (see Appendix B). It is likely that most of the prey collected were those of *L. hesperus* spiders, because the integrity of their prey is preserved after consumption, whereas *Tegenaria* spp. spiders usually crumble their prey rendering most remains unrecognizable as consumed prey (pers. obs.). Prey consumption was quantified as the number and biomass of prey consumed per microhabitat over time. A detailed list of the number and biomass of prey consumed on a monthly basis over one year is presented in Appendix C.

2.4 Results

2.4.1 Lifecycle and Natural History

Latrodectus hesperus has an annual lifecycle presented in Fig. 2.1. Females lay most of their egg sacs from May to July and spiderlings start emerging at the end of June.

During the egg-laying period, 60-80% of females had egg sacs and many of them were seen guarding 2 or sometimes even 3 egg sacs. On one occasion in May we observed a female making an egg sac. In a laboratory setting, females lay on average 8.581 ± 2.605 egg sacs (mean \pm SD; range: 2-13, N = 31; data from 2004-2005) over a period of 2-6 months (median: 4), from which 0-122 spiderlings emerge, depending on the laying sequence. Juveniles grow during the summer and autumn months, and both females and males start maturing in late summer. Most of the adult males are found from August to November, which indicates the peak of the mating season. Males and females were seen sharing webs during this time and we observed one instance of copulation in August. Most females mate during this period and wait until the following spring and summer to lay eggs. Juveniles of both sexes are present throughout the autumn and winter and those that overwinter reach maturity the following spring. Females may live for up to 1 year post-emergence if they do not succumb to winter storms or cold snaps, whereas most males die soon after the mating season. A few dead adult females were found on the ground under logs in March, July and December (note that the small decrease in the number of females during July was primarily due to anthropogenic disturbance; see Fig. 2.1). In September and March, we found one adult female wrapped in silk on another female's web, which is evidence of cannibalism; no other traces of cannibalism were found.

The proportion of logs occupied by *L. hesperus* webs increased over time from 58-69% in March-June to 77-96% starting in July, with a peak in August-September. This indicates that not all potential microhabitats are always occupied. The average number of webs per log was near unity from March to July and increased to approximately 2 from August to December, which is when large juveniles begin dispersing to establish their own territories. Some webs were very extensive and covered the entire space available under of a log. The level of web occupancy by spiders ranged from 67.1% in April to 93.1% in August (median: 82.3%), and it increased with the total number of webs (GLM: $F_{1,8} = 6.936$, $P = 0.030$, $R^2 = 0.397$). Occupied webs had between 1-5 spiders from March to June and between 1-8 spiders from July to December (Fig. 2.2). The average group size on occupied webs ranged from 1 to 2 depending on the

time of year: it was closer to 1 until June and increased to 1.5-2 per web in July. Group composition varied across logs and months, yielding over 30 possible combinations of sexes and maturity levels. Overall, the majority of groups involved associations among and between adult and subadult females, adult females and juveniles, and adult females with adult or subadult males (compare Fig. 2.1 and Fig. 2.2). In March and April, individuals of different age classes and sexes form small groups, including juveniles. In May and June, adult females predominate and usually live solitarily on a web. In July and August, juveniles emerge and associate with each other and with adult females (small juveniles associated with each other, whereas medium and large ones tended to associate with females), and subadult and adult males share webs with females. From September to December, adult and/or subadult females form groups that vary in size from 2 to 8 individuals (some of the large groups were composed of only adult females).

There was a positive relationship between the size of a log and both the total number of spiders and the number of adult females per log between July and December (GZLMs: all $P < 0.05$), but no significant relationship between March and June (all $P > 0.05$), except for the number of adult females in March that was significantly higher under larger logs ($P = 0.021$). There was also a positive relationship between log size and the number of subadult females per log from October to December (all $P < 0.01$), and with the total number of juveniles per log in July ($P = 0.026$). The number of webs per log was strongly positively correlated with log size throughout the study period ($P < 0.05$ in each month), except in May ($P = 0.092$). In all cases where the relationships were significant, the slopes of the regressions were always >1 , indicating that log size is not the only factor involved in determining the distribution of spiders.

From October to December, there were more *L. hesperus* spiders under logs that were occupied by *Tegenaria* spp. spiders than under those that were not (GZLMs: all $P < 0.05$), and this relationship was close to being significant in September ($P = 0.061$). Likewise, there was a positive relationship between the number of *L. hesperus* spiders and the number of *Tegenaria* spp. spiders under a log during this period, as well as in August and September (GZLMs: all $P < 0.01$). *Latrodectus hesperus* and *Tegenaria* spp.

spiders often build their webs either in contact with or in close proximity to one another; Funnel-sheet webs of *T. agrestis* and *T. duellica* were typically found under the 3-dimensional cobwebs of *L. hesperus*, and were smaller in size. On two occasions, in July and September, we observed *L. hesperus* spiders preying upon *T. duellica* subadult males.

The distribution of all spiders and that of only adult females under logs were significantly different from a random distribution from October to December (Kolmogorov-Smirnov tests: all $P < 0.05$), and in July when considering all spiders ($P = 0.021$). During these months, there was an over-representation of unoccupied logs and logs occupied by ≥ 2 spiders and an under-representation of logs with 1 spider, which is indicative of an aggregated distribution. The difference found in July reflects the presence of many newly emerged spiderlings sharing webs. The spatial distribution of *L. hesperus* spiders varied over time between clumped (Standardized Morisita index of dispersion: values > 0.5) and random (values ≤ 0.5 and ≥ -0.5) depending on the type of spider considered (Fig. 2.3). The overall distribution of spiders was clumped during the whole year except in May and June when it was random. Adult and subadult females were clumped with respect to each other from August to December as well as in May, and juveniles were clumped in July (a time of peak emergence) and randomly distributed thereafter.

2.4.2 Distribution Over Several Years

The overall density of *L. hesperus* spiders and webs varied between 2002 and 2005 and was higher in September than in June (Fig. 2.4a). In September, the majority of spiders were adult and subadult females, and in June adult females predominated. In contrast, the density of *Tegenaria* spp. spiders (i.e. *T. agrestis* and *T. duellica* combined) was fairly constant over time. *Latrodectus hesperus* spiders showed a tendency to form groups in September and live solitarily in June, which is analogous to the results of the year-long study in 2006 (see 2.4.1). The overall distribution of *L. hesperus* spiders across microhabitats was significantly different from a random distribution in September 2002-2005 (Kolmogorov-Smirnov tests: 2002: $Z_{152} = 2.326$, $P < 0.0001$; 2003: $Z_{212} = 2.628$, $P < 0.0001$; 2004: $Z_{257} = 3.530$, $P < 0.0001$; 2005: $Z_{238} = 3.952$, $P < 0.0001$) but not in June

2004 and 2005 (2004: $Z_{243} = 1.093$, $P = 0.184$; 2005: $Z_{240} = 0.998$, $P = 0.272$). At each census date, there was an over-representation of unoccupied logs and logs occupied by more than one spider. This suggests that (1) microhabitats are not limited for *L. hesperus* spiders and (2) spiders commonly share logs and their spatial distribution tends to be aggregated. Their tendency to aggregate is further supported by positive scores above 0.5 for the standardized Morisita Index of Dispersion (Sep. 2002: $I_p = 0.564$; Sep. 2003: $I_p = 0.558$; Sep. 2004: $I_p = 0.565$; Sep. 2005: $I_p = 0.564$). The overall level of log occupancy by *L. hesperus* webs was relatively low in this study site, and it was higher in September (range from 2002-2005: 50.1-57.2%) than in June (2004: 32.3%; 2005: 30.5%). Web coverage under logs also varied across years, with a median value between 20-30% in both September (overall range: 1-100%; 2002: 26.8%; 2003: 21.2%; 2004: 24.8%; 2005: 30.9%) and June (2004: 24.2%; 2005: 27.2%). Mean web area per log increased with log area, both in September (log-transformed data; 2002: $R^2 = 0.192$, $P < 0.0001$; 2003: $R^2 = 0.142$, $P < 0.0001$; 2004: $R^2 = 0.061$, $P = 0.002$; 2005: $R^2 = 0.166$, $P < 0.0001$) and in June (2004: $R^2 = 0.099$, $P = 0.001$; 2005: $R^2 = 0.182$, $P < 0.0001$). Furthermore, the number of *L. hesperus* spiders per web was positively correlated with web area in June and September of each year (GZLMs on log-transformed variable: all $P < 0.05$), but there was no effect of log area (log-transformed variable: all $P > 0.1$).

In September of each year, web sharing was common among *L. hesperus* spiders (i.e. mainly adult and subadult females): the density of spiders was higher compared to that of webs (Fig. 2.4a; 1.4 - 2 × more spiders than webs), the average spider group size was >1, and the median group size was 1 in 2003 and 2004 and >1 in 2002 and 2005 (Fig. 2.4b). In June, however, the densities of adult females and webs were similar, and most spiders occupied webs individually (1.2 – 1.3 × more spiders than webs; Fig. 2.4b). The distribution of spider group sizes in September 2002-2004 overlapped with that of September 2006 in an adjacent habitat (see Fig. 2.2; Kolmogorov-Smirnov tests: all $P > 0.1$), but not in September 2005 ($Z_{137} = 1.432$, $P = 0.033$): there was a greater number of large group sizes in 2005 compared to 2006. Logs occupied by *L. hesperus* spiders were larger in terms of surface area than those devoid of spiders in most years (log-transformed data; Sep. 2002: $t_{150} = 1.050$, $P = 0.295$; Sep. 2003: $t_{210} = 3.646$, $P = 0.0003$;

Jun. 2004: $t_{241} = 6.096$, $P < 0.0001$; Sep. 2004: $t_{255} = 7.714$, $P < 0.0001$; Jun 2005 $t_{238} = 5.567$, $P < 0.0001$; Sep. 2005: $t_{236} = 6.310$, $P < 0.0001$). At all survey dates, there were more *L. hesperus* spiders under larger logs (GZLMs: all $P < 0.05$), and the slopes of these regressions were all greater than 1. Furthermore, in June and September 2004-2005, there were more *L. hesperus* spiders under logs that were farther from the vegetation than under those that were close, suggesting that these spiders prefer to be in the open (GZLMs; all $P < 0.0001$). In September 2004-2005, there were more *L. hesperus* spiders under logs occupied by *Tegenaria* spp. spiders (GZLM: both $P < 0.01$), but not in June 2004-2005 (both $P > 0.05$). These results are again similar to those of the yearlong study of *L. hesperus* spiders conducted in 2006.

2.4.3 Cohabitation Dynamics

New unoccupied microhabitats that were placed around natural microhabitats in January 2003 were quickly colonized by *L. hesperus*, *T. agrestis*, and *T. duellica* spiders. Figure 2.5 shows the rate of change in densities of spiders and webs from 2003 to 2005. Within 5 months, 63% of the new microhabitats were occupied by *L. hesperus* spiders, and by July all of them were occupied. From that point onwards, >80% of the new microhabitats were occupied at all times. Starting in 2003, we see a seasonal pattern in the distribution of *L. hesperus* and *Tegenaria* spp. spiders (Fig. 2.5) similar to that of spiders living under natural microhabitats (see Fig. 2.1). Females and males co-occurred in August and September, when mating took place, and females laid egg sacs from May to July. Juveniles then started emerging in June, grew and matured during the summer and fall, and the density of adult females peaked in September-October (Fig. 2.5a, b). Note that the overall density of spiders was much higher than that of spiders found under natural microhabitats (Fig. 2.1), probably because our artificial microhabitats provided more 3-dimensional space for web construction than most of the logs occupied by *L. hesperus* spiders.

The distribution of *T. agrestis* and *T. duellica* spiders followed different trajectories, and overall they were found at much lower densities than *L. hesperus* spiders

(Fig. 2.5c). *Tegenaria duellica* adult and subadult spiders were found year-round at fairly constant densities (with small peaks in the late fall and early spring and lower levels in the summer), whereas *T. agrestis* adults and subadults occurred at very low densities, except in the fall and early winter when the density of adult females sharply increased and in 2005 reached very high levels. *Tegenaria* spp. juveniles from different age classes were found year-round.

Within six months of the start of the study, *L. hesperus* spiders had colonized the whole space available under a microhabitat, and there was on average 1 web per microhabitat (Fig. 2.5d). Their webs were usually as voluminous as the underside of a microhabitat (with extensions outside during the summer months) and several individuals cohabitated on a web. The density of *Tegenaria* spp. webs varied over time and peaked in the fall (Fig. 2.5d), which corresponds to a time of increase in the number of *T. agrestis* females building individual webs. *Tegenaria* spp. funnel-sheet webs are prone to damage and many were destroyed after being abandoned by spiders, whereas *L. hesperus* cobwebs are made of stronger silk and thus tend to persist over several months. Small rodents and garter snakes were occasionally seen living under the sheds, and crows would typically roost on the sheds at dusk. All of these are potential predators or sources of web damage.

Latrodectus hesperus spiders shared webs and lived in groups mostly during the summer and the fall (Fig. 2.6). Changes in the distribution of group sizes over time were driven by adult and subadult females, and juveniles. Median group size was around 2 from January to June, as adults and subadults shared webs with one other conspecific, except during the first year of the study (2003) when spiders were slowly colonizing the sheds and median group size was 1 (Fig. 2.6a). In July, there was a sharp increase in group size due to the emergence of juveniles that cohabitated on their mother's web and sometimes formed large groups (Fig. 2.6c). Median group size was high again in late summer, fall, and early winter, when maturing adult and subadult females shared webs and were often found in groups of 3 or 4 (especially in 2004-2005; Fig. 2.6b). Group size peaked in October and November for adult and subadult females, when the density of *L.*

hesperus and *Tegenaria* spp. spiders was highest (except for the post-emergence peak in the summer).

The rate of cannibalism among *L. hesperus* spiders was relatively low throughout the study period. Dead *L. hesperus* spiders were found under microhabitats primarily between November and March, and it is likely that they had succumbed to winter storms and cold weather, since there were no traces of cannibalism (i.e. silk wrapping, puncture wounds). However, some dead spiders were also found in the summer, most of which were adult females with occasional subadults and juveniles. Among these, some were wrapped in *L. hesperus* silk and had clearly been consumed by conspecifics. *Latrodectus hesperus* adult and subadult females preyed upon *T. agrestis* and *T. duellica* adults (females and males) and juveniles year round, with most predation events occurring in the fall and early winter when spider densities are highest. Overall, we noticed few predation events by *L. hesperus* spiders on *Tegenaria* spp. spiders given the extent of interspecific cohabitation under microhabitats and the length of the study (2 direct observations of predation events and 11 consumed *Tegenaria* spp. prey collected). No predation by *Tegenaria* spp. spiders on *L. hesperus* spiders was ever observed.

2.4.4 Prey capture

The number and biomass of prey captured by *L. hesperus* spiders in 2005 is shown in Fig. 2.7 (see also Appendices B and C for calculation details and raw data). The majority of prey capture took place between May and September, a period when females lay eggs and juveniles emerge and grow (Fig. 2.7a; see also Fig. 2.1). Overall, conspecifics comprised a small fraction of their diet. *Latrodectus hesperus* spiders fed primarily on beetles and weevils (order Coleoptera; 60.8% of total catch) that ranged in length from 4.6 to 24.2 mm, with a majority of small prey (median size: 7.8 mm). This in turn represented 87.8% of the total prey biomass. The second most abundant order of prey were Hymenoptera, including paper wasps (*Polistes* sp.), sand wasps (*Bembix* sp.), bumble bees (*Bombus* sp.), ichneumonid wasps (Ichneumonidae), sphecid wasps (Sphecidae) and ants (Formicidae). The majority of these prey were captured from May to September, which corresponds to their season of activity. They represented 26.5% of

the total catch and 10.0% of the total prey biomass, and ranged in size from 4.9 (ants) to 20.7 mm (paper wasps), with many large (wasps and bees; median size: 14.1 mm) and many small prey (ants; median size: 6.0 mm). The remaining orders of arthropod prey each represented <5% of the total prey catch and <1% of the total prey biomass. These included, by order of abundance as prey: Isopoda, Araneae, Dermaptera, Orthoptera, Lepidoptera and Diptera. Spiders that were preyed upon included lycosids (primarily *Pardosa* spp., *Alopecosa kochii*, *Arctosa perita*, and *Trochosa terricola*), *L. hesperus* adults and juveniles, *T. agrestis* and *T. duellica* adults and juveniles, and one *Habronattus americanus* male and one *Antrodiaetus pacificus* female. Overall, median prey size varied over time in accordance with the availability of different types of prey (Fig. 2.7a, c). The majority of prey were between 6-14 mm in size, which is within 0.6-1.4 average body lengths of an adult *L. hesperus* female. From May to October, when most of the prey capture takes place, median prey size ranged from 7.5-9.8 mm, and from November to April it was between 6.9-9.1 mm. An analysis of the differences in mean prey size per microhabitat over time showed an effect of month, as prey size peaked in the summer (repeated-measures GLM: $F_{10,130} = 2.082$, $P = 0.030$; data for January were excluded from the analysis because of their high variance; Fig. 2.7c).

2.5 Discussion

The results of this study demonstrate that *Latrodectus hesperus* spiders from coastal British Columbia show facultative group-living behaviours. Group living has never been reported in the genus *Latrodectus*, although many social and subsocial spider species belong to the same family, the Theridiidae (Avilés 1997; Agnarsson 2004). *Latrodectus hesperus* spiders associate and form groups during a significant portion of their life by sharing webs (i.e. spiders built large common cobwebs which they co-occupied) and live solitarily the rest of the time, on individual webs. Most of the groups are composed of adult and subadult females, or juveniles at post-emergence. In the fall and early winter, when the density of adult and subadult females is highest, maturing females and adult females share sometimes quite extensive webs and live in close proximity. In contrast, adult and maturing females usually live alone in late spring and

early summer, when egg laying takes place. In summer, juveniles emerging from egg sacs form groups prior to dispersal. Cannibalism is rare among group members as spiders tolerate the proximity of neighbours. We review the main questions addressed in this study and discuss important issues arising from the results presented here.

2.5.1 Main Characteristics of Group Living in *L. hesperus*

Our data suggest that *L. hesperus* spiders do not associate simply in response to ecological constraints such as limited microhabitat availability, since many microhabitats were left unoccupied despite the fact that they provided similar environmental conditions as occupied ones, and spiders were spatially clustered. An aggregated distribution of individuals may result from a number of causes, including limited movement or dispersal and attraction between co-occurring individuals (Prokopy & Roitberg 2001; Krause & Ruxton 2002). In our study, group membership varied from month to month as individuals moved between microhabitats to leave or join new groups (we did not mark individuals and follow their movements). Results from a related field experiment showed that in the fall adult females often move between microhabitats, and settle at different locations either alone or with other individuals (see Chapter 3). This suggests that *L. hesperus* spiders form dynamic groups with frequent modulations in size and composition, unlike the stable group structures of social species (Avilés 1997). It remains to be investigated to what extent *L. hesperus* juveniles disperse from their natal sites, and how different age classes behave in response to changing conditions. In a previous study, we collected adult *L. hesperus* females in and above pitfall traps placed in an open sandy habitat from April-June and in September-October, and juveniles from July-October and in March, which suggests that these spiders are active dispersers (M. Salomon & R. G. Bennett, unpublished data). In social spiders, individuals do not disperse prior to the mating season and form groups of related individuals, whereas in subsocial species, individuals cease to live in groups at some point in their life and disperse in search of new foraging and reproductive opportunities (Roeloffs & Riechert 1988; Avilés & Gelsey 1998). Environmental factors such as prey availability or predation risk may influence the timing of dispersal and duration of the group-living phase (e.g. Gundermann et al. 1993; Jones & Parker 2000; Kim 2000), which may also hold true for *L. hesperus*. For instance,

spiders may congregate in microhabitats where prey is abundant. However, in this study we found no major differences in prey abundance across artificial microhabitats occupied by *L. hesperus* spiders.

Attraction among conspecifics (or arrestment in some cases) has also been shown to lead to group living in spiders and other animals (Stamps 1988). In our study, we created a situation where several empty microhabitats were available and followed their colonization by spiders, in an effort to examine the patterns of group formation. *Latrodectus hesperus* spiders spontaneously aggregated and formed groups in these new sites, and their tendency to associate and dissociate in different seasons persisted over several years. It is likely that the presence of webs in a microhabitat produced by established spiders caused incoming spiders to remain in that site and in some cases form groups, as attraction to silk has been documented in web-building spiders (Hodge & Storfer-Isser 1997; Schuck-Paim & Alonso 2001). Conspecific webs (and their occupants) may provide information about microhabitat quality and also facilitate settlement by newcomers. The density of spiders in these microhabitats was in fact much higher than that of spiders living under natural microhabitats, mostly because more space was available for settlement and web construction. This suggests that group size may be constrained by microhabitat size in *L. hesperus*. Additional support for this claim comes from the positive relationship between microhabitat size and the number of spiders. Other microhabitat characteristics that were not assessed in this study may also influence the propensity of group vs. solitary living among *L. hesperus* spiders, such as the amount of 3-dimensional space available for web construction under a log, and perhaps more importantly the availability of hiding places in the form of cracks and crevices where spiders can retreat between foraging bouts, seek protection from adverse conditions, and also overwinter. Our future research will examine the importance of these factors in more detail.

The design of *L. hesperus* cobwebs is conducive to web sharing and thus group living. Spiders that choose to associate and join a group can expand the tangle component and build additional anchor threads onto a pre-existing structure, without necessarily

having to build a separate structure. *Latrodectus hesperus* spiders built large communal cobwebs that often took up a lot of the space available in a microhabitat and on which they either lived alone or with other conspecifics. Individuals sharing webs were frequently seen moving between different parts of a web, interacting with other group members and taking up new positions, and not defending a particular location on a web. These behaviours are reminiscent of some non-territorial social species in the genus *Anelosimus* that share large cobwebs (e.g. Pasquet & Krafft 1989; Avilés & Tufino 1998). It would be interesting to examine what portion of a web is built by each member of a group in *L. hesperus*, and whether individuals vary their level of investment into web construction and silk production. Asymmetries in individual investment may cause conflict when some individuals reap the benefits of group living without contributing much to the group effort (i.e. cheating; Franks 1995).

Overall, there was little cannibalism among *L. hesperus* spiders living in groups, despite their frequent interactions and close proximity. Adult and/or subadult females were commonly seen living very close to each other on a web (i.e. less than 2 units of body lengths apart), and conspecifics constituted a very minor portion of their general diet. This suggests that *L. hesperus* spiders living in this habitat express tolerance behaviours towards conspecifics, which is a trait characteristic of social species (Hodge & Uetz 1995). The benefits gained from group living (if any) may reinforce mutual tolerance and group cohesion. Such associations are surprising, because adult and subadult spiders often express cannibalistic tendencies (Wise 2006) and group living in non-permanently social spider species usually involves associations between juveniles (e.g. Pekár & Král 2001). In highly cannibalistic and food-limited animals such as spiders, an individual's degree of cannibalism is determined by the trade-off between the relative nutritional value of conspecifics as prey versus other potential prey (for spiders it is often high), and the costs associated with their capture (Mayntz & Toft 2006; Montserrat et al. 2006). In *L. hesperus*, the level of tolerance between interacting group members changes depending on an individual's nutritional state (see Chapter 3), as fluctuating prey availabilities influence an individual's hunger level and increases the likelihood of aggression and cannibalism (Sirot 2000).

Studies have shown that the amount of cannibalism between group members may also depend on their degree of kinship, favouring the formation of groups of related individuals through kin selection (Reeve 1989; Bilde & Lubin 2001). It is not known whether groups of *L. hesperus* spiders are composed of close kin. However, results of laboratory experiments with *L. hesperus* have shown that unrelated females readily associate and form groups in the same way as spiders living in their natural habitat (see Chapter 6). We intend to conduct further research on this topic to test whether kin recognition is present in *L. hesperus* (as in some social and subsocial species; e.g. Bilde & Lubin 2001), and if so, examine how kin selection influences group living.

2.5.2 Value of Group Living

An obvious question that emerges from the results of this study is: what are the reasons for and outcomes of group living in *L. hesperus*? Conflicts of interest typically arise between group members sharing common resources such as food or shelter, and these may compromise the integrity of a group (Strassmann & Queller 1989). Yet, group living may also provide a variety of benefits to the individual, which generally promote group maintenance. Some of the main reasons invoked for the evolution of social behaviour in spiders that pertain to facultative group-living spiders such as *L. hesperus* include differential foraging, web building, protection and information sharing (reviewed in Whitehouse & Lubin 2005). The social organization of a species is usually determined by the interplay between different ecological factors. Although our inferences about the costs and benefits of group living in *L. hesperus* are limited by the lack of empirical evidence from this study, we draw from the results of other studies on this species to discuss these relationships.

Group living may increase a spider's access to prey either by enhancing prey detection or facilitating prey capture (e.g. Rypstra 1989). In *L. hesperus*, group living between adult females provides foraging benefits in the form of enhanced prey capture success at certain group sizes (see Chapter 6). Therefore, it may be advantageous for adult and subadult females to form groups during the fall to secure food resources before

the winter. Conversely, in the spring and summer females may prefer to live individually to forage on abundant prey and lay eggs. An individual's propensity to live in a group vs. solitary may be determined by a combination of factors influencing foraging opportunities. Early instars of laboratory-reared *L. hesperus* spiderlings that are kept on the same web engage in group-foraging activities, whereby large prey items are captured and consumed as a group, whereas small prey are captured and consumed individually (pers. obs.). Repeated interactions between young individuals may favour the retention of social behaviours at the adult stage (Gundermann et al. 1993).

Web building (i.e. silk production, web construction, web maintenance) is an energetically costly activity for a spider (Tanaka 1989), and one of the main benefits of group living comes from sharing these costs (e.g. Lloyd & Elgar 1997). *Latrodectus hesperus* spiders that live in groups usually share cobwebs, therefore it is likely that they save on some of the costs associated with web building. Furthermore, their cobwebs are resilient three-dimensional structures made of strong flexible silk (Blackledge et al. 2005) that may offer good protection against predators. As groups often build larger webs than solitary individuals, joining or forming a group may enhance an individual's anti-predator potential. Individuals living in a group may assume safer positions close to the centre of a web and use neighbours as sentinels (Rayor & Uetz 1990). It would be interesting to measure predation pressure at different times of year and determine whether it drives group living in *L. hesperus*. For egg-laying females, it is possible that an increased cost of parasitism to egg sacs associated with group living favours solitary living (see e.g. Hieber & Uetz 1990), whereas non-reproducing individuals may form groups to be better protected against predators. Finally, another reason for joining a group is the fact that the presence of conspecifics at a site may reflect its quality in terms of resource distribution and risks, which may reduce the cost of habitat assessment and favour settlement by incoming conspecifics (Valone & Templeton 2002). Salomon (2007) showed that *L. hesperus* females invest more silk into microhabitats occupied by conspecifics compared to empty ones, suggesting that their presence may convey information about the status or quality of a site.

2.5.3 Influence of Heterospecific Spiders on Group Living

The presence of *T. agrestis* and *T. duellica* spiders had no major influence on the group-living behaviour of *L. hesperus* spiders. However, the distribution of *L. hesperus* spiders was positively correlated with the presence of *Tegenaria* spp. spiders in the fall, when each species reaches high population densities. These species co-occurred under natural and artificial microhabitats and built their webs either close to or in direct contact with one another. Some *Tegenaria* spp. spiders are found on *L. hesperus* webs, despite the predation risks from adult and subadult females. *Latrodectus hesperus* spiders were seen preying upon both *T. agrestis* and *T. duellica* adults and juveniles, but the opposite has not been observed. *Latrodectus hesperus* is the dominant spider predator in this system (but note that *Tegenaria* spp. spiders may prey upon *L. hesperus* juveniles, as was observed once). Native *L. hesperus* spiders and introduced *T. agrestis* and *T. duellica* spiders have only been in contact for a short time as *Tegenaria* spp. spiders were introduced in western North America in the first half of the twentieth century (Vetter et al. 2003), and their intriguing associations deserve further attention. Because *T. agrestis* and *T. duellica* are both alien species that take up much space in the native habitat of *L. hesperus*, it would be worth assessing their impact on the native fauna by conducting exclusion experiments and studying populations at different locations.

2.5.4 Conclusion

This study provides a new example of facultative group living in a territorial animal that was previously considered to be purely solitary. Species such as *L. hesperus* are especially useful study organisms to investigate the role of different selective pressures in shaping the evolution of sociality, because of the facultative nature of their grouping tendencies. Further research is needed to characterize the factors that modulate individuals' social strategies in different contexts. Studies such as this one that are mostly observational provide a useful basis for establishing the social organization of a particular species, from which manipulative experiments can be devised that test specific hypotheses about the evolution of group living.

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Figure 2.1. Natural lifecycle of *Latrodectus hesperus* in coastal British Columbia, Canada. Changes over time in densities (number per m²) of (a) males and females (adults and subadults); (b) juveniles, egg sacs, and webs; (c) large, medium and small juveniles (aF: adult females; saF: subadult females; aM: adult males; saM: subadult males; Juv: juveniles; Eggs: egg sacs)

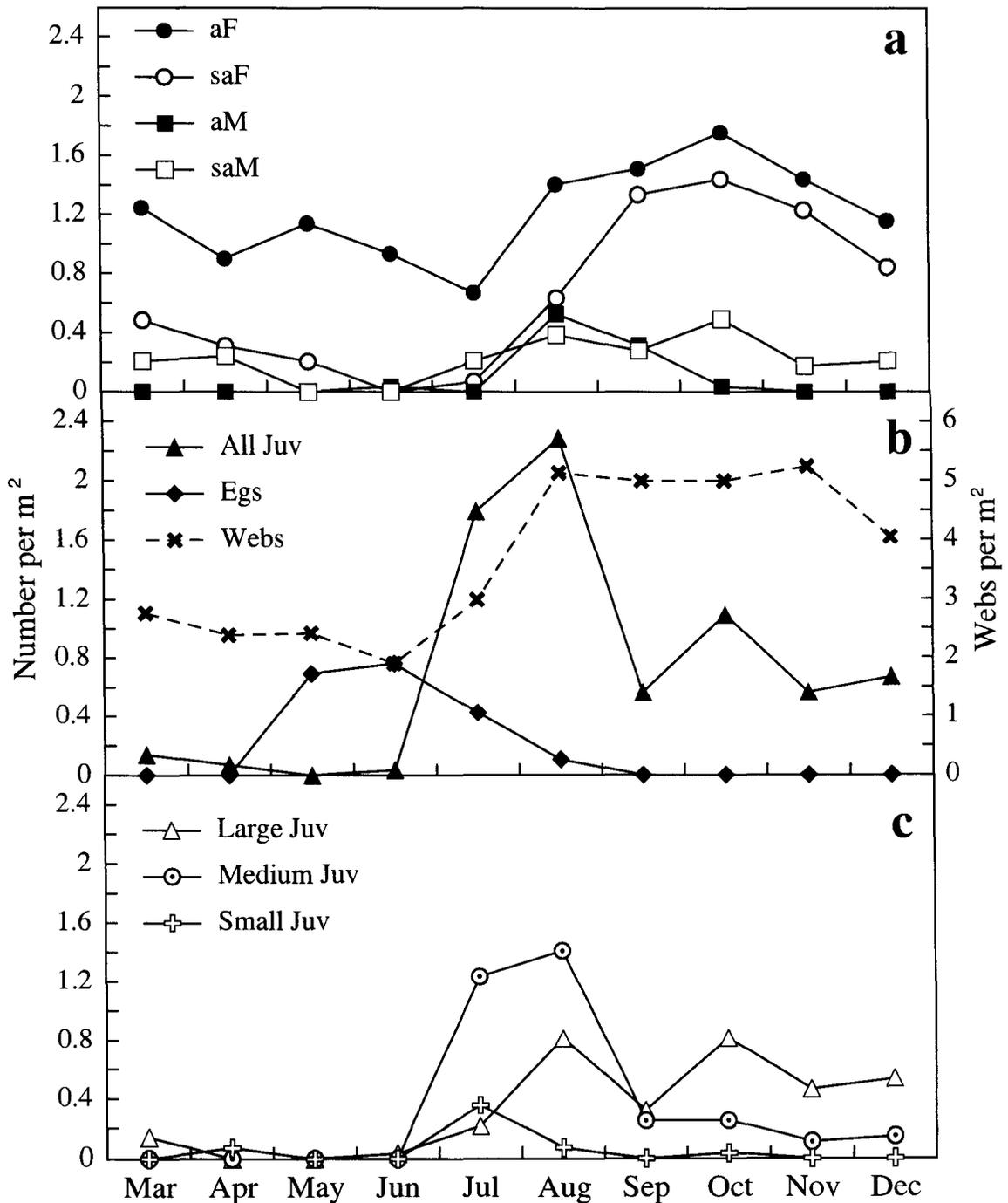


Figure 2.2. Distribution of *L. hesperus* spider group sizes (number of spiders per occupied web) in natural microhabitats on a monthly basis in 2006. Box plots show medians (centre bold lines), means (filled squares), 25th and 75th percentiles (bottom and top of boxes, respectively), and 10th and 90th percentiles (cap of lower and upper whiskers, respectively)

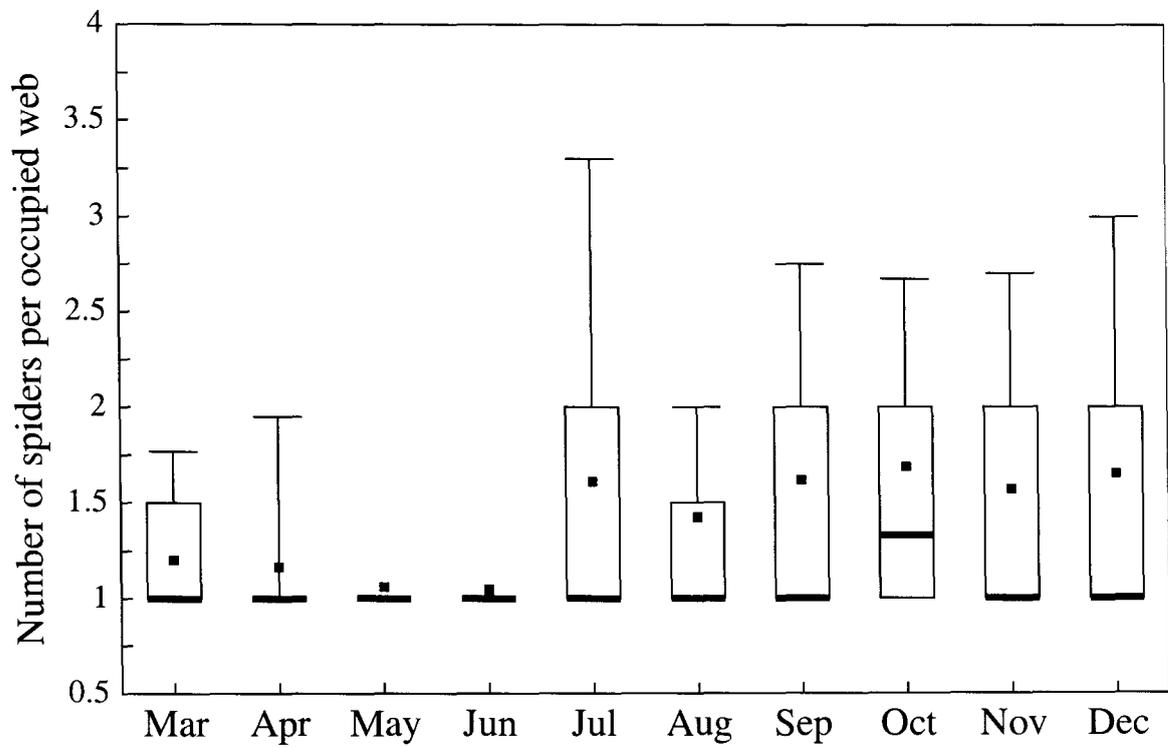


Figure 2.3. Spatial distribution of *L. hesperus* spiders (all spiders, adult and subadult females (aF+saF), and juveniles (Juv)) in 2006. Values on the y-axis represent the Standardized Morisita Index of dispersion, which ranges from -1 to +1, with 95% confidence intervals at -0.5 and +0.5 (see methods for a detailed explanation of the index). Note that the juvenile (Juv) curve only starts in July, because too few individuals were found from March to June (see Fig. 2.1b) to calculate a meaningful value of this index

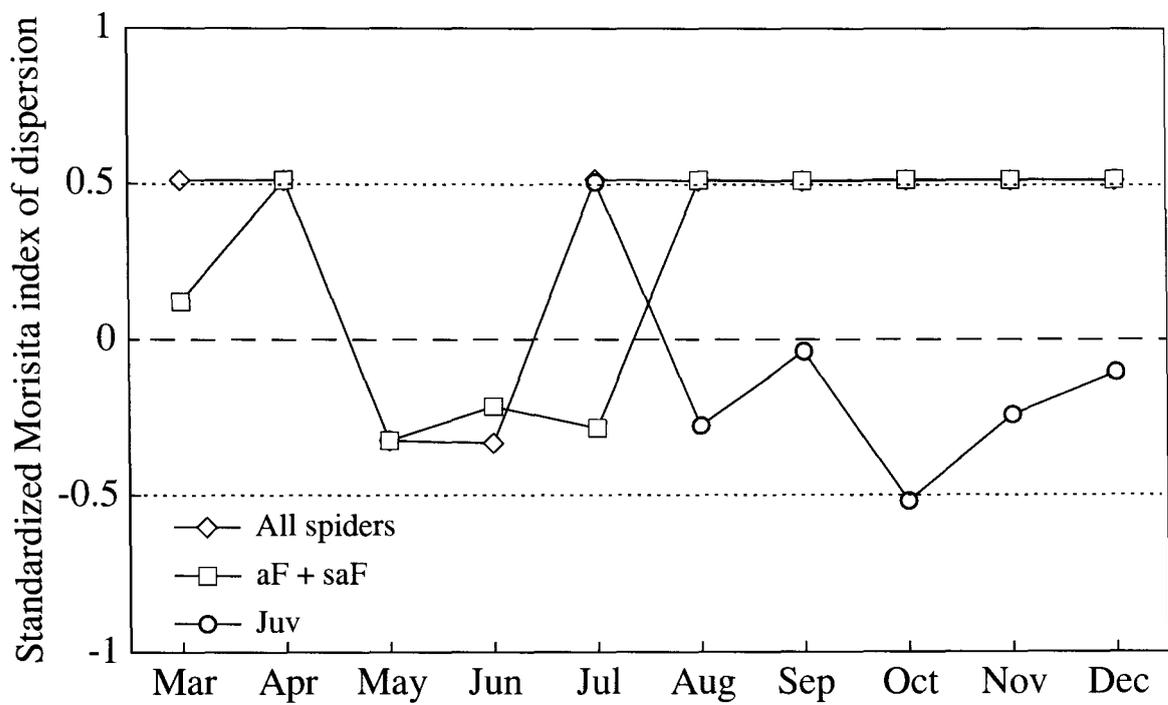


Figure 2.4. Distribution of *L. hesperus* spiders in September and June from 2002 to 2005: (a) Changes over time in densities (number per m²) of *L. hesperus* spiders and webs and *Tegenaria* spp. spiders (i.e. *T. agrestis* and *T. duellica*; aF+saF: adult and subadult *L. hesperus* females); (b) Distribution of *L. hesperus* spider group sizes (number of spiders per occupied web; refer to Fig. 2.2 for box plot specifications)

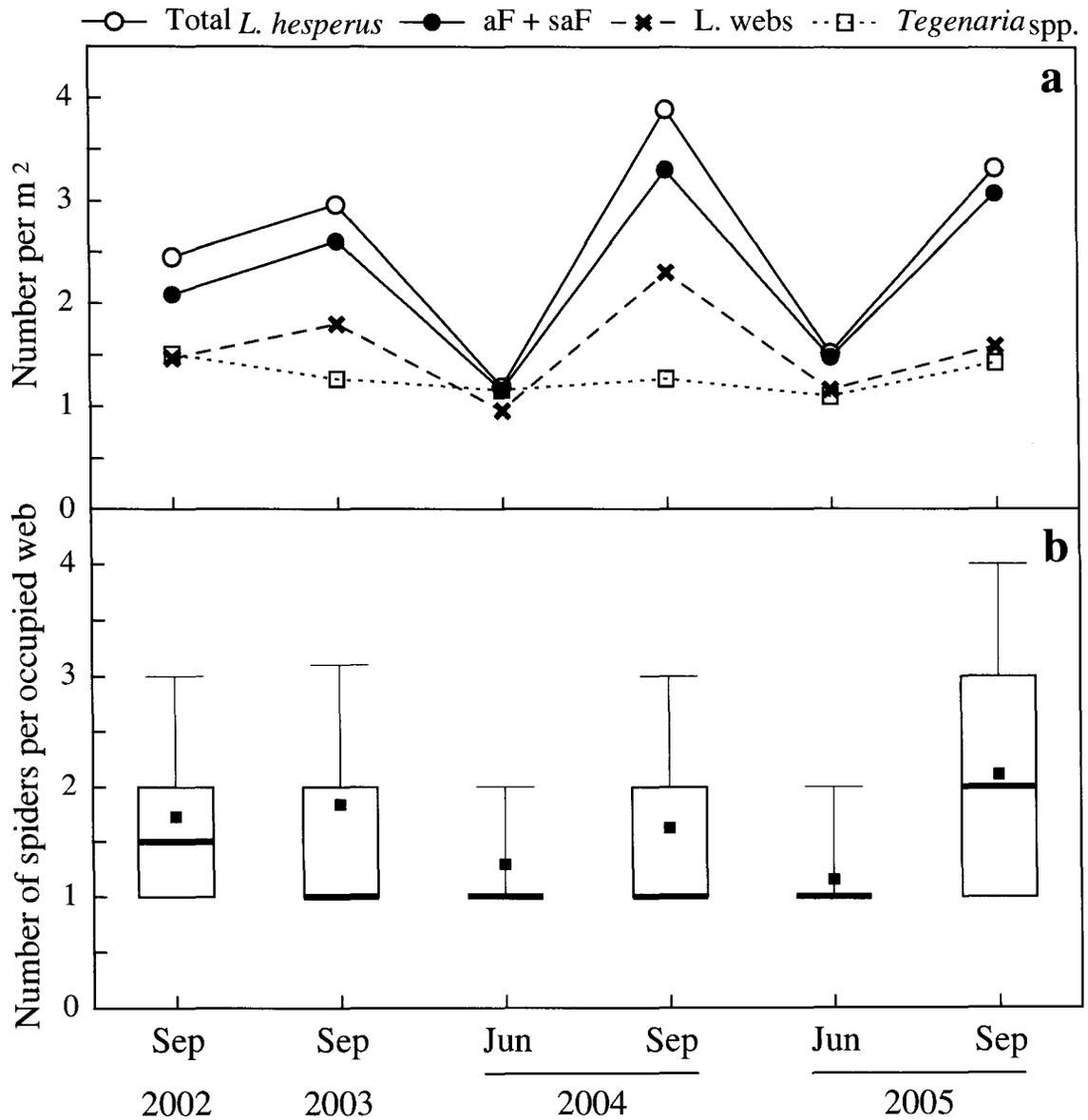


Figure 2.5. Changes over time in densities (number per m²) of spiders and webs from 2003-2005 in artificial microhabitats for (a) *L. hesperus* adult females, subadult females, and adult and subadult males combined; (b) *L. hesperus* juveniles and egg sacs; (c) *T. duellica* and *T. agrestis* adult and subadult spiders, and *Tegenaria* spp. juveniles; (d) *L. hesperus* and *Tegenaria* spp. webs. Each data point represents a month of the year, abbreviated as the first letter of the month on the x-axis (refer to Fig. 2.1 for an explanation of the abbreviations used on the graphs)

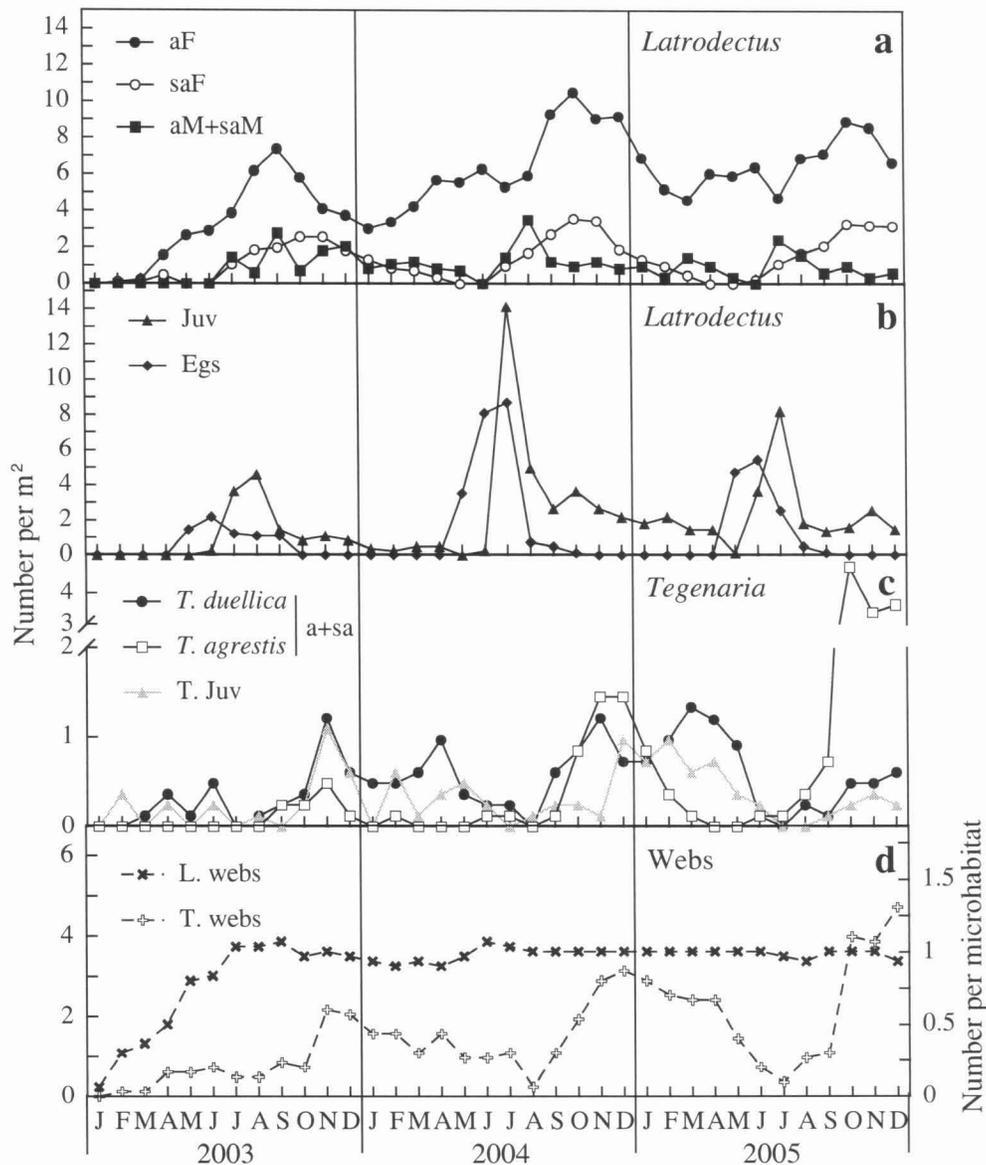


Figure 2.6. Distribution of *L. hesperus* spider group sizes (number of spiders per occupied web) in artificial microhabitats on a monthly basis from 2003 to 2005 for (a) all spiders; (b) adult and subadult females; (c) juveniles. (Refer to Fig. 2.2 for box plot specifications)

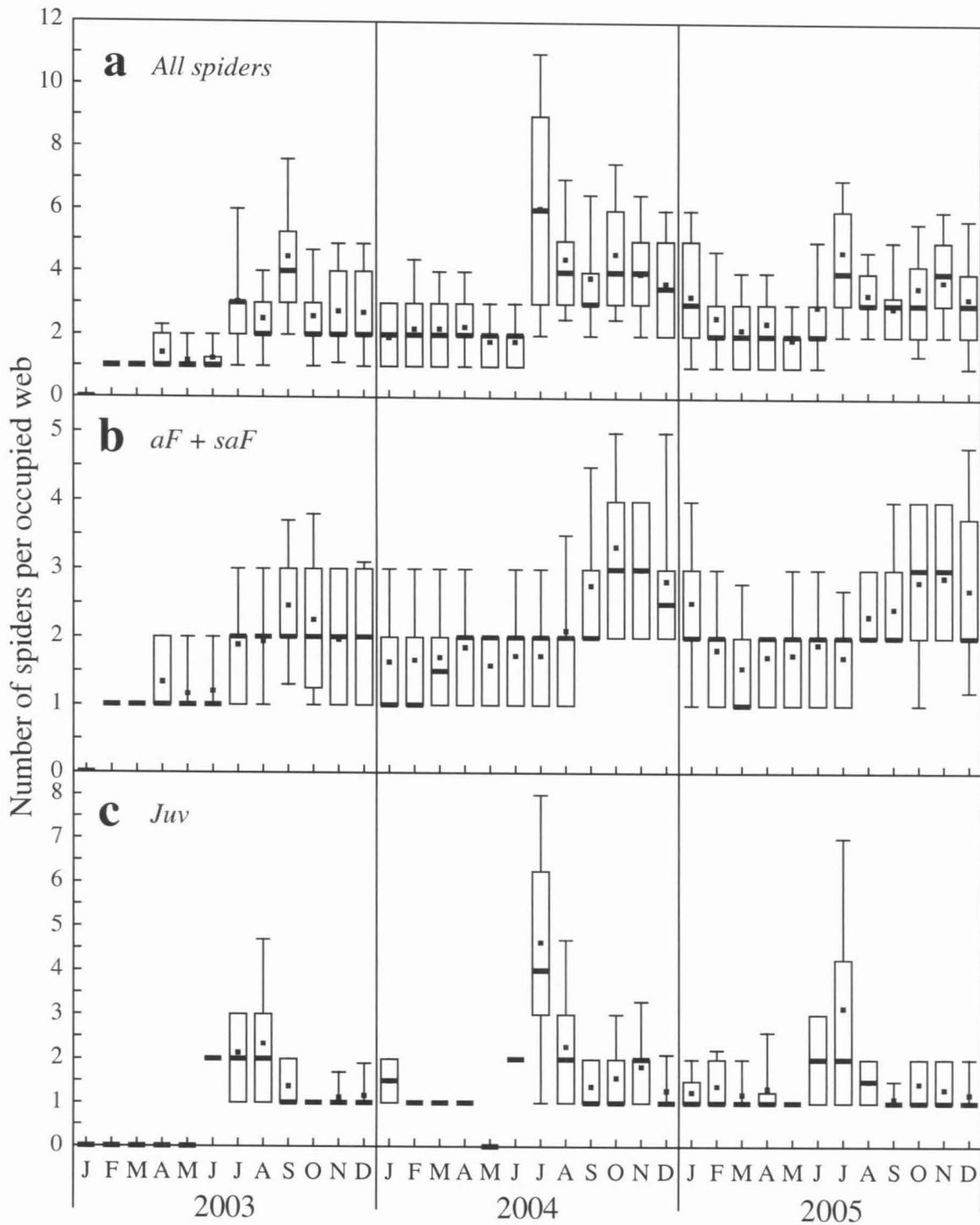
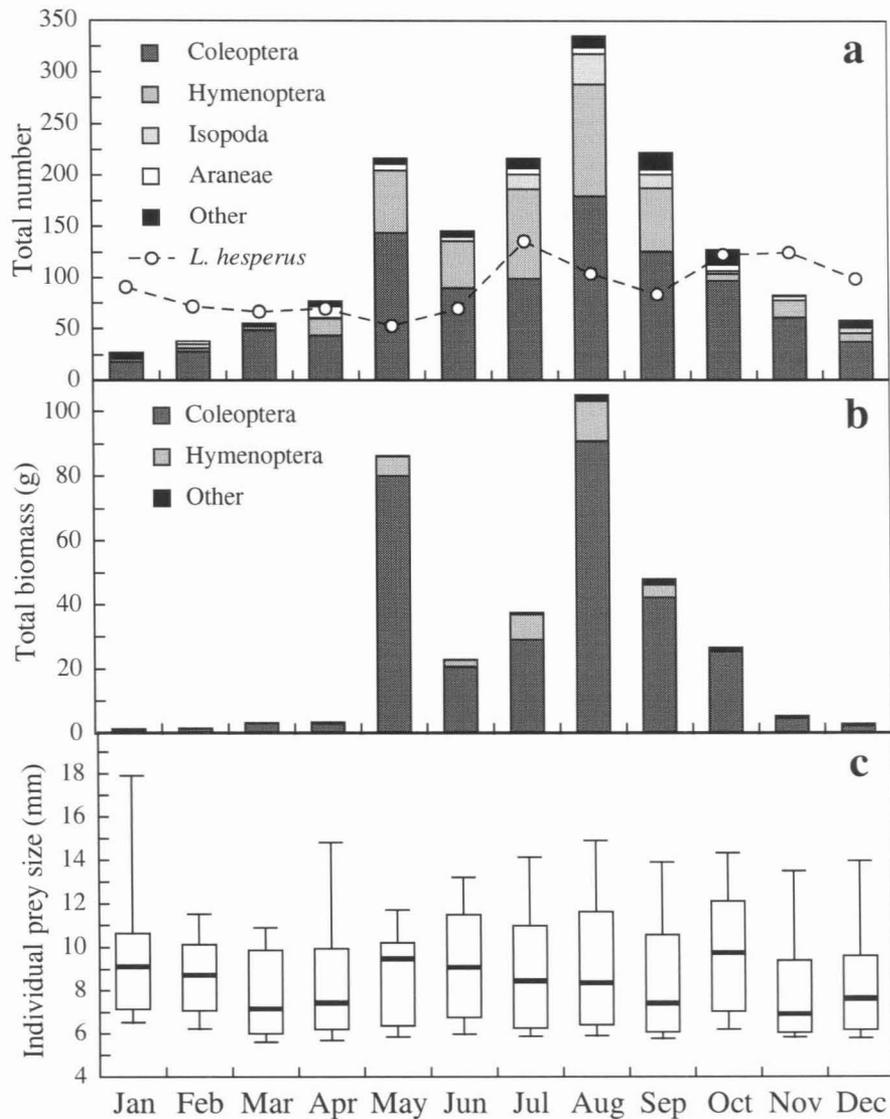


Figure 2.7. Prey captured by *L. hesperus* spiders on a monthly basis in 2005: (a) total number of prey; (b) total prey biomass; (c) prey size (body length) distribution. Also represented in (a) is the total number of *L. hesperus* spiders (i.e. predators) present under the sheds. In (a) and (b), prey are grouped according to their taxonomic order and the 4 most abundant orders are shown with the rest grouped into a single category, “Other” (i.e. Dermaptera, Orthoptera, Lepidoptera, and Diptera). For (b), only the 2 most abundant orders are shown and the remainder is lumped into “Other”. Data for Araneae prey are omitted from (c), since they are not based on body length (see Appendix B). (Refer to Fig. 2.2 for box plot specifications)



2.8 Appendices

2.8.1 Appendix A

Table A2.1. List of plant species present at Island View Beach in the open habitat where *L. hesperus* and *Tegenaria* spp. spiders co-occur (non-exhaustive list). The status column indicates whether the species is native or introduced in western Canada

Family & Species	Common Name	Status
Apiaceae		
<i>Lomatium nudicaule</i> (Pursh) Coul. & Rose.	Indian consumption plant	Native
Asteraceae		
<i>Achillea millefolium</i> L.	Yarrow	Native
<i>Ambrosia chamissonis</i> (Less.) Greene	Silver burweed	Native
<i>Grindelia integrifolia</i> DC. ⁽²⁾	Entire-leaved gumweed	Native
<i>Hypochaeris radicata</i> L.	Hairy cat's-ear	Introduced
Berberidasceae		
<i>Mahonia aquifolium</i> (Pursh) Nutt. ⁽¹⁾	Tall Oregon-grape	Native
Convolvulaceae		
<i>Convolvulus soldanella</i> L. R. Br.	Beach morning-glory	Native
Cyperaceae		
<i>Carex macrocephala</i> Willd. Ex Spreng. ⁽²⁾	Large-headed sedge	Native
Fabaceae		
<i>Cytisus scoparius</i> (L.) Link	Scotch broom	Introduced
Grimmiaceae		
<i>Racomitrium canescens</i> Hedw. Brid.	Roadside rock moss	Native
Liliaceae		
<i>Allium acuminatum</i> Hook. ⁽¹⁾	Hooker's onion	Native
Nyctaginaceae		
<i>Abronia latifolia</i> Eschsch.	Yellow Sand-Verbena	Native
Plumbaginaceae		
<i>Armeria maritime</i> (Mill.) Willd.	Thrift, Sea pink	Native

Poaceae		
<i>Aira praecox</i> L.	Early hairgrass	Introduced
<i>Aira caryophylla</i> L.	Silver hairgrass	Introduced
<i>Bromus</i> sp. L. ⁽¹⁾	Brome	Introduced
<i>Festuca rubra</i> L.	Red fescue	Native/Introduced
<i>Leymus triticoides</i> (Buckley) Pilg.	Creeping wild rye	Native
<i>Poa</i> spp. L.	Bluegrasses	?
<i>Vulpia myuros</i> (L.) C. C. Gmel.	Foxtail fescue	Introduced
Polygonaceae		
<i>Polygonum paronychia</i> Cham. & Schtdl.	Black or beach knotweed	Native
<i>Rumex acetosella</i> L.	Sheep sorrel	Introduced
Rosaceae		
<i>Rosa nutkana</i> C. Presl ⁽¹⁾	Nootka rose	Native
Scrophulariaceae		
<i>Linaria genistifolia</i> L. Mill. ssp. <i>dalmatica</i> ⁽²⁾	Dalmatian toadflax	Introduced

(1) Species only found in Island View Beach Regional Park

(2) Species only found in the Tsawout First Nations area of Island View Beach

2.8.2 Appendix B

2.8.2.1 Methods for measuring prey capture in *L. hesperus*

We collected prey from under the sheds at Island View Beach on a monthly basis in 2005, identified them to order level and measured them. We measured the total body length of each prey item and calculated its dry mass using taxonomic order-specific regression equations that were either available from the literature or derived from our own data (see Table A2.1). For Araneae prey we measured the combined length of the tibia and patella of the first pair of legs (an index of size in spiders) instead of total body length, since they were not always intact (some specimens had a missing abdomen). To then calculate the biomass of these prey, we developed three sets of regression equations for each type of Araneae prey that was collected: *Tegenaria* spp., *Latrodectus hesperus* and Lycosidae. For the two Araneae prey specimens that did not belong to either of these

prey types (i.e. one *Habronattus americanus* and one *Antrodiaetus pacificus*), we used the regression equations developed for Lycosidae, which we judged to be sufficiently accurate for the purpose of this study. For both *Tegenaria* spp. and *L. hesperus* prey, we measured and regressed tibia-patella length of leg pair 1 (in mm) against wet weight (in mg) using data from field-collected adult females (86 *L. hesperus*; 28 *Tegenaria* spp.: 15 *T. agrestis* and 13 *T. duellica*). To calculate dry weight from wet weight, we weighed field-collected adult females to the nearest 0.1 mg, sacrificed them by freezing them, dried them in an oven at 60 °C for 96 h and re-weighed them (32 *L. hesperus*; 16 *Tegenaria* spp.: 8 *T. agrestis* and 8 *T. duellica*). For Lycosidae, we measured and weighed spiders from different species, genders and age classes collected in pitfall traps at Island View Beach between March and June 2003 as part of a separate study (N = 32; species: *Pardosa* spp., *Alopecosa kochii*, *Arctosa perita*, and *Trochosa terricola*; equal representatives of each of the four genera; M. Salomon & R. G. Bennett, unpublished data). We measured the tibia-patellar lengths of their first pair of legs, dried them using the protocol described above and weighed them once fully dry.

Table A2.2. List of regression equations used to calculate dry prey biomass (y) in mg based on total body length measurements (x) in mm for different orders of arthropods. For Araneae prey, the regression equations were based on tibia-patella length of leg pair I (tp) and wet prey biomass (w)

Taxonomic order	Regression equation	R	R ²	Source
Coleoptera	$\ln(y) = -3.460 + 2.790 * \ln(x)$	0.98	—	Rogers et al. 1977
Hymenoptera	$\ln(y) = -3.871 + 2.407 * \ln(x)$	0.97	—	Rogers et al. 1977
Lepidoptera	$\ln(y) = -4.037 + 2.903 * \ln(x)$	0.99	—	Rogers et al. 1977
Orthoptera	$\ln(y) = -3.020 + 2.515 * \ln(x)$	0.97	—	Rogers et al. 1977
Dermaptera	$y = 0.0015 * (x)^{3.497}$	—	0.96	Hóðar 1996
Isopoda	$y = 0.0101 * (x)^{2.844}$	—	0.96	Hóðar 1996
Diptera	$\ln(y) = -3.293 + 2.366 * \ln(x)$	0.96	—	Rogers et al. 1977
Hemiptera	$\ln(y) = -2.998 + 2.270 * \ln(x)$	0.98	—	Rogers et al. 1977
Araneae				Empirically derived
<i>Latrodectus hesperus:</i>	$\ln(w) = 1.948 + 2.032 * \ln(tp)$ (P < 0.0001, N = 86)	—	0.23	
	$\ln(y) = -1.846 + 1.132 * \ln(w)$ (P < 0.0001, N = 32)	—	0.92	
<i>Tegenaria spp.:</i>	$\ln(w) = 3.038 + 1.253 * \ln(tp)$ (P = 0.007, N = 28)	—	0.22	
	$\ln(y) = -1.745 + 1.100 * \ln(w)$ (P < 0.0001, N = 16)	—	0.87	
Lycosidae:	$\ln(y) = -0.679 + 2.643 * \ln(tp)$ (P < 0.0001, N = 32)	—	0.65	

2.8.2.2 References

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- Rogers, L. E., Buschbom, R. L. & Watson, C. R.** 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, **70**, 51-53.

2.8.3 Appendix C

Table A2.3. Number and biomass of prey consumed by *L. hesperus* spiders on a monthly basis in 2005. Each column represents a different order of arthropod prey belonging either to the insects, arachnids or malacostraca. The first row of each cell has the number of prey and the second row has prey biomass (in mg). Data are presented as means \pm SE per microhabitat (N = 30)

	Coleoptera	Hymenoptera	Isopoda	Orthoptera	Dermaptera	Lepidoptera	Diptera	Araneae
January	0.600 \pm 0.156	0.100 \pm 0.305	0.033 \pm 0.183	0.033 \pm 0.183	0.000 \pm 0.000	0.067 \pm 0.254	0.000 \pm 0.000	0.067 \pm 0.365
	23.954 \pm 11.361	1.240 \pm 0.840	0.151 \pm 0.151	3.948 \pm 3.948		11.307 \pm 9.495		4.709 \pm 4.709
February	0.933 \pm 0.197	0.100 \pm 0.305	0.133 \pm 0.346	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.100 \pm 0.305
	47.360 \pm 16.437	0.844 \pm 0.523	0.825 \pm 0.408					3.385 \pm 2.305
March	1.633 \pm 0.222	0.100 \pm 0.305	0.000 \pm 0.000	0.033 \pm 0.183	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.067 \pm 0.254
	104.494 \pm 32.141	0.333 \pm 0.239		0.708 \pm 0.708				2.744 \pm 2.162
April	1.467 \pm 0.202	0.533 \pm 0.629	0.033 \pm 0.183	0.000 \pm 0.000	0.133 \pm 0.346	0.033 \pm 0.183	0.000 \pm 0.000	0.367 \pm 0.556
	98.767 \pm 35.844	4.743 \pm 1.662	0.107 \pm 0.107		0.732 \pm 0.356	1.174 \pm 1.174		9.216 \pm 3.267
May	4.800 \pm 0.526	2.033 \pm 5.720	0.000 \pm 0.000	0.000 \pm 0.000	0.133 \pm 0.346	0.000 \pm 0.000	0.033 \pm 0.183	0.200 \pm 0.407
	2734.523 \pm 956.62	199.865 \pm 176.063			0.403 \pm 0.221		0.420 \pm 0.420	4.435 \pm 0.973
June	3.000 \pm 0.314	1.533 \pm 1.634	0.000 \pm 0.000	0.000 \pm 0.000	0.200 \pm 0.407	0.000 \pm 0.000	0.000 \pm 0.000	0.133 \pm 0.346
	522.348 \pm 132.345	68.009 \pm 23.292			1.410 \pm 0.605			1.988 \pm 0.973
July	3.300 \pm 0.463	2.933 \pm 3.723	0.467 \pm 0.730	0.033 \pm 0.183	0.200 \pm 0.484	0.000 \pm 0.000	0.067 \pm 0.365	0.200 \pm 0.484
	797.942 \pm 336.131	267.479 \pm 113.172	6.664 \pm 2.770	0.579 \pm 0.579	2.905 \pm 2.043		1.702 \pm 1.702	9.393 \pm 5.075
August	6.000 \pm 0.732	3.633 \pm 4.056	0.967 \pm 1.326	0.167 \pm 0.379	0.067 \pm 0.254	0.133 \pm 0.346	0.000 \pm 0.000	0.200 \pm 0.407
	3029.621 \pm 877.72	415.356 \pm 168.236	38.329 \pm 20.971	14.079 \pm 6.836	0.576 \pm 0.434	7.747 \pm 3.699		5.118 \pm 2.658
September	4.200 \pm 0.490	2.067 \pm 4.201	0.433 \pm 1.006	0.233 \pm 0.504	0.133 \pm 0.346	0.133 \pm 0.346	0.033 \pm 0.183	0.167 \pm 0.379
	1405.033 \pm 596.94	139.780 \pm 88.505	15.980 \pm 13.412	22.577 \pm 10.210	0.531 \pm 0.307	9.170 \pm 4.803	0.250 \pm 0.250	6.328 \pm 2.884
October	3.233 \pm 0.389	0.233 \pm 0.504	0.100 \pm 0.305	0.267 \pm 0.521	0.133 \pm 0.346	0.067 \pm 0.254	0.033 \pm 0.183	0.200 \pm 0.407
	849.174 \pm 202.981	3.636 \pm 1.775	0.343 \pm 0.205	23.532 \pm 10.316	0.879 \pm 0.442	4.671 \pm 3.373	0.394 \pm 0.394	7.659 \pm 4.902
November	2.033 \pm 0.273	0.567 \pm 1.331	0.000 \pm 0.000	0.033 \pm 0.183	0.000 \pm 0.000	0.000 \pm 0.000	0.000 \pm 0.000	0.133 \pm 0.434
	157.085 \pm 50.133	11.417 \pm 5.168		3.750 \pm 3.750				7.123 \pm 5.231
December	1.233 \pm 0.223	0.300 \pm 0.651	0.167 \pm 0.379	0.033 \pm 0.183	0.067 \pm 0.254	0.067 \pm 0.254	0.000 \pm 0.000	0.067 \pm 0.254
	76.144 \pm 39.307	5.146 \pm 3.840	0.782 \pm 0.340	3.259 \pm 3.259	0.295 \pm 0.221	4.255 \pm 3.098		3.040 \pm 2.132

Chapter 3: COHABITATION DYNAMICS AMONG WEB-BUILDING SPIDERS AS A FUNCTION OF PREY AVAILABILITY AND POPULATION DENSITY *

* This study is co-authored by Maxence Salomon & Samantha Vibert

3.1 Abstract

A group of animals represents a dynamic and somewhat unstable structure, as group composition and interactions between members may vary depending on the current ecological context, which determines the net payoff of group living. Few studies have examined the dynamic nature of group-living relationships and the constraints associated with them, especially in sedentary and territorial animals such as web-building spiders. We conducted a field experiment to investigate the dynamics of group living in the western black widow spider, *Latrodectus hesperus*, and tested the hypothesis that prey availability and population density influence cohabitation dynamics among females. To address this hypothesis we first assessed grouping tendencies in a natural population of *L. hesperus* spiders, and then examined changes in cannibalistic, foraging, web-building, movement, and spacing behaviours in spiders held at different prey availabilities and population densities. We also compared the influence of prey availability on associations between conspecifics versus between *L. hesperus* and co-occurring heterospecific spiders (*Tegenaria agrestis* and *T. duellica*). Our results show that both prey availability and population density influence the dynamics of group living in *L. hesperus*. An increase in prey availability decreased the level of cannibalism between conspecifics and the amount of movement between groups, suggesting that this factor affects group stability and the level of tolerance. Furthermore, spiders living at high densities moved more and reduced their territory size by sharing webs relative to those kept at low density, but there was no effect of population density on foraging outcome and cannibalism. We discuss our findings in the context of the behavioural plasticity associated with social interactions, and consider how dynamic relationships influence the adaptive value of grouping.

3.2 Introduction

Social interactions range widely from territorial and agonistic displays towards conspecifics in solitary species to cooperative and synchronized behaviours in social

group-living species, with a majority of intermediate forms (Krause & Ruxton 2002). A group usually constitutes a heterogeneous assemblage of individuals, which may involve disparities between group members in terms of resource exploitation and/or susceptibility to adverse factors, and result in conflicts of interest. Hence, a group of individuals is sometimes an unstable entity, which may dissociate and re-associate over time depending on the relative payoff of a particular group-living strategy. The selective environments controlling the evolution of such a diverse array of social strategies is structured by both intrinsic (primarily genetic) and extrinsic (ecological) factors (Alexander 1974; Cangialosi & Uetz 1987; Griffin & West 2003). Ecological factors such as prey availability, climate, habitat topology, and predation pressure may all influence the formation and maintenance of group-living relationships, although sometimes in conflicting ways (e.g. Uetz & Hodge 1990; Arnold & Owens 1999; Clutton-Brock et al. 1999). To examine the evolutionary basis of different group-living strategies one has to analyze the constraints associated with them under opposing environmental conditions.

One possible way of addressing this question is to examine the dynamics of group living in the context of microhabitat selection. This approach considers the influence of specific microhabitat attributes such as the spatiotemporal distribution of resources (e.g. food) and residents (e.g. predators, competitors) on group-living behaviours, and provides a measure of an animal's social nature and its potential for modulation. A suitable microhabitat constitutes an optimal combination of microhabitat factors perceived as indicators of profitability. One such factor is the presence of other conspecifics, which may shape microhabitat settlement decisions via positive or negative interactions (e.g. Pärt & Doligez 2003). Individuals with similar resource requirements may all congregate in the same favourable sites, which may cause conflict over finite resources and involve competitive interactions (Lubin et al. 2001). The outcome of these interactions is determined by both the nature of the contested resources and the characteristics of the individuals, such as their social tendency, foraging experience, and the level of phenotypic asymmetries. The inherent trade off between the availability of resources and the proximity of other individuals may cause individuals to compromise and coexist (Pereira et al. 2003) or tolerate each other and associate (Robertson et al. 1998). In some

situations, the presence of other microhabitat occupants may in fact initiate positive interactions by facilitating or enhancing resource acquisition, which will favour group formation and/or maintenance (Stephens & Sutherland 1999).

Web-building spiders are excellent model organisms for studying group-living dynamics in the context of microhabitat selection. Few species have evolved any degree of tolerance towards conspecifics due to the predominance of territoriality and cannibalism, so the rare examples of group living behaviours are worth further investigation (Avilés 1997). Furthermore, they are mostly sedentary animals that build webs as part of their microhabitat settlement tactic, which makes it convenient for assessing settlement decisions.

Two of the main factors that may constrain the extent of grouping among web-building spiders include population density and prey availability. The way they operate often depends on the nutritional requirements of individuals (Wagner & Wise 1997). Some spiders will only associate under favourable conditions when such constraints are relaxed, allowing for a reduction in territory size, while others that are less susceptible to changing conditions will establish more permanent societies (Uetz & Hieber 1997). Previous studies have shown that group living among spiders has the potential to increase individual fitness by enhancing foraging returns (e.g. Pekár et al. 2005), reducing web-building costs (e.g. Jakob 1991), and/or improving protection from predation and parasitism (e.g. Hieber & Uetz 1990). Few studies, however, have considered the dynamic nature of these relationships resulting from the ecological context in which they evolve. Furthermore, although intraspecific associations between spiders have been well characterized, little is known about associations between different co-occurring species.

Here, we investigate the dynamics of group living in the western black widow spider, *Latrodectus hesperus* Chamberlin & Ivie (Araneae: Theridiidae), a web-building species found in western North America (Kaston 1970). Recent evidence suggests that at least some populations in coastal British Columbia have an aggregated spatial distribution at certain times of the year, wherein adult and subadult females exhibit

communal behaviours by building clusters of webs or more commonly by sharing webs (see Chapter 2). Furthermore, these spiders co-occur and share microhabitats with two congeneric species of introduced European house spiders: *Tegenaria agrestis* Walckenaer, the hobo spider and *T. duellica* Simon, the giant house spider (Araneae: Agelenidae). In sympatry, these species often build webs that are adjacent or affixed to one another, despite the associated mortality risks of cannibalism and predation (*L. hesperus* is the dominant predator of the three species and it preys upon both *Tegenaria* species (pers. obs.)).

To examine the dynamics of cohabitation among *L. hesperus* spiders, we first surveyed a natural population to determine the extent of cohabitation, and then conducted a semi-natural field experiment in which we manipulated two factors that are hypothesized to modify spacing requirements and territorial behaviour among females: (1) population density (and composition), and (2) prey availability. For the first one, we varied the initial density of conspecific females and also the presence of *Tegenaria* spp. females. Variations in population density often change the nature and rate of interactions between spiders (e.g. agonism vs. tolerance), which may influence group-living dynamics. For the second one, we kept females on different feeding regimes (high food vs. food-deprived) to examine nutritional state-dependent grouping behaviours. We measured the effects of our manipulations on the following variables: (a) the rate of cannibalism and predation, (b) individual foraging success, (c) web-building behaviours, (d) the rate of movement between microhabitats, and (e) the spatial arrangement of individuals across microhabitats. We predict that group living would arise and be maintained at high prey availability, because females are more likely to tolerate the presence of neighbours, even when space is limited at high population density. Furthermore, females should form different grouping relationships at high vs. low population density, due to the associated changes in resource availability.

3.3 Materials and Methods

3.3.1 Study System

Latrodectus hesperus is a cobweb-weaving spider that occurs both in natural habitats and in association with human habitations in western North America. It is a nocturnal predator that feeds on a variety of ground-dwelling arthropods (see Chapter 2). *Tegenaria duellica* and *T. agrestis* are funnel-web spiders of European origin that have recently been introduced to the Pacific Northwest and have now become invasive (Vetter et al. 2003). In their introduced range both species are mainly synanthropic although they also occur in natural habitats in association with *L. hesperus* spiders. Sympatric populations of these three species are found along the southern coast of British Columbia where individuals often co-occur and share microhabitats. High densities of adult and subadult females are observed in late summer and autumn (pers. obs.).

3.3.2 Study Area

The study was conducted on Cordova Spit, a sandy spit located on the land of the Tsawout First Nation on southern Vancouver Island, British Columbia, Canada (48°35' N, 123°22' W, at sea level). The spit is structurally complex with a predominance of bushes and trees at the base (*Cytisus scoparius*, *Malus fusca*, *Pseudotsuga menziesii*), an extensive area dominated by grasses and sedges in the centre (*Carex macrocephala*, *Leymus cinereus*), and at the tip a large open sandy area with widely spaced patches of short plants (predominantly *Abronia latifolia*, *Ambrosia chamissonis*, *Convolvulus soldanella*, *Grindelia integrifolia*, *Hypochaeris radicata*, *Polygonum paronychia*, *Rumex acetosella*, and stabilized patches of *Racomitrium canescens*) and driftwood, bordered by a narrow strip of Douglas Firs (*Pseudotsuga menziesii*) and their associated understory vegetation. A sandy beach surrounds the spit. *Latrodectus hesperus*, *T. duellica* and *T. agrestis* spiders primarily inhabit the open sandy parts, where they build their webs on the underside of and underneath logs of driftwood that are patchily distributed throughout this habitat. They are the dominant web-building spiders in these microhabitats, although we have also observed a few other species of web-builders (families Theridiidae and

Linyphiidae), and a variety of cursorial spiders (families Lycosidae, Salticidae, Dysderidae, and Corinnidae).

3.3.3 Survey of a Natural Population

We surveyed an aggregation of driftwood logs covering an area of 611.5 m² in the open sandy area at the end of the spit, approximately 20-40 m from our experimental site (see 3.3.4), for the presence of *L. hesperus*, *T. duellica*, and *T. agrestis* spiders and their webs. This was done in mid-August 2004, just before starting the experiment. All logs that were at least 30 cm in length and detached from the substrate were turned over and surveyed (previous research has shown that these spiders only occupy logs that are at least this size; see Chapter 2). We recorded the following parameters: number of *L. hesperus*, *T. duellica*, and *T. agrestis* spiders, sex and age class, mean length and width of their webs to estimate total area, nearest-neighbour distances between individuals and webs, and total area available under each log (mean length \times width). From these data, we quantified the spatial distribution of individuals and their webs using dispersion indices based on (1) individual counts (the standardized Morisita index of dispersion, I_p ; see Krebs 1999) and (2) distances (the nearest-neighbour index, R , followed by Donnelly's modified Z test). The former index presents scores ranging from -1 to +1; 0 denotes a random distribution of individuals, positive values indicate a tendency to aggregate and negative values a uniform distribution, with 95% confidence intervals at +0.5 and -0.5. We then compared the distribution of nearest-neighbour distances between webs to the distribution of distances between their corresponding logs using a Wilcoxon signed-ranks test, to assess their spatial arrangement with respect to the logs. To determine the influence of microhabitat size on the level of space occupancy by *L. hesperus* spiders, we regressed web area against log area (log-transformed) using a general linear model (GLM). We used a generalized linear model (GZLM) with a Poisson distribution, a log-link function, and an overdispersion parameter to examine the relationship between the number of spiders per occupied web and web area. Finally, we compared the mean number of spiders per occupied web between species with a Mann-Whitney U test.

3.3.4 Field Experiment

3.3.4.1 Experimental design

To examine the dynamics of cohabitation among and between species, we conducted a field experiment in their natural habitat from the end of August to early October 2004, when females of all 3 species co-occur (pers. obs.). We chose to work under semi-natural conditions, because it was not possible to control for space limitation and prey availability in spiders' natural microhabitats. Twelve circular enclosures (310 cm in diameter; 7.55 m² area; 9 m apart) bound by white plastic Templast walls (30 cm in height, sunk 10 cm deep) were placed in a line on the sand, in the open area at the end of the spit (see Fig. 3.1). The smooth surface of the plastic prevented the emigration of *L. hesperus* and *Tegenaria* spp. females, as determined from preliminary trials. All the vegetation was removed from the enclosures and the sand was levelled off. Within each enclosure, we placed 6 rectangular wooden sheds (125 cm length × 15 cm width × 8 cm height; open at both ends) in a radial configuration around the centre that served as spider microhabitats. The size of a shed corresponded to the mean dimensions of a log of driftwood occupied by these spiders, as determined from our survey data (mean ± SE; length = 144.03 ± 10.06 cm, width = 17.36 ± 0.88 cm, N = 110). Each shed was built with a removable wooden lid fitting onto the sides, to which was stapled a roof made of aluminium meshing (mesh size: 2 mm) to allow the observation of spiders without turning over the sheds and disturbing them and their webs. Preliminary experiments confirmed that adult spiders readily settled in these microhabitats and attached their webs onto the meshing through which they were unable to pass.

Only adult females were used in the experiment. All females were collected from driftwood logs in a sandy habitat located 800-m away from our experimental site. Spiders were kept in separate Petri dishes (14 cm diameter; 2.5 cm height) containing moist cotton wicks for about 10 days before the start of a trial, at 24 ± 3°C and 30 ± 5% RH. We used *T. agrestis* and *T. duellica* spiders indiscriminately, because in these habitats they form similar ecological associations with *L. hesperus* spiders (pers. obs.). After the experiment, all surviving spiders were returned to the collection site.

The experiment followed a 2×3 factorial design, with 2 feeding regimes (well fed vs. poorly fed) and 3 starting spider densities (low conspecific (1 *L. hesperus* spider per microhabitat); high conspecific (2 *L. hesperus* spiders per microhabitat); and high heterospecific (1 *L. hesperus* + 1 *Tegenaria* spp. spider per microhabitat)). All treatment combinations were randomly assigned to the enclosures. Poorly-fed spiders were starved for 10 days prior to the start of the experiment and kept unfed throughout, whereas well-fed spiders were given 1 large house cricket, *Acheta domesticus* (mean weight \pm SE = 403.487 ± 12.541 mg, N = 90) each every other day from the day they were collected to the end of the experiment. During the experiment, we fed spiders in the well-fed treatment shortly before dusk (starting on day 1), by introducing the appropriate number of crickets under each shed and closing off the ends with wooden panels for 30 min to ensure that spiders perceived the presence of prey; subsequently the crickets were free to wander in and out of the sheds. The same procedure was applied to sheds in the poorly-fed treatment, except that no prey were introduced. Our prey supplementation treatments provided standardized information about prey availability, but did not exclude the possibility that spiders would feed on other prey in the enclosures.

All spiders were marked for individual identification with small dots of whiteout paint on their legs and dorsum in distinct combinations of colour and dotting patterns. They were then introduced either alone or in pairs under the sheds on the first day of the experiment at 1200 hours (side of introduction determined randomly). Spiders that died during the experiment were not replaced. Spiders were randomly assigned to the treatment groups and pairs of spiders introduced under the same shed were selected so as to minimize size differences, as this may influence the outcome of interactions (e.g. Buddle et al. 2003). In the two high initial spider density treatments, mean size differences between paired spiders were not different across the different enclosures (GLM: 2 *L. hesperus*: $F_{6,40} = 1.855$, $P = 0.113$; 1 *L. hesperus* + 1 *Tegenaria* spp.: $F_{6,40} = 0.964$, $P = 0.351$). Furthermore, the mean size of *L. hesperus* spiders did not differ between feeding regimes ($F_{1,189} = 2.895$, $P = 0.091$) and trials ($F_{1,189} = 0.125$, $P = 0.724$).

We ran 2 separate 15-day trials: from 23 August-07 September and from 20 September-05 October. Each trial had 2 replicates of each of the 6 initial spider density/feeding regime treatment combinations (4 replicates of each in total). We surveyed all enclosures on a daily basis starting the day after spider introduction (day 1) by opening the lids of the sheds to record our observations and carefully turning sheds over to collect any consumed prey or dead spiders. Heavy rain prevented us from conducting our normal survey during 1 day in trial 1 (day 7), so we simply mapped the spatial distribution of spiders and collected any consumed prey and dead spiders.

3.3.4.2 Variables measured

3.3.4.2.1 Survival, cannibalism and predation

To test whether feeding regime and initial spider density influenced the rate of cannibalism and survival, we surveyed sheds daily, recorded all spider deaths, and identified dead spiders based on their markings. We assigned a cause of death based on (1) our observations of cannibalistic and predation events, and (2) inspections of spider carcasses in the laboratory. If a dead spider was wrapped in silk on the web of another spider and being consumed, we recorded the identity of the predator and waited until the prey had been discarded to collect it (usually within 1-2 days). If spiders were found dead on the ground, we examined them under a dissecting microscope for any signs of cannibalism such as silk wrapping and puncture wounds. The effects of our treatments on spider survival rate were analyzed with survival analysis using Cox's regression method, stratified by trial (see Hosmer & Leshow 1999). We also examined whether differences in size between individuals had any bearing on cannibalistic events using paired t-tests.

3.3.4.2.2 Spider body condition

Body condition is a measure of a spider's physiological state, which is used as an indicator of energy intake, growth rate, and reproductive status (Jakob et al. 1996). We weighed all spiders before and after the experiment to the nearest 0.1 mg, and measured the length of the tibia and patella on one of their front legs using callipers (precision: 0.01

mm) as an index of size. The body condition of each spider used in the experiment was calculated as the residuals of a regression of weight over size for (1) all *L. hesperus* spiders, and (2) all *Tegenaria* spp. spiders (both variables log-transformed; *L. hesperus*: $y = 1.447x + 3.029$, $R^2 = 0.109$, $P < 0.0001$; *Tegenaria* spp.: $y = 1.413x + 2.621$, $R^2 = 0.258$, $P = 0.0002$). The slopes of the regressions did not differ between feeding regimes (GLM: feeding regime \times spider size: *L. hesperus*: $F_{1,188} = 2.048$, $P = 0.154$; *Tegenaria* spp.: $F_{1,44} = 0.847$, $P = 0.362$), but the difference in elevation was significant (feeding regime: *L. hesperus*: $F_{1,189} = 150.932$, $P < 0.0001$; *Tegenaria* spp.: $F_{1,45} = 16.253$, $P = 0.0002$). Thus, at the start of the experiment well-fed *L. hesperus* and *Tegenaria* spp. spiders were in better condition than poorly-fed ones. However, we did not detect any difference in spider body condition across initial spider density treatments (*L. hesperus*: $P = 0.339$) and trials (*L. hesperus*: $P = 0.246$; *Tegenaria* spp.: $P = 0.321$). The body condition of surviving spiders at the end of the experiment was calculated using the same method as above.

3.3.4.2.3 Foraging returns

To determine a spider's foraging success, we recorded the number of prey items captured and consumed by each spider on a daily basis, and calculated the biomass they represent. Prey were collected from the ground under the microhabitats as soon as spiders had discarded them. Insect prey were identified to taxonomic order, their total length measured with callipers (precision: 0.01 mm) and weighed to the nearest 0.1 mg. We estimated an insect prey's initial dry weight (mg) from its total length (mm) using Rogers et al.'s (1977) regression equations, applying different coefficients to each taxonomic order of insect prey. To determine the initial dry weight of dead *L. hesperus*, *Tegenaria* spp., and *Pardosa* sp. spiders that were preyed upon by other spiders, we used separate genus-specific (family-specific in the case of *Pardosa* sp.) regression equations developed in a previous study (see Chapter 2) to derive dry weights from spiders' initial wet weights at the start of the experiment. We then used these dry weight estimates to compare the total mass acquired from insect prey capture versus predation on *L. hesperus* and *Tegenaria* spp. spiders.

The total number of prey and the total prey mass consumed per capita were compared between treatments using general linear mixed models (GLMM), with feeding regime and initial spider density as between-subject factors, day as within-subject factor, and mean number of spiders per microhabitat as a covariate (log-transformed).

We also compared the initial and final body weight of surviving spiders before and after the experiment as a means of assessing the effect of our prey supplementation and initial spider density treatments on foraging returns. We used a GLMM with final weight as a response variable (log-transformed), feeding regime and initial spider density as predictors, and initial spider weight as a covariate (log-transformed). Another GLMM analyzed the effect of these same treatments on final body condition, with initial condition as a covariate (both log-transformed).

3.3.4.2.4 Analysis of web building

To investigate the web-building behaviours of *L. hesperus* and *Tegenaria* spp. spiders, we marked the location of each cobweb and funnel-sheet web under a given microhabitat and measured their size on a daily basis. This provided data on the changes in web size and the occurrence of new webs. We measured web length and width and multiplied them to obtain web area, and recorded the number of web occupants and their identities based on their markings. The 3-dimensional configuration of *L. hesperus* webs was assessed in terms of thread density. We indexed thread density by assigning categorical values to each web as follows: 0 = no web; 1 = just a few threads; 2 = web with capture threads; 3 = very dense web. Finally, we evaluated the latency to onset of web construction, defined as the point in time at which a functional web (i.e. density of 2) was found under a given microhabitat.

Because we were unable to measure web parameters on a rainy day in trial 1, data analyzes were run with missing data. We used separate GLMMs to assess the effects of feeding regime and initial spider density (between-subject factors), and day (within-subject factor) on (1) the mean number of webs per microhabitat, (2) the mean area per web, (3) the mean thread density per web, and (4) the mean number of spiders per web.

3.3.4.2.5 Movement behaviour

Throughout the experiment we recorded the position of each spider on a daily basis by flagging consecutive locations on the lids of the sheds. Spiders were seen moving between microhabitats after dusk using either direct routes or walking along the walls of the enclosures. The movement behaviour of *L. hesperus* and *Tegenaria* spp. spiders were analyzed separately. We examined the effects of feeding regime and initial spider density on their daily travels in terms of (1) the number of moves per capita, and (2) the distance moved per capita. To assess the distance moved per capita, we assigned a value of 0 to those spiders that remained under the same microhabitat over 24 h (this is a conservative measure since most spiders did move within a microhabitat), 1 to those that had moved to an adjoining microhabitat, and 2 or 3 to those that had travelled to microhabitats that were 2 or 3 positions over, respectively. These two response variables were analyzed using separate GLMMs, with feeding regime and initial spider density as between-subject factors, and day as a within-subject factor. We also compared the total number of moves per capita over the course of the experiment between treatment groups using a general linear model (GLM), with trial as a random factor.

3.3.4.2.6 Spatial distribution

We assessed the spatial distribution of spiders by recording the number of microhabitats occupied and the number of spiders per occupied shed on a daily basis. We used GLMMs to assess the effect of feeding regime and initial spider density (between-subject factors) and day (within-subject factor) on (1) the mean number of occupied microhabitats and (2) the mean number of spiders per occupied microhabitat.

3.3.4.3 Statistical analysis

All statistical analyses were conducted with SPSS v. 13 (SPSS Inc., Chicago, USA). Given the large size of our dataset, we wrote small programs to parse and systematically verify the raw data prior to analysis. Data were tested for normality and homoscedasticity, and transformations or non-parametric tests were used where

appropriate. We ran GLMs and GLMMs with trial number as a random factor, and GLMMs had a first-order autoregressive covariance structure with enclosure (plot) number as a random subject factor. We first ran the full models with all interaction terms and then chose the best-fitting models based on differences in Akaike's information criterion (AIC) scores.

3.4 Results

3.4.1 Survey of a Natural Population

We examined a total of 110 driftwood logs and found 69 *L. hesperus* webs occupied by 77 spiders, and 64 *Tegenaria* spp. webs occupied by 34 spiders (15 *T. agrestis*, 7 *T. duellica*, and 12 undetermined *Tegenaria* spp. juveniles). Nineteen logs (17.3%) only had *L. hesperus* webs, 12 logs (10.9%) only had *Tegenaria* spp. webs, 31 logs (28.2%) had both types of webs, and 48 logs (43.6%) were devoid of webs. Under occupied logs, there were on average 1.488 ± 0.798 *Tegenaria* spp. webs (mean \pm SD; median = 1, range: 1-4, N = 43) and 1.380 ± 0.697 *L. hesperus* webs (median = 1, range: 1-4, N = 50).

The overall distribution of spiders under these logs was consistently more aggregated than random (standardized Morisita index of dispersion: $I_p = 0.503$), which was also the case when *L. hesperus* spiders were considered separately ($I_p = 0.513$), whereas *Tegenaria* spp. spiders were uniformly distributed with respect to each other ($I_p = -0.467$). The spatial patterns of logs, *L. hesperus* webs, and *Tegenaria* spp. webs were all significantly clumped based on nearest-neighbour distances (logs: $R = 0.711$, $Z = -5.930$, $P < 0.0001$; *L.* webs: $R = 0.619$, $Z = -6.062$, $P < 0.0001$; *T.* webs: $R = 0.531$, $Z = -7.061$, $P < 0.0001$). The distribution of *Tegenaria* spp. webs was more clumped than that of the logs they occupied ($Z = -2.214$, $N = 64$, $P = 0.027$), whereas *L. hesperus* webs and their corresponding logs were equally spaced out ($Z = -0.882$, $N = 69$, $P = 0.378$).

Web occupancy was higher on *L. hesperus* webs (85.5%; 59/69 webs) than on *Tegenaria* spp. webs (51.6%, 33/64 webs). The median number of spiders on occupied *L. hesperus* and *Tegenaria* spp. webs was in both cases 1, but there were on average more spiders on *L. hesperus* than on *Tegenaria* spp. webs (mean \pm SD; L. webs: 1.254 ± 0.544 ; T. webs: 1.030 ± 0.174 ; Mann-Whitney U test: $U = 803.5$, $P = 0.022$, $N_L = 59$, $N_T = 33$). Furthermore, the number of *L. hesperus* spiders per occupied web was positively correlated with web area (GLZM on log-transformed data: $\chi^2_{57} = 11.748$, $P = 0.0006$). *Latrodectus hesperus* webs were significantly larger than *Tegenaria* spp. webs (mean area \pm SD; L. webs: 670.957 ± 71.082 cm²; T. webs: 394.375 ± 53.721 cm²; GLM on log-transformed data with log area as a covariate: $F_{1,130} = 26.746$, $P < 0.0001$), and covered a larger proportion of the area available under a log (L. webs: $20.147 \pm 18.904\%$; T. webs: $9.128 \pm 8.360\%$). The amount of space available under a log was a moderate but highly significant predictor of web area for both web types (GLM on log-transformed data; L. webs: $\beta = 0.553$, $R^2 = 0.352$, $F_{1,67} = 36.438$, $P < 0.0001$; T. webs: $\beta = 0.582$, $R^2 = 0.204$, $F_{1,62} = 15.930$, $P = 0.0002$).

3.4.2 Field Experiment

3.4.2.1 Survival, cannibalism and predation

There was a positive effect of feeding regime on the rate of survival of *L. hesperus* spiders, but no effect of initial spider density, and no interaction between these factors (Table 3.1; Fig. 3.2). Overall, well-fed spiders survived longer than poorly fed ones, regardless of their initial density. Since spider survival rates were homogenous between trials, we pooled the data from each trial. At the end of the experiment, the proportion of surviving individuals was greater in well-fed than in poorly-fed groups (Fisher's exact test (2-tailed): $P = 0.0007$), but there was no difference across initial spider density treatments (Log-likelihood ratio test: $G_2 = 0.132$, $P = 0.936$). On average, $22.222 \pm 3.602\%$ of poorly-fed *L. hesperus* spiders died (mean \pm SE; averaged across replicates and initial spider density treatments), whereas only $5.556 \pm 2.135\%$ of them died in the well-fed groups. The final number of *L. hesperus* spiders per microhabitat at the end of the experiment overlapped with the initial spider density in the well-fed

treatment, whereas it decreased in the poorly-fed treatment (Fig. 3.3); however, in the high initial density treatment (2 *L. hesperus* spiders per microhabitat) the final density was higher than 1 spider per microhabitat, indicating that crowding was maintained. With regard to *Tegenaria* spp. spiders, neither feeding regime (Cox regression: $\chi^2 = 0.128$, d.f. = 1, $P = 0.721$) nor trial ($\chi^2 = 1.966$, d.f. = 1, $P = 0.161$) had any effect on their survival rate. Furthermore, their mortality rate was higher than that of *L. hesperus* spiders, with $37.500 \pm 7.979\%$ of spiders dying in well-fed groups and $45.833 \pm 4.167\%$ in poorly fed groups. In the heterospecific spider initial density treatments, the probability of surviving was higher for *L. hesperus* spiders than for *Tegenaria* spp. spiders (Cochran-Mantel-Haenzel test: $\chi^2 = 8.412$, d.f. = 1, $P = 0.004$).

The leading cause of mortality among *L. hesperus* spiders was cannibalism, accounting for 96.3% of deaths (26/27). Most cannibals preyed upon one conspecific during the experiment (76.2%, 16/21), but a few preyed upon 2 conspecifics (23.8%, 5/21), and this pattern was conserved between trials ($G_1 = 0.022$, $P = 0.882$). For *Tegenaria* spp. spiders, most of the mortality was due to predation by *L. hesperus* spiders, which accounted for 85.0% of deaths (17/20). Another 10.0% (2/20) of deaths among *Tegenaria* spp. spiders were due to cannibalism. The remaining deaths (1 *L. hesperus* spider and 1 *Tegenaria* spp. spider) were due to unknown reasons: these spiders were found dead on the ground, unconsumed, and without any visible signs of predation on their carcasses. Since the enclosures were placed in the natural habitat of *L. hesperus* and *Tegenaria* spp. spiders, aerial predators of these spiders were able to visit the enclosures, whereas ground-active ones might have been constrained by the walls of the enclosures.

Cannibalism between *L. hesperus* spiders occurred in microhabitats occupied by 2-4 spiders (including the victim). In the 1 *L. hesperus* spider and 1 *L. hesperus* spider + 1 *Tegenaria* spp. spider initial density treatments all cannibalistic events happened in microhabitats occupied by 2 spiders, whereas in the 2 *L. hesperus* spiders initial density treatment cannibalism occurred in microhabitats with 2 (37.5%), 3 (56.3%), or 4 (6.3%) spiders.

Overall, *L. hesperus* cannibals were significantly larger than their conspecific victims in the poorly-fed group (Wilcoxon signed-ranks test on log-transformed response variable: $Z_{19} = 3.018$, $P = 0.003$), but not in the well-fed group ($Z_7 = 0.338$, $P = 0.735$). *Tegenaria* spp. spiders that were preyed upon by *L. hesperus* spiders were not any smaller than those that survived (GLM on log-transformed response variable: $F_{1, 45} = 0.611$, $P = 0.439$, power = 0.119), and there was no difference between trials ($F_{1, 45} = 1.837$, $P = 0.182$, power = 0.264).

3.4.2.2 Foraging

During the experiment, spiders that were successful in capturing prey caught on average 2.371 ± 1.247 prey (\pm SD; $N = 89$) in the well-fed treatments, and 1.175 ± 0.446 ($N = 40$) in the poorly fed treatments. The majority of these prey were the supplemented crickets ($N = 203$). The rest of the prey included cannibalized conspecifics ($N = 26$), *Tegenaria* spp. spiders ($N = 17$), and also other arthropods seeking shelter under the sheds, including moths ($N = 18$), ground beetles ($N = 3$), paper wasps ($N = 2$), and on single occasions a termite alate, an ant, and a *Pardosa* sp. spider. Spiders in the poorly fed groups captured most of these other arthropod prey (poorly fed: 69.2%, well fed: 30.8%; $\chi^2 = 3.947$, d.f. = 1, $P = 0.047$).

As expected, our prey supplementations had a positive effect on prey intake rate in *L. hesperus* spiders, resulting in higher mean daily per capita prey capture success and prey mass acquired in well-fed than in poorly-fed groups, but no difference across initial spider density treatments (Table 3.2). Furthermore, there was an interaction between feeding regime and time, such that prey capture success fluctuated over time for well-fed spiders, especially early on in the experiment, while there was no major change over time for poorly-fed spiders. The mean number of *L. hesperus* spiders per occupied microhabitat had no effect on either of these two response variables (both $P > 0.1$), so this parameter was removed from the final models. Overall, the largest biomass of prey consumed by *L. hesperus* spiders was the supplemented cricket prey (75.45% of total prey mass), followed by cannibalized *L. hesperus* spiders and preyed upon *Tegenaria* spp. spiders (16.27%), and other types of prey (8.28%).

The same pattern was observed when analyzing the effect of our treatments on mean overall weight gain (final vs. initial weight) in surviving *L. hesperus* spiders: there was a positive effect of feeding regime (GLMM: $F_{1,64.8} = 27.719$, $P < 0.0001$) and initial weight (log-transformed; $F_{1,157.4} = 245.937$, $P < 0.0001$), but no effect of initial spider density ($F_{2,36.3} = 0.571$, $P = 0.570$), and no interaction between these factors (term removed from the final model). At the end of the experiment, well-fed *L. hesperus* spiders were in better condition than poorly-fed ones (GLMM on log-transformed response variable; $F_{1,10.4} = 84.610$, $P < 0.0001$), and there was no difference across initial spider density treatments ($F_{1,12.2} = 0.377$, $P = 0.694$). There was an interaction between feeding regime and initial body condition on final body condition (GLMM on log-transformed response variable; interaction: $F_{1,141.2} = 5.372$, $P = 0.022$; feeding regime: $F_{1,72.2} = 21.362$, $P < 0.0001$; initial body condition: $F_{1,158.7} = 163.738$, $P < 0.0001$), but no effect of initial spider density ($F_{2,31.0} = 2.352$, $P = 0.112$). Well-fed spiders experienced a greater increase in body condition than poorly-fed spiders, and the magnitude of this difference was greater for spiders in low initial body condition.

We observed 8 feeding events among *Tegenaria* spp. spiders (5 in trial 1 and 3 in trial 2), all of which involved supplemented cricket prey in the well-fed group. Three spiders captured 2 consecutive prey items each, and 2 others caught 1 prey each. In addition, there were 2 cannibalistic events, 1 among poorly-fed and 1 among well-fed spiders.

3.4.2.3 Web building

Latrodectus hesperus spiders constructed large webs that often spanned the entire space available under a microhabitat. The mean area per web increased with time over the first 4-6 days of the experiment (GLMM on log-transformed response variable: $F_{14, 247.2} = 16.770$, $P < 0.0001$; Fig. 3.4b). Initial spider density had an effect on mean web area ($F_{2, 23.2} = 11.625$, $P = 0.0003$), such that spiders from the 2 *L. hesperus* spiders initial density treatment built larger webs than those kept at a lower density or with *Tegenaria* spp. spiders (Bonferroni-adjusted pairwise comparisons: $P = 0.005$, $P = 0.0004$,

respectively), while there was no difference between the latter 2 groups ($P = 0.893$). This difference is mostly due to the fact that there were more spiders and thus greater web coverage at higher initial densities. Despite the lack of statistical difference in mean web area between spiders in the 1 *L. hesperus* spider initial density treatment and those kept with *Tegenaria* spp. spiders (see above), webs in the latter group were marginally smaller by the end of the experiment (see Fig. 3.4b), although there was no interaction between initial spider density and time ($P = 0.090$). Feeding regime had no bearing on mean web area ($F_{1,23.2} = 0.926$, $P = 0.346$).

Webs that were built early on were fused together to form larger webs in the high initial density treatment, whereas spiders in the other two treatments built small webs at the onset and progressively increased their size, a pattern supported by the divergent trends over time between initial spider densities in the number of webs per microhabitat (Fig. 3.4a) and the overall increase in web size over time (Fig. 3.4b). The average number of *L. hesperus* webs per microhabitat varied across initial spider density treatments during the first 4 days of the experiment (GLMM on log-transformed response variable: initial spider density \times day: $F_{28,249.4} = 2.394$, $P < 0.0001$). It progressively increased over time up to 1 web per microhabitat in the 1 *L. hesperus* spider and the 1 *L. hesperus* + 1 *Tegenaria* spp. spider initial density treatments, whereas in the 2 *L. hesperus* spiders initial density group it decreased down to 1 web per microhabitat (Fig. 3.4a). In all treatment groups it soon reached a constant average of 1 web per microhabitat (range: 0.95-1.05). There was no effect of feeding regime on this response variable ($F_{1,20.1} = 0.065$, $P = 0.801$). At the end of the experiment, a greater proportion of *L. hesperus* webs in the 2 *L. hesperus* spiders initial density treatment covered the whole area under a microhabitat than in the other two density groups ($G_2 = 34.624$, $P < 0.0001$), although there was no difference between feeding regimes ($G_1 = 2.305$, $P = 0.129$).

There was an effect of time (GLMM: $F_{14,236.5} = 15.332$, $P < 0.0001$), feeding regime ($F_{1,32.3} = 61.401$, $P < 0.0001$) and initial spider density ($F_{2,32.3} = 6.433$, $P = 0.004$) on average thread density. Well-fed spiders clearly built denser webs than poorly fed ones, and spiders in the 2 *L. hesperus* spiders initial density treatment built denser webs

than those at a lower conspecific density (Bonferroni-adjusted pairwise comparison: $P = 0.004$), but there was no detectable difference with spiders kept with *Tegenaria* spp. spiders ($P = 0.103$). Thread density increased over time, and towards the end of the experiment, some webs made by well-fed spiders were so dense that we would have liked to assign them to a new and higher thread density category.

Large webs typically occupied by several spiders did not consist of separate silken entities. Instead, these webs were formed of a single three-dimensional unit with a series of intermingled threads. Webs that reached the highest thread density were characterized by the presence of 2-3 distinct densely woven tangled areas where spiders resided (usually 1 per individual). Most of the prey capture took place in these areas, and they were interconnected via a network of anchor lines, which spiders used to move along a web. The size of these silken areas varied over time: during the first half of experiment they were on average 25-30% of the length of a microhabitat, and by the end of the experiment, some of them reached 40-60%, while others had fused with neighbouring areas.

Spiders started building webs within the first day of the experiment and most webs were functional (i.e. able to catch prey) by that time. However, some webs remained sparse and small with few silk threads until the third or fourth day, and a few webs built by poorly-fed spiders stayed that way during the whole experiment. Since spiders shared webs and often moved between microhabitats, it was not possible to attribute a particular web-building effort to a specific spider. However, the changes in web size and density over time indicate that spiders spent time and energy producing silk and building webs at several locations.

Latrodectus hesperus webs were often occupied by 2-3 females, and sometimes even up to 4-5 at a time. The average number of *L. hesperus* spiders per occupied web differed across initial spider density treatments (GLMM on log-transformed response variable: $F_{2,29.4} = 40.784$, $P < 0.0001$; Fig. 3.4c), such that there were more spiders per web in the 2 *L. hesperus* spiders initial density treatment than in the lower density

treatment (Bonferroni-adjusted pairwise comparison: $P < 0.0001$) and that with *Tegenaria* spp. spiders ($P < 0.0001$), but there was no difference between the latter two groups ($P = 0.655$). Spiders in the 2 *L. hesperus* spiders initial density treatment were more likely to share webs than to build individual webs. Furthermore, the mean number of spiders per occupied web varied over time and feeding regime (feeding regime \times day: $F_{14,200.4} = 2.098$, $P = 0.013$; day: $F_{14,200.4} = 1.990$, $P = 0.020$; feeding regime: $F_{1,27.5} = 4.629$, $P = 0.040$), as it stayed relatively constant over time among well-fed spiders, whereas it decreased between the first and second half of the experiment for poorly-fed spiders. Web ownership varied widely, as spiders assumed different positions on a given web and also moved between microhabitats and webs.

Tegenaria spp. spiders built webs that were smaller than *L. hesperus* webs, reaching a maximum size corresponding to 65% of the area available under a microhabitat (with most within 20-40%), compared to a maximum size of 100% for *L. hesperus* webs. Furthermore, they increased in size over time (GLMM on log-transformed response variable: $F_{14,51.3} = 3.235$, $P = 0.001$), and underwent minor increases and decreases in size due to their higher susceptibility to breakage. However, there was no effect of feeding regime ($F_{1,6.0} = 0.040$, $P = 0.848$). These webs were typically located under *L. hesperus* webs, and both web types were usually attached to each other. The average number of *Tegenaria* spp. webs increased over time from 0.45 to about 1 per microhabitat (GLMM on log-transformed response variable: $F_{14,55.4} = 9.337$, $P < 0.0001$) but there was no difference between feeding regimes ($F_{1,6.0} = 0.091$, $P = 0.773$).

3.4.2.4 Movement behaviour

Latrodectus hesperus spiders regularly moved between webs and microhabitats. The mean per capita number of moves between microhabitats decreased over time (GLMM on log-transformed response variable: $F_{14,167.8} = 16.735$, $P < 0.0001$; Fig. 3.5), and was positively affected by both feeding regime ($F_{1,20.0} = 7.538$, $P = 0.012$) and initial spider density ($F_{2,20.0} = 8.093$, $P = 0.003$). This decrease in the number of moves occurred mostly during the first 5 days of the experiment, and was especially pronounced during

the first 2 days, after which it stayed at a constant low. Poorly fed spiders had a higher tendency to move than well-fed ones, and those in the 2 *L. hesperus* spider initial density treatment moved more than those kept with *Tegenaria* spp. spiders (Bonferroni adjusted pairwise comparison: $P = 0.002$), while spiders in the 1 *L. hesperus* spider treatment showed an intermediate rate of movement ($P > 0.05$). The mean number of spiders per microhabitat had no effect on their tendency to move and was thus removed from the final model (log-transformed: $P = 0.649$). The total number of moves per capita differed between feeding regimes (GLM on log-transformed response variable: $F_{1,19} = 10.377$, $P = 0.004$) and initial spider density treatments ($F_{2,19} = 7.799$, $P = 0.003$), such that poorly-fed spiders moved more often overall, and spiders in the 2 *L. hesperus* spider initial density treatment moved more than those kept with *Tegenaria* spp. spiders (Tukey's HSD test: $P = 0.002$), while there was no difference with the 1 *L. hesperus* spider initial density treatment ($P = 0.079$).

When considering the magnitude of movement per capita (i.e. the distance travelled between microhabitats), we found an effect of time (GLMM on log-transformed response variable: $F_{14,178.3} = 8.062$, $P < 0.0001$) and initial spider density ($F_{2,123.0} = 14.999$, $P < 0.0001$), but no effect of feeding regime ($F_{1,123.0} = 1.029$, $P = 0.312$). Spiders in the 2 *L. hesperus* spiders initial density treatment covered more distance than those in the other 2 treatments (Bonferroni-adjusted pairwise comparisons: $P < 0.0001$ and $P = 0.006$), while there was no difference between the latter 2 groups ($P = 0.076$). The amount of per capita distance moved fluctuated widely over time: there was an initial decrease during the first few days, followed by an increase and subsequent decrease again.

With regard to the movement behaviour of *Tegenaria* spp. spiders, both the mean number of moves per capita and the mean distance moved per capita decreased over time (number of moves: $F_{14,50.8} = 6.505$, $P < 0.0001$; distance moved: $F_{14,50.3} = 5.791$, $P < 0.0001$), but there were no differences between feeding regimes (number of moves: $F_{1,6.0} = 0.840$, $P = 0.395$; distance moved: $F_{1,6.0} = 0.523$, $P = 0.497$). In both cases, most of the decrease over time took place during the first half of the experiment. Neither the mean

number of *L. hesperus* spiders per microhabitat, nor the mean number of *Tegenaria* spp. spiders per microhabitat had an effect on their movement behaviours (all $P > 0.1$).

3.4.2.5 Spatial Distribution

Not surprisingly, mean microhabitat occupancy by *L. hesperus* spiders varied between initial spider density treatments (GLMM: $F_{2,20.0} = 11.351$, $P = 0.001$): there were more spiders in the 2 *L. hesperus* spiders density group that usually occupied more microhabitats than in the other 2 groups (Bonferroni-adjusted pairwise comparisons: both $P = 0.002$). In the 2 *L. hesperus* spiders initial density treatment, on average >90% of microhabitats were occupied at all time, whereas in the other two density treatments it ranged from 70-80%. There was also an effect of time ($F_{14,166.2} = 2.375$, $P = 0.005$), mainly due to fluctuations over the first 2 days of the experiment which subsequently stabilized. However, there was no effect of feeding regime ($F_{1,20.0} = 0.040$, $P = 0.844$).

The mean number of *L. hesperus* spiders per occupied microhabitat was influenced by initial spider density (GLMM on log-transformed response variable: $F_{2,19.8} = 49.433$, $P < 0.0001$), which again was accounted for by the 2 *L. hesperus* spiders initial density treatment that was higher than the other two (Bonferroni-adjusted pairwise comparisons: both $P < 0.0001$). In this treatment group, there were more spiders overall, and each occupied microhabitat held on average 2 individuals (range: 1.8-2.2; Fig. 3.6a), compared to an average ratio closer to unity in the other two density groups (range: 1.1-1.4). The number of spiders per occupied microhabitat in the latter two initial spider density treatments was always >1, indicating that individuals did not settle under all available microhabitats and had a tendency to aggregate. These levels of microhabitat occupancy were generally maintained over the duration of the experiment. There was also an interaction between time and feeding regime on this response variable (feeding regime \times day: $F_{14,169.6} = 2.363$, $P = 0.005$; day: $F_{14,169.6} = 3.156$, $P = 0.0002$; feeding regime: $F_{1,20.9} = 3.866$, $P = 0.063$; Fig. 3.6b). The number of spiders per occupied microhabitat was similar between feeding regimes during the first half of the experiment, but it subsequently diverged due to a decrease in the poorly fed group associated with a

lower spider survival rate (see Fig. 3.2) causing an increase in microhabitat space per capita.

There was a decrease over time in microhabitat occupancy by *Tegenaria* spp. spiders (GLMM: $F_{14,49.7} = 2.870$, $P = 0.003$) due mostly to an increase in mortality from predation by *L. hesperus* spiders, but no difference between feeding regimes ($F_{1,6.0} = 0.126$, $P = 0.735$). The mean number of spiders per occupied microhabitat stayed constant over time (GLMM on log-transformed response variable: $F_{14,52.1} = 0.710$, $P = 0.754$; range: 1.2-1.8) and did not differ between feeding regimes ($F_{1,6.0} = 0.001$, $P = 0.996$).

3.5 Discussion

The results of this study show that the dynamics of cohabitation among *Latrodectus hesperus* spiders are governed by state-dependent interactions. Both factors that were manipulated (prey availability and population density) influenced group-living interactions and had different effects on the variables used to characterize cohabitation dynamics among *L. hesperus* females. Prey availability modified the likelihood of cannibalism, individual foraging success, web-building behaviours and the amount of movement between microhabitats. Population density influenced web building and movement behaviours, and spatial distribution, but had no effect on survival rate and foraging behaviours.

3.5.1 Survival and Cannibalism

Our manipulation of prey availability lead to divergent levels of survival due to cannibalism: food-deprived spiders did not survive as long as those that were kept on a high-food diet, as they succumbed to more cannibalism. The proportion of cannibalism among poorly-fed spiders (21.9%) was much higher than that of well-fed spiders (5.2%), the latter of which is more characteristic of a background level of mortality. These findings agree with previous research in spiders showing that high prey availability reduces the likelihood of cannibalism (Rypstra 1986). Furthermore, larger individuals

usually preyed upon smaller ones in the poorly fed treatment, a pattern that is consistent with previous findings in spiders (Heiling & Herberstein 1999; Buddle et al. 2003) and other arthropods (Elgar & Crespi 1992; Pfennig 1997). Because cohabitation involves interactions between individuals of different size and stature, size asymmetries may increase the chances of a positive outcome for the larger individual. Furthermore, cannibalism may be viewed as a foraging tactic used when less costly alternatives are not offered, which provides nutritious benefits (Mayntz & Toft 2006). Well-fed spiders that shared microhabitats were unlikely to cannibalize each other, even at high densities, because the net payoff of doing so is marginal since their foraging requirements are satisfied. Food deprivation *per se* was not a significant mortality factor, as it only accounted for 1 spider death (3.7%) in the poorly fed treatment, perhaps caused by physiological stress.

We found no evidence of density-dependent cannibalism. There was no difference in the survival rate of spiders kept at high vs. low initial conspecific densities, nor was there any effect of the presence of *Tegenaria* spp. spiders. This is surprising given that a high population density unavoidably increases the frequency of interactions between individuals, which had been shown to cause aggression levels to escalate in territorial animals such as spiders (e.g. Moya-Laraño et al. 2002). In addition, when food is limited, as in our poorly fed treatment, and co-occurring individuals overlap in resource use, density-dependent effects often come into play and influence the outcome of interactions between individuals (Wise 1993). Was our high-density treatment not high enough, preventing us from demonstrating a potential density-dependent mortality effect? Our findings do not support this claim. If we compare the average number of *L. hesperus* spiders per microhabitat measured in the natural population (mean \pm SD = 0.700 ± 1.097) to that of our experimentally low (0.917 ± 0.126) and high (1.667 ± 0.252) conspecific density treatments at the end of the experiment, we find that our high-density manipulation brought at least a two-fold increase in density, while keeping it close to the natural level in the low-density treatment. Since this two-fold increase in density was accompanied by a substantial reduction in microhabitat availability, spiders were kept at high densities throughout.

Similarly, the presence of *Tegenaria* spp. spiders did not modify the rate of cannibalism between *L. hesperus* spiders. Therefore, these spiders do not represent an alternative source of prey that would serve to alleviate some of the pressures leading to cannibalism, as seen between species that show intra-guild predatory interactions (e.g. Wise & Chen 1999; Denno et al. 2004). Despite that, *L. hesperus* spiders preyed upon *Tegenaria* spp. spiders at a higher frequency than on conspecifics, perhaps because of the high mobility of *Tegenaria* spp. spiders, which may have intensified interspecific interference.

3.5.2 Foraging

One postulated reason for the occurrence of cohabitation leading to group living is that the proximity of conspecifics may facilitate prey capture (Whitehouse & Lubin 2005). In web-building spiders this has been shown to occur both directly, via an increase in per capita prey intake rate and average prey size in the case of cooperating spiders (Rypstra & Tirey 1991; Kim et al. 2005), and also indirectly, when the presence of close neighbours enhances prey detection and thus increases the chances of successful prey capture (Uetz 1989).

In our experiment, well-fed *L. hesperus* spiders did not capture more prey or a greater biomass of prey at higher conspecific densities or when sharing a web with another individual. However, and more importantly, an increase in spider density (both in terms of conspecifics and heterospecifics) did not have any negative impact on per capita prey intake rate. Therefore, we found no evidence of competition for prey between spiders kept at high densities (see e.g. Lubin et al. 2001), even though most of them shared webs when living under a same microhabitat. Our data indicate that *L. hesperus* spiders in the high-density treatment did not interfere with each other's prey capture, despite the fact that they were more likely to share microhabitats than to live alone. We did not observe any prey stealing or fights over prey ownership prior to consumption. Furthermore, prey were always caught and consumed by a single spider; there was no prey sharing.

Tegenaria spp. spiders caught few prey compared to *L. hesperus* spiders and, despite their prey-compacting behaviour (pers. obs.), we are confident that we uncovered all of their prey during the experiment. Therefore, this begs the question of whether the presence of *L. hesperus* spiders has any negative effects on their feeding behaviours. The short duration of our experiment does not allow us to form any definite opinion about the nature of the interactions between these species, as spiders can generally withstand long periods of food deprivation (Nakamura 1987). Because most *Tegenaria* spp. webs are built underneath *L. hesperus* webs, the presence of overhanging *L. hesperus* silk may hinder prey capture, although it may also provide protection or enhance foraging success if prey escaping from one type of web contacts an adjacent one. Our future research will investigate in more detail the foraging interactions between *Tegenaria* spp. and *L. hesperus* spiders to determine whether they associate opportunistically or antagonistically.

3.5.3 Web Building

Collectively, our results indicate a reduction in territory (i.e. web) size with increasing spider density, due to web sharing. *Latrodectus hesperus* females shared webs that grew larger over time and eventually covered the whole space available under a microhabitat. Furthermore, there were more spiders per occupied web at high density. At low conspecific density and in the presence of *Tegenaria* spp. spiders, *L. hesperus* webs were smaller than at high conspecific density, but they still covered a large portion of a microhabitat. Some spiders kept at high conspecific density initially built separate webs, but they soon fused their webs with neighbouring ones. A similar pattern was observed in natural settings, where *L. hesperus* spiders built spacious webs occupied by several individuals, even though microhabitat availability was high. This behaviour is reminiscent of some social spiders that associate and form groups by sharing large webs (Avilés 1997). As in social spiders, web ownership and defence is limited in *L. hesperus*, and spiders often change positions on a large shared web or relocate onto neighbouring webs. The results of the natural population survey showed that web size was positively

correlated with microhabitat size, which suggests that spider group size may be constrained by microhabitat size.

Thread density increased with both prey availability and population density, suggesting that spiders invest more energy into silk production and web construction when in the presence of neighbours and when well fed, which has also been shown in a laboratory setting (Salomon 2007). The presence of *Tegenaria* spp. spiders had no effect on the web-building behaviour of *L. hesperus* spiders, partly because *Tegenaria* spp. funnel-sheet webs can fit underneath *L. hesperus* cobwebs, as seen in the natural population.

3.5.4 Movement and Spatial distribution

Latrodectus hesperus females frequently moved between webs and microhabitats over the course of the experiment and web ownership changed because spiders did not maintain and protect a single location. This is unlike the behaviour of a territorial spider (Riechert 1981) or a social spider (Avilés 1997), in which mature individuals would maintain more stable positions to enhance either territory defence or group cohesion, respectively. However, there was an overall decrease in the amount of movement over time, associated with more permanent microhabitat settlement. The duration of a spider's stay in a microhabitat was context-dependent, and was influenced by both prey availability and population density. Well-fed spiders moved less than those that were food-deprived. Furthermore, poorly-fed spiders moved at a greater rate and also further away, abandoning webs and relocating onto either unoccupied or occupied webs. The same was true for spiders kept at high conspecific density compared to those at low density, although the presence of *Tegenaria* spp. spiders did not alter their rate of movement.

This overall movement strategy is consistent with risk-sensitivity foraging, which has been observed in other sedentary spiders (Wagner & Wise 1997; Nakata & Ushimaru 1999; Chmiel et al. 2000). A spider's decision to leave a microhabitat is determined by the balance between the costs of moving (spending energy travelling, increased mortality

risks, building a new web) and the benefits of finding an alternative microhabitat, which may be of better quality and thus provide fitness payoffs. For well-fed spiders, staying at a given location may be an optimal strategy, because it reduces the chance of encountering less favourable microhabitat conditions, while also minimizing the mortality risks and energy expenditures associated with movement (e.g. Lubin et al. 1993). Conversely, under food deprivation, maintaining a high level of movement activity may be the best tactic, because it increases the chance of encountering prey.

Latrodectus hesperus spiders build webs that are energetically costly to produce (Salomon 2007), thus relocation is an expensive strategy because another web has to be built at a new site. This cost may be alleviated if a spider relocates onto an existing web. In the experiment, spiders often relocated onto other webs that were either vacant or occupied by conspecifics. Because spiders often shared webs and thus had a tendency to aggregate, some microhabitats were left unoccupied, suggesting that the presence of neighbours caused them to stay at a microhabitat and allowed them to profit from group living interactions (e.g. economy of silk) or harvest public information about microhabitat quality (Pärt & Doligez 2003). However, joining an unfamiliar web then incorporates a new cost, that of interacting with a potential web occupant, which in some spiders causes web eviction and relocation (Smallwood 1993; Jakob 2004). Spiders kept at high density moved more overall regardless of prey availability, perhaps due to a higher rate of encounter between neighbours causing repeated web and microhabitat shifts. However, the small size of our enclosures and limited number of microhabitats may also have facilitated frequent moves.

3.5.5 Conclusion and Perspective

This study offers new insight into group living interactions among territorial spiders by exploring the dynamic nature of these interactions and the ecological factors that control them. Our findings suggest that *L. hesperus* females form different types of associations depending on the availability of prey and the density of individuals. The longitudinal experimental approach that we used constitutes a reliable method of examining how animals interact and partition resources under different environmental

scenarios. These data invite further investigation on cohabitation dynamics among other territorial animals to clarify the nature of interactions between co-occurring individuals and the conditions that favour the evolution of antagonism vs. tolerance. Our future research will investigate group living dynamics at different times of the year, such as at the height of the reproductive season, to determine how the proximity of conspecifics may affect reproductive decisions.

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Table 3.1. Effect of different predictors on the survival rate of *L. hesperus* spiders, analyzed using the Cox regression method

Source	df	χ^2	P
Whole model	5	14.675	0.012
Feeding regime	1	9.023	0.003
Initial spider density	2	0.327	0.849
Feeding regime × Initial spider density	2	0.715	0.699

Table 3.2. GLMM analyses of the effects of different factors on (a) the daily number of prey captured per capita, and (b) the daily mass of prey captured per capita (log-transformed), by *L. hesperus* spiders

Source	df	F	P
(a) Number of prey captured			
Feeding regime	1, 135.8	118.528	< 0.0001
Initial spider density	2, 133.2	2.522	0.084
Day	14, 178.7	2.039	0.017
Feeding regime × Day	14, 178.7	1.916	0.027
(b) Mass of prey captured			
Feeding regime	1, 122.1	126.037	< 0.0001
Initial spider density	2, 121.1	0.661	0.518
Day	14, 177.3	1.677	0.064
Feeding regime × Day	14, 177.3	1.750	0.050

Figure 3.1. The circular enclosures used in the experiment contained 6 evenly-spaced wooden sheds that served as spider microhabitats

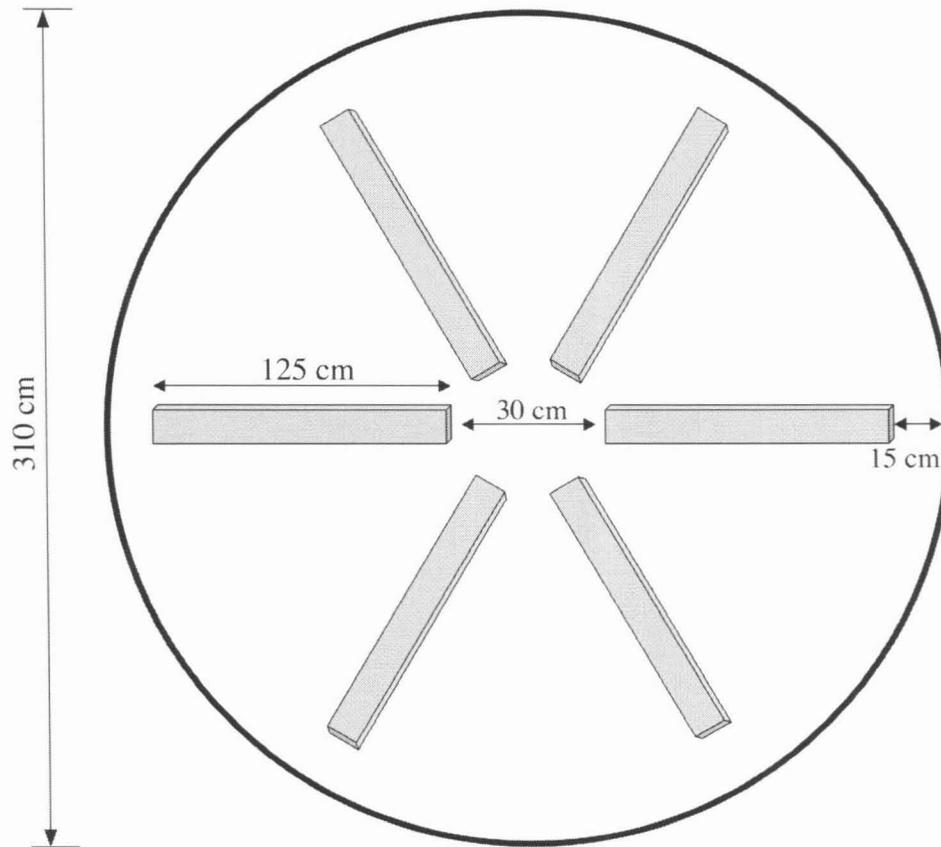


Figure 3.2. Survival rate of *L. hesperus* spiders kept on two different feeding regimes (well fed vs. poorly fed), and 3 different initial spider densities: (a) 1 *L. hesperus* spider per microhabitat; (b) 2 *L. hesperus* spiders per microhabitat; (c) 1 *L. hesperus* + 1 *Tegenaria* spp. spider per microhabitat

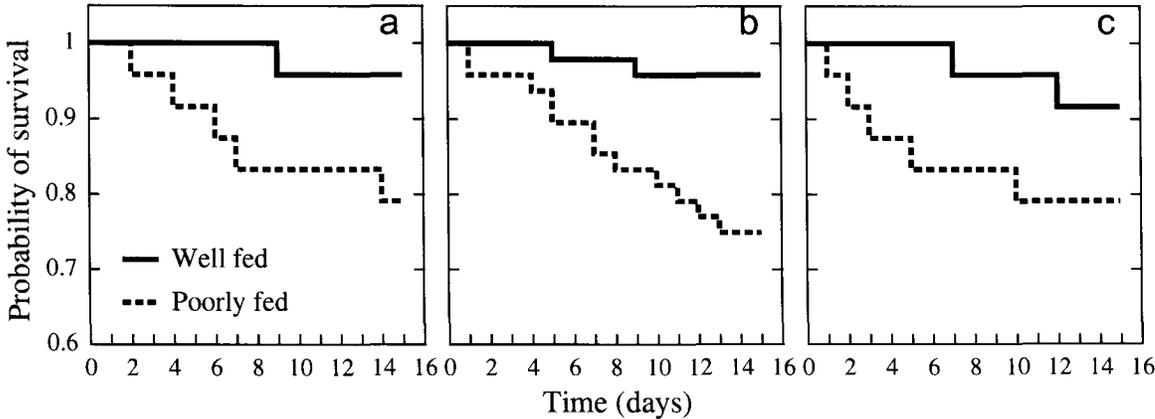


Figure 3.3. Final *L. hesperus* spider density at the end of the experiment (mean number of spiders per microhabitat \pm SD) as a function of feeding regime and initial spider density

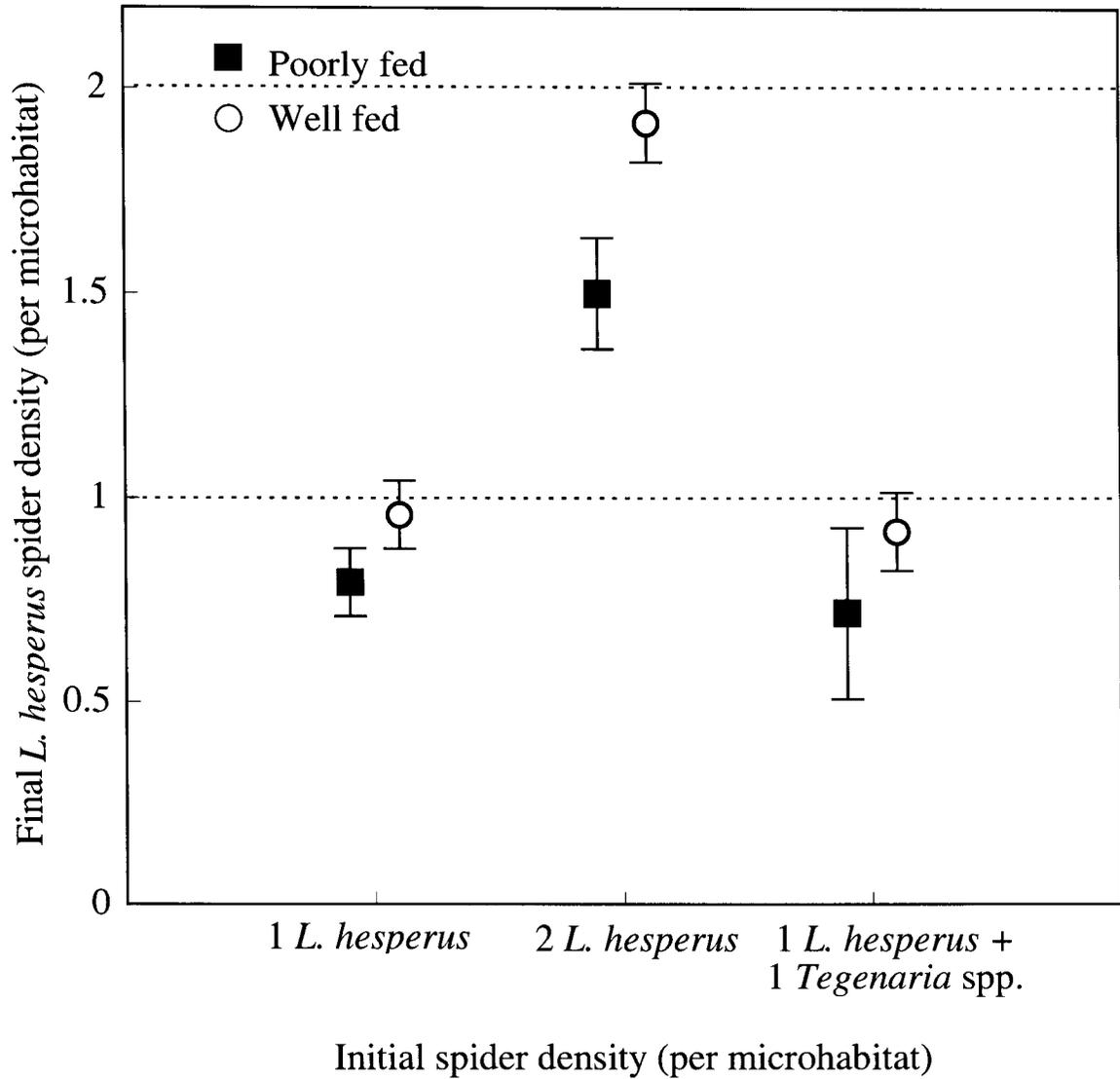


Figure 3.4. Web-building dynamics of *L. hesperus* spiders as a function of initial spider density (number per microhabitat): (a) Mean (\pm SE) number of webs per microhabitat; (b) Mean (\pm SE) area per web; (c) Mean (\pm SE) number of spiders per occupied web. The dotted line in (c) corresponds to the total area under a microhabitat available for web building

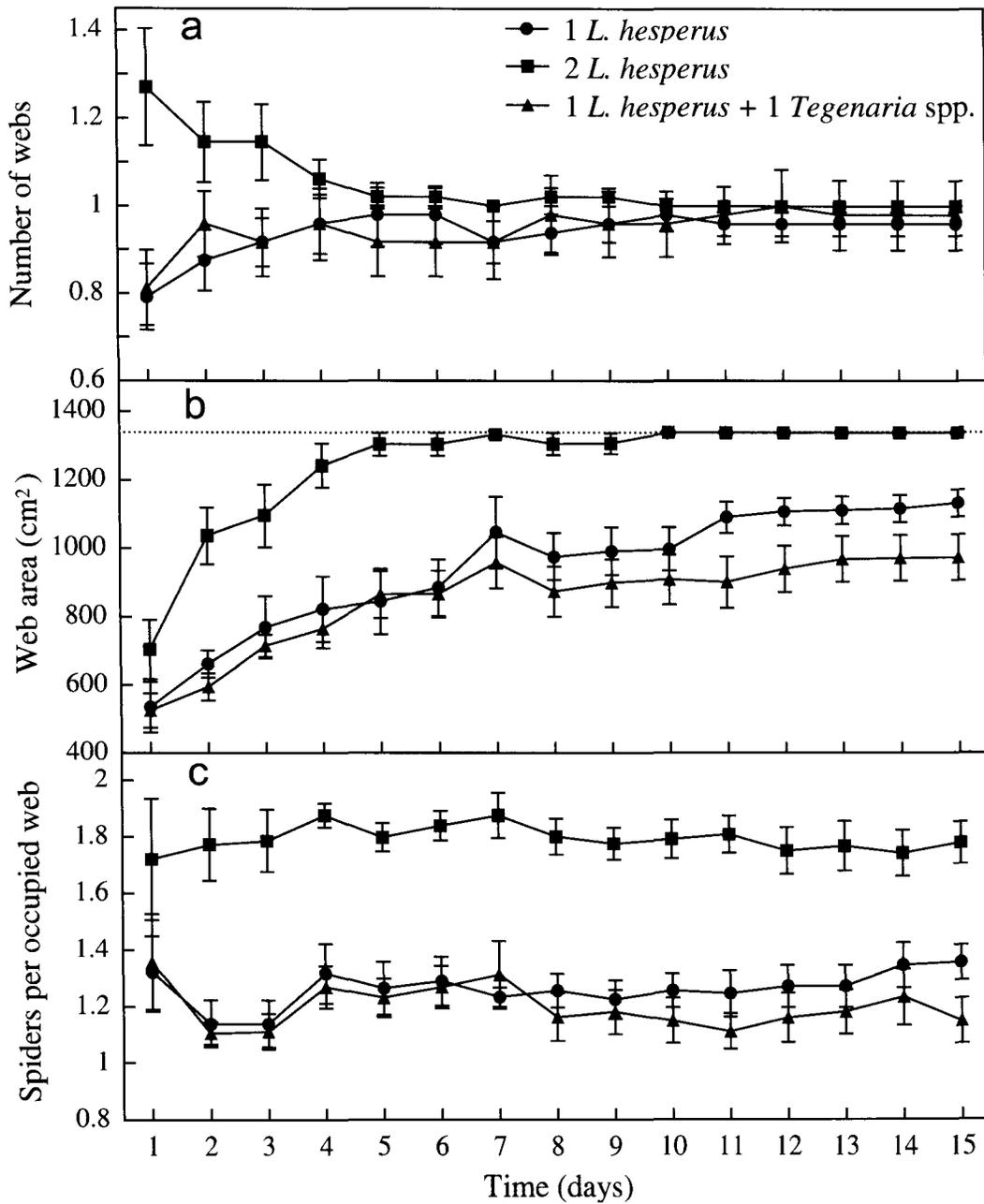


Figure 3.5. Change over time in mean (\pm SE) per capita number of moves by *L. hesperus* spiders kept at 2 different feeding regimes (well fed vs. poorly fed) and 3 different initial spider densities: (a) 1 *L. hesperus* spider per microhabitat; (b) 2 *L. hesperus* spiders per microhabitat; (c) 1 *L. hesperus* and 1 *Tegenaria* spp. spider per microhabitat

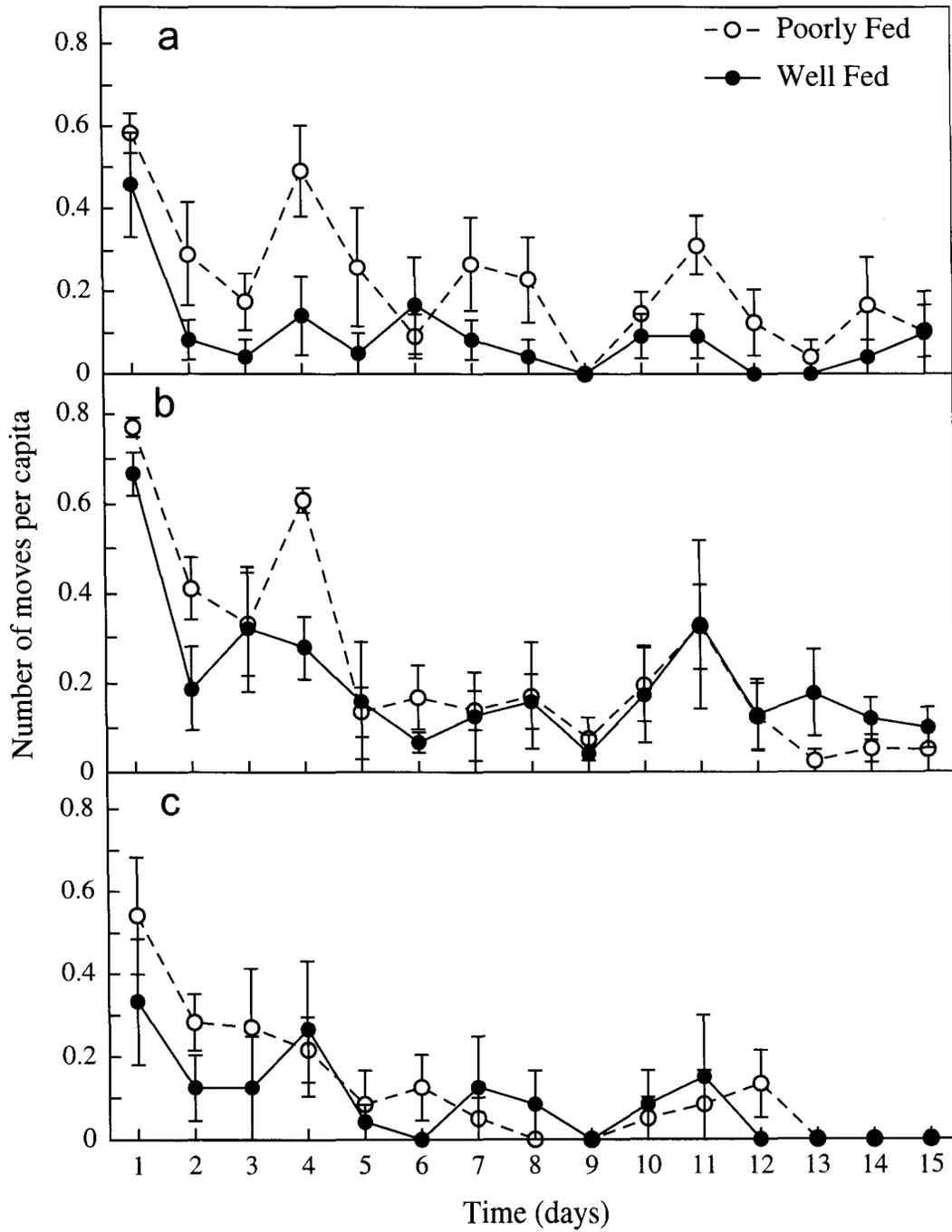
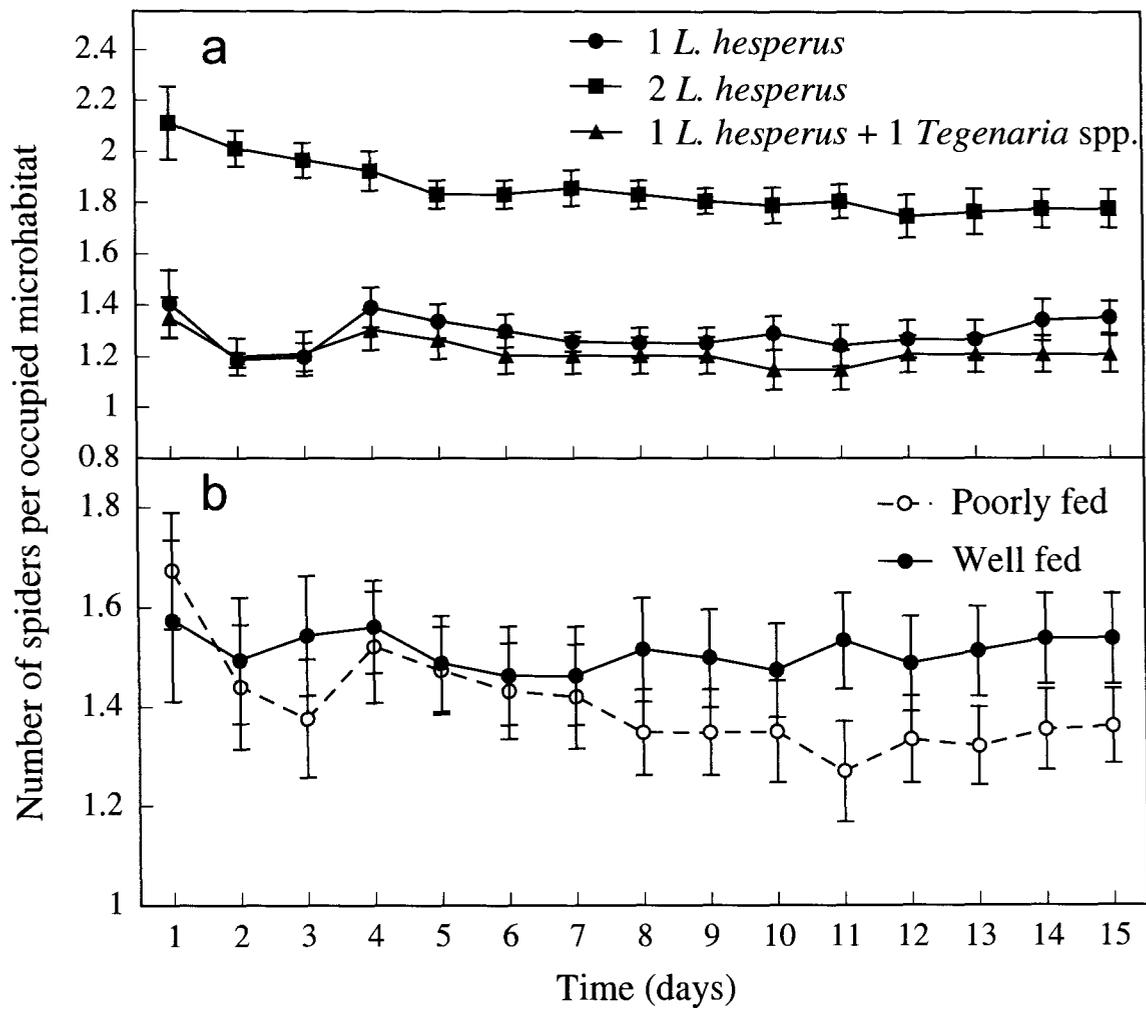


Figure 3.6. Change over time in mean (\pm SE) number of *L. hesperus* spiders per occupied microhabitat across (a) initial spider density treatments, and (b) feeding regimes



**Chapter 4: COMBINED INFLUENCE OF NEIGHBOURS
AND FEEDING STATE ON MOVEMENT DECISIONS
MADE BY A WEB-BUILDING SPIDER**

4.1 Abstract

It is well recognized that feeding rate has a major influence on the amount of movement between microhabitats for many animals. However, the role of other extrinsic and intrinsic factors, and particularly how these factors may interact, is not well understood. This three-part study examines the movement behaviour of a web-building spider, *Latrodectus hesperus*, by assessing microhabitat tenacity in established spiders and by testing how the presence of conspecific neighbours and the combined influence of feeding state (a function of prior feeding experience) and neighbour presence influence microhabitat residence time in unestablished spiders. The results show that naturally established spiders did not leave their microhabitats readily, emphasizing the importance of choosing a profitable location. Unestablished spiders stayed longer in microhabitats occupied by conspecifics than in empty ones, and there was practically no cannibalism even though neighbours shared webs. Furthermore, feeding state and neighbour presence showed an interactive effect on microhabitat residence time. When spiders were housed alone, microhabitat residence time increased with feeding state. However, in the presence of conspecifics, spiders had a low propensity to move, regardless of feeding state. Together, these results demonstrate the combined importance of grouping dynamics and feeding state in shaping movement decisions in a territorial animal. The presence of neighbours may be a source of social information that could facilitate microhabitat exploitation, depending on an individual's feeding state.

4.2 Introduction

An animal can maximize the fitness returns from its habitat by adopting a specific movement strategy to best exploit resources across different microhabitats. Optimality modelling predicts that an individual should leave a microhabitat when its current feeding rate is less than the net benefit of foraging in a different microhabitat (Charnov 1976; Green 1984), and indeed, feeding rate has been shown to affect microhabitat residence

time for a variety of animal taxa (e.g. insects: Bonser et al. 1998; spiders: McNett & Rypstra 1997; fish: Wildhaber et al. 1994; birds: Alonso et al. 1995). However, feeding rate is just one component of fitness that arises from microhabitat exploitation.

A more realistic model would include other factors that may concurrently influence microhabitat residence time, be they intrinsic to an individual (e.g. body condition, foraging behaviour, life history), or ecological (e.g. biotic interactions, habitat structure, climate). However, few empirical studies have explicitly examined the role of such factors in shaping microhabitat residence time (Brown 1988; Nishimura 1991; Miyashita 2005; Stenberg & Persson 2005). Therefore, our understanding of what motivates an individual to move from a given microhabitat is limited. Another important factor to consider is the amount of information available to an individual about its habitat (Dall et al. 2005). An individual's knowledge of future opportunities may be constrained by inadequate habitat sampling or stochastic variation in resource availability (Wildhaber et al. 1994; Beachly et al. 1995). Microhabitat residence time may therefore depend on the state of an individual, such as its feeding state, which is determined by recent foraging history and body condition (Nonacs 2001; Nakata & Ushimaru 1999; Hahn et al. 2006). Likewise, the presence of other microhabitat occupants (neighbours) may contribute to an individual's decision about residence time, either because occupancy provides indirect information about microhabitat quality ('social information'; Danchin et al. 2004; Dall et al. 2005), or because the presence of neighbours *per se* affects individual fitness (e.g. Stamps 1991). Few studies have empirically tested whether grouping dynamics influence microhabitat residence time, and those that have focused mainly on group-foraging and -breeding species (e.g. Livoreil & Giraldeau 1997; Smith et al. 1999; but see Smallwood 1993; Ovadia & zu Dohna 2003; Stenberg & Persson 2005). Furthermore, none has examined the combined influence of grouping and feeding state.

Here, I investigate how both the presence of neighbours and an individual's feeding state affect microhabitat residence time in a territorial web-building spider, the western black widow spider, *Latrodectus hesperus* Chamberlin & Ivie, which is native to western North America (Kaston 1970). Web-building spiders constitute a particularly apt

model system for this study. First, they generally have a sedentary mode of foraging that involves an investment into web building, which renders movement between microhabitats costly and limited (Tanaka 1989; Lubin et al. 1993). Since low mobility precludes accurate microhabitat sampling, spiders may use neighbours as quality indicators. Second, because spiders are able to survive for extended periods without food (Nakamura 1987), the relationship between feeding state and microhabitat residence time is not obvious. Some studies report that movement between microhabitats for feeding purposes is infrequent (Provencher & Riechert 1991), while others find the amount of movement to be inversely correlated with feeding state (Wagner & Wise 1997; Chmiel et al. 2000). Third, the presence of other microhabitat occupants (especially conspecifics) may strongly influence a spider's movement decisions. The large majority of spider species are territorial and cannibalistic (Whitehouse & Lubin 2005); thus, interactions between spiders sharing a microhabitat may cause conflict and result in forced or voluntary microhabitat departure (e.g. Smallwood 1993). Conversely, the proximity of conspecifics may be a source of prey, protection, or public information, promoting longer residence times in occupied microhabitats.

I conducted three separate experiments to determine (1) how likely *L. hesperus* spiders are to move from their microhabitat, (2) how they adjust their movement strategy according to the presence of conspecific neighbours and (3) whether their strategy depends on the combined influence of neighbour presence and feeding state. In the first experiment, I determined the propensity of naturally established females to leave a microhabitat by subjecting them to different regimes of physical disturbance, as this has previously been shown to cause movement in spiders (Chmiel et al. 2000; Nakata & Ushimaru 2004). Given the costs of moving, I predict a high threshold level of relocation following disturbance. In the second experiment, I assessed the influence of previously established conspecifics on microhabitat residence time in a natural setting. If the presence of conspecifics is detrimental, individuals should leave a microhabitat sooner than when living alone, whereas if their presence is correlated with profits, residence times should be longer in occupied sites. In the final experiment, I examined the combined influence of neighbour presence and feeding state on microhabitat residence

time, by testing well-fed and poorly-fed spiders in occupied and unoccupied microhabitats. Here, I predict that spiders will express risk-sensitive behaviours: poorly-fed spiders should be risk-prone and thus inclined to relocate and search for new foraging opportunities if they do not encounter suitable microhabitat conditions, whereas well-fed spiders should be risk averse and remain longer in a microhabitat irrespective of its relative quality, at least on the short term (Caraco & Gillespie 1986). Furthermore, the level of microhabitat occupancy should be used as an indicator of microhabitat quality and thus influence movement decisions, because the presence of neighbours affects the costs or benefits of microhabitat exploitation.

4.3 Experiment 1: Microhabitat Tenacity in Established Spiders

4.3.1 Methods

This field experiment was conducted in late July 2002 in Garry oak meadows of Mt. Maxwell Provincial Park on Salt Spring Island, British Columbia, Canada (48°48' N, 123°31' W, elevation: 280-350 m). These meadows consist of open grassy areas with scattered oak trees and patches of rocky outcrops on which *L. hesperus* spiders commonly build their cobwebs, with silken retreats in the interstices of the rock.

I first conducted a survey of *L. hesperus* webs in a large meadow (area: c. 2500 m²) and recorded which of the webs were occupied and the types of occupants present on them (gender and age class). Sixty webs occupied by single females (some of which had egg sacs) that did not share anchor points with other webs were randomly chosen for the experiment. All females were marked with whiteout paint on their abdomens at night without removing them from their webs, and were given 36 h to recover from handling before the experiment began (none relocated during this time). To examine their movement behaviours, I experimentally damaged cobwebs by repeatedly cutting selected silk threads with scissors. Females and their webs were randomly assigned to one of three experimental groups (N = 20 in each), and manipulations were done every day between 1000 and 1400 hours for 4 consecutive days. In the control group, webs were left intact,

except that I touched a few silk threads on each web with scissors to control for the effects of handling. In the half-web removal group, I cut all the threads in either the upper or lower half of a web (determined randomly) and removed them. In the whole-web removal group, I cut and removed all silk threads of a web. Retreats were left intact, and females were always in their retreats during these manipulations.

For each test subject, I measured the following variables on the first day of the experiment and 24 h after each manipulation: location of the spider and its web, web area, and distance travelled since last census. To determine daily web area, I measured the mean vertical and horizontal lengths of each web and multiplied them. Before each manipulation, the location of a web's boundaries was marked on the substrate with pieces of tape next to the anchor points of the outermost silk threads. As well, I censused each experimental microhabitat during a 1-min period every night between 2230 and 0030 hours to determine the location of each marked female. The day following each manipulation, I recorded whether each female had moved, and if so I searched the environs until I found a newly occupied microhabitat with a cobweb and a marked female. All *L. hesperus* webs immediately surrounding an experimental microhabitat were flagged to facilitate the location of new microhabitats, and determine whether relocating spiders moved onto existing webs. Because so few females relocated (Table 4.1), I was able to find the location of each newly established web.

I used Fisher's exact tests (2-tailed) to compare the proportion of microhabitat relocation between treatment groups during each 24-h period and overall. I also assessed changes in a spider's daily web area (log-transformed measurement) over time using a general linear model (GLM) with day as the within-subject variable, treatment as the between-subject variable, and initial web area as a covariate.

4.3.2 Results

There was no difference in the proportion of microhabitat relocation between treatment groups, neither during each 24-h time interval nor overall (Table 4.1), and the collective daily relocation rate was very low (0-10%). None of the spiders in the

unmanipulated control group relocated. Similarly, the large majority of spiders in the half-web and whole-web removal groups did not relocate their webs, but instead repaired the damage to their webs or built a new web at the same site the night following each manipulation (web construction took place soon after dusk). Egg sac ownership did not affect the overall likelihood of relocation across treatment groups (Cochran-Mantel-Haenszel test: $P = 0.217$). Spiders did not relocate very far, as every individual that moved relocated to a microhabitat that was adjacent to its original location. No individual relocated either onto a conspecific's web (although relocating spiders may have intruded into a conspecific's web and left soon after) or into a microhabitat previously abandoned by another test spider, and none of those that moved twice came back to a former location.

Physical disturbance influenced web-building behaviour: changes in mean daily web area varied significantly across the different treatment groups (treatment \times day: $F_{5,0,140.3} = 3.097$, $P = 0.011$; Fig. 4.1). Web area stayed constant over time in the control and half-web removal groups, but decreased in the whole-web removal group starting on the third day of manipulation. Spiders in the whole-web removal treatment built smaller webs relative to those in the control and half-web removal groups (Bonferroni-adjusted pairwise comparisons: $P = 0.001$, $P = 0.002$, respectively), but there was no difference between the latter two groups ($P = 1.000$).

4.4 Experiment 2: Effect of Neighbours on Microhabitat Residence Time

4.4.1 Methods

This field experiment was conducted in early August 2004 at Cordova Spit, on southern Vancouver Island, British Columbia, Canada ($48^{\circ}35'$ N, $123^{\circ}22'$ W, at sea level). The experimental site was located in a large, open sandy area with interspersed clusters of driftwood logs under which *L. hesperus* commonly build their cobwebs. Females were

collected from logs 1 week before the experiment, kept indoors at $24 \pm 3^\circ\text{C}$ in 15-ml tubes, and fed 1 cricket (*Acheta domesticus*) each on the collection day. Forty-four rectangular wooden sheds used as microhabitats (dimensions: 125 cm length \times 15 cm width \times 8 cm height) were lined up next to each other on the sand, away from any driftwood cluster, at 150-cm intervals along a NW-SE transect. Any vegetation was removed from underneath the sheds, and the sand was levelled off. Sheds were open at both ends and consisted of a removable lid and 2 vertical sides, to which was stapled a roof made of aluminium meshing (mesh size: 2mm; impermeable to females) under which spiders readily attached their webs. This design allowed for the monitoring of spiders present under a shed (the observation unit) by simply opening the lid, without disturbing them or damaging their webs.

Each shed was randomly assigned to 1 of 2 microhabitat occupancy treatment groups (N = 22 per group): (1) alone (the control), or (2) with an established conspecific. Control sheds remained empty until the start of the experiment, whereas in the treatment group, 1 ‘cue’ spider (a *L. hesperus* female) was introduced under each shed 72 h prior to the experiment with 1 cricket as a prey, and allowed to settle and build a web. During this time, all shed openings were closed off with pieces of wood to prevent spiders from leaving. All cue spiders had built a web after 72 h, and all crickets had been consumed and their carcasses removed. Spiders were marked with whiteout paint before introduction for individual identification: cue spiders were marked on the abdomen and test spiders were marked on both front legs. At the end of the 72-h acclimation period at 1400 hours, all pieces of wood covering the openings were removed, the dimensions of cue spiders’ webs were measured, and the experiment was started by introducing 1 *L. hesperus* female under each shed (side of introduction determined randomly). In both treatment groups, test spiders were assigned to a shed on the basis of their size (combined tibia-patella length of the first leg pair) to minimize the size difference between test and cue spiders, which may promote agonistic interactions (Wise 2006). There was no detectable difference in test spider size between treatment groups (t-test: $t_{42} = 0.194$, $P = 0.847$). The experiment ran for 48 h, during which time each shed was checked every 2 h to record whether each spider was still present underneath, the distance between

individuals sharing a shed, and the occurrence of cannibalism. None of the cue spiders left their sheds during the experiment.

For analysis, I compared the proportion of test spiders staying at vs. leaving a microhabitat between treatment groups using Fisher's exact tests (2-tailed), both after 24 h and at the end of the experiment, after 48 h. Next, I used survival analysis (the product-limit Kaplan-Meier method with a log-rank test) to determine whether the presence of neighbours had any effect on the rate of microhabitat departure. Finally, I tested whether microhabitat residence times differed between treatment groups using a Mann-Whitney U test.

4.4.2 Results

In each treatment group, >50% of *L. hesperus* test spiders vacated their microhabitats during the course of the experiment (a few of them were seen under driftwood logs surrounding the experimental site). After 24 h, significantly more control spiders in unoccupied microhabitats had left compared to those that were housed with a conspecific ($P = 0.015$; Table 4.2). The same trend persisted at the end of the 48-h trial, but was not statistically significant ($P = 0.104$).

The level of microhabitat occupancy had a significant effect on the rate of departure ($\chi^2 = 7.127$, d.f. = 1, $P = 0.008$; Fig. 4.2), such that spiders departing from unoccupied microhabitats left sooner relative to those that were housed with a conspecific. The rate at which spiders left from unoccupied microhabitats was constant during the first 16 h, with some individuals leaving during the daytime, whereas in the conspecific group, spiders waited until dusk to vacate their microhabitats (Fig. 4.2). Furthermore, the timing of departures varied across treatment groups: in the control group more than 80% of departing spiders had left by the end of the first night, while a similar proportion left each night in the conspecific treatment (Table 4.2; Fig. 4.2). A comparison of microhabitat residence times between treatments showed a similar difference: spiders introduced under occupied microhabitats stayed longer than control spiders ($P = 0.005$).

All test spiders in the control treatment built some webbing. However, it was not possible to determine whether those in the conspecific treatment had spun any webbing, because cue spiders built webs that spanned 91-100% of the area under a shed before the experiment. This implies that 2 *L. hesperus* females present at a same microhabitat were sharing a web. During cohabitation, neighbours stayed relatively close to each other (mean distance over time \pm SD = 44.214 \pm 10.775 cm; i.e. 28-43% of the length of a microhabitat).

4.5 Experiment 3: Effects of Multiple Factors on Microhabitat Residence Time

4.5.1 Methods

This experiment was done in September in a laboratory setting for practical reasons. The experiment followed a 2 \times 2 factorial design, with 2 feeding states (well fed vs. poorly fed) and 2 microhabitat occupancy levels (alone (the control) vs. with a conspecific spider) as independent factors. Virgin *L. hesperus* females were reared from eggs laid by field-collected females, and were fed fruit flies (*Drosophila melanogaster*) during the first 3 instars and blowflies (*Phaenicia sericata*) thereafter, and kept in large dishes (diameter: 14 cm; height: 2.5 cm). Females matured within 4-6 weeks of the experiment. Spiders were reared, maintained, and experimentally tested at 28°C \pm 2°C, 40 \pm 5% RH, under a reversed 10D: 14L photoperiod (corresponding to September lighting conditions). Upon reaching maturity, 24 *L. hesperus* test females were randomly assigned to each microhabitat occupancy treatment (total N = 48) and marked on the abdomen with whiteout paint. There was no difference in spider size between treatment groups (t-test: $t_{46} = 0.653$, $P = 0.517$). Within each group, half of the females were maintained on a high-food diet and the other half were kept on a low-food diet for 12 days prior to experimental testing, after which they were switched to the opposite diet for an additional 12 days and tested a second time (the order of diets was randomly assigned). Well-fed

spiders were fed 2 blowflies every other day, and poorly-fed spiders were given 1 blowfly every 12 days (i.e. a 7-fold difference in feeding rate). To ensure that spiders in each diet group consumed the same number of prey, any blowfly that had not been caught within 8 h of feeding was presented to the spider until it initiated a standard prey capture sequence leading to consumption. Cue spiders were kept on the same diet as the test spiders.

The experimental microhabitats (i.e. sheds) consisted of 75-cm sections of black PVC tubing (inner diameter: 9 cm) cut in half longitudinally, under which spiders readily built their webs. Autoclaved sand was glued onto the inside walls to provide a rougher lining that increased the adherence of silk threads. The sheds were placed on a 5-cm thick Styrofoam base with black construction paper covering it, which was replaced between trials. Spiders were allowed to exit their sheds, but were prevented from moving to another shed by blind-ended 10-cm extensions made of stiff clear plastic sheeting shaped as half-cylinders which closed off both shed openings. Sheds were washed with laboratory soap and rinsed between trials. A video camera placed above the sheds monitored any spiders that moved from the sheds into one of the plastic extensions, where spiders were visible and their marks recognizable (low-intensity red lights were turned on during the dark phase and full-spectrum white lights were used during the light phase).

In the conspecific treatment, 1 'cue' female marked on one of the front legs was introduced under each shed and allowed to build a web for 72 h before each trial. During this time, both shed openings were closed off with a vertical sheet of plastic that was too slippery for web attachment. Sheds in the control treatment were left empty. All spiders were sized with callipers (tibia-patella length of leg pair I; precision: 0.01 mm), and test spiders were weighed before each trial to the closest 0.1 mg. To decrease the likelihood of cannibalism, test and cue spiders were paired so as to minimize size differences. At the start of each trial, the plastic sheets were removed from the openings, 1 test spider was introduced under a shed (side of introduction determined randomly), and the 2 plastic extensions were fixed onto the openings. Trials began at the onset of the dark phase and

lasted 48 h. Sixteen replicates were tested in each trial (4 from each diet × microhabitat occupancy combination), over a total of 6 trials. Data were gathered from the video footage by recording the time at which a spider first left a shed and its identity (cue vs. test); further movement by test spiders that had exited their sheds was not analysed. After each trial, the sheds were dismantled and checked for cannibalism. Replicates where one occupant had preyed upon the other were excluded from analysis (N = 2), as well as those in which cue spiders spent more than 120 consecutive min outside a shed (N = 2).

To assess differences in spider body condition (i.e. the relationship between weight and size) across treatment groups, I used a GLM with feeding state as within-subject variable, microhabitat occupancy level as between-subject variable, spider weight as the response variable, and spider size as the covariate (both log-transformed). I analysed differences between treatment groups in the proportion of spiders that had left their microhabitats after 24 h and 48 h using (1) McNemar's test to compare between diet groups and (2) Fisher's exact test (2-tailed) to compare between microhabitat occupancy treatments. For each diet group, I compared the rate of microhabitat departure between microhabitat occupancy treatments using the Kaplan-Meier survival analysis with a log-rank test, both during the first 24 h and over the whole 48 h. Finally, I compared microhabitat residence times between microhabitat occupancy treatments using the Mann-Whitney U test, and between diet groups using the Wilcoxon signed-ranks test.

4.5.2 Results

Latrodectus hesperus test spiders were in better condition when well fed than when poorly fed ($F_{1,45} = 6.468$, $P = 0.014$), but there was no detectable difference across microhabitat occupancy treatments ($F_{1,45} = 1.770$, $P = 0.190$, power = 0.356), nor was there an interaction between these two factors ($F_{1,45} = 1.175$, $P = 0.284$, power = 0.286). However, there was an interaction between feeding state and spider size ($F_{1,45} = 8.806$, $P = 0.005$): the slope of the relationship between spider weight and size was steeper when spiders were well fed.

Overall, 35-63% of test spiders vacated their microhabitats during the course of the experiment, and the majority of departures took place at night (>70% in each group). The proportion of microhabitat departures was concurrently determined by microhabitat occupancy level and feeding regime. After 24 h, fewer spiders in unoccupied microhabitats had left when well fed than when poorly fed ($P = 0.021$; Table 4.2), but there was no difference between diet groups for spiders housed with a conspecific ($P = 1.000$). After 48 h, there was no difference across diet groups in both the control ($P = 0.227$) and conspecific treatment ($P = 1.000$). Within each diet group there was no difference between microhabitat occupancy treatments in the proportion of spiders that had vacated their microhabitats after 48 h (both $P > 0.1$). However, after 24 h fewer poorly fed spiders housed with a conspecific had left compared to those in the control group ($P = 0.011$); yet, there was no difference when spiders were well fed ($P = 0.428$).

A graphical representation of the rate of microhabitat departure across treatment groups clearly shows a combined influence of feeding state and microhabitat occupancy (Fig. 4.3). Well-fed spiders displayed equivalent rates of departure whether alone or with a conspecific (Fig. 4.3a), whereas departure rates diverged between treatments when spiders were poorly fed (Fig. 4.3b), as fewer spiders vacated their microhabitats when a conspecific was present than when residing alone. For well-fed spiders, the rate of microhabitat departure did not vary between microhabitat occupancy treatments over 48 h ($\chi^2 = 0.479$, d.f. = 1, $P = 0.489$), but varied marginally among poorly fed spiders ($\chi^2 = 3.716$, d.f. = 1, $P = 0.054$). Likewise, within the first 24 h there was a significant difference between poorly-fed spiders ($\chi^2 = 7.062$, d.f. = 1, $P = 0.008$), but not between well-fed ones ($\chi^2 = 0.892$, d.f. = 1, $P = 0.345$). Feeding state also affected the timing of microhabitat departure (Table 4.2; Fig. 4.3). When poorly fed, most departing spiders in unoccupied microhabitats left during the first night, while a similar proportion of spiders housed with a conspecific left during each night. In contrast, there were no clear differences in the timing of departures among well-fed spiders, although more spiders in occupied microhabitats left on the second night.

Poorly fed spiders stayed longer at microhabitats occupied by conspecifics ($P = 0.026$), but residence time did not vary between well-fed spiders ($P = 0.500$). Feeding state also caused some variation in residence time: in the control treatment, spiders stayed longer at a microhabitat when well fed than when poorly fed ($Z = -2.722$, $P = 0.006$), but there was no difference between diet groups for spiders housed with a conspecific ($Z = -1.007$, $P = 0.314$).

4.6 Discussion

This study provides empirical evidence that the presence of neighbours and individual feeding state concurrently influence movement decisions. The results show that *Latrodectus hesperus* spiders were reluctant to move once established (Exp. 1), and unestablished individuals showed divergent movement tactics depending on the level of microhabitat occupancy (Exp. 2): they delayed relocation in the presence of conspecifics compared to when they were alone. This effect was mediated by a spider's feeding state: poorly fed spiders were prone to adjust their microhabitat residence time according to the presence of conspecifics (Exp. 3), suggesting a feeding state-dependent movement strategy that varies with microhabitat occupancy level.

4.6.1 Movement Behaviour of Established Spiders

The results clearly indicate that, once established, *L. hesperus* females are reluctant to move, even under high levels of disturbance to their webs. It is therefore expected that individuals at the pre-established phase (the context of Experiments 2 and 3) should employ movement strategies that achieve rapid location of profitable microhabitats, because subsequent relocation is unlikely. This lack of movement suggests that the cost of leaving a microhabitat may outweigh the cost of web damage, which may be explained in two ways.

First, moving between microhabitats involves mortality risks, entails the possibility of not encountering another suitable location, and for spiders involves building

a new web (Tanaka 1989; Lubin et al. 1993). In this study, the variable micro-topology of outcrops may limit the availability of suitable sites, and the various vertebrates that visit outcrops (e.g. feral sheep, snakes, birds; pers. obs.) may kill spiders during their travels. Likewise, web building is energetically costly for *L. hesperus* spiders (Salomon 2007), and individuals that relocate their webs do not recycle silk. Consequently, if the high level of tenacity is due to moving costs, the use of social information for microhabitat selection should be of great value as it offsets the need for habitat sampling (Danchin et al. 2004).

Second, key aspects of microhabitat quality, such as microhabitat structure or prey capture rate, may compensate for the cost of web repair and delay relocation (e.g. Hodge 1987; Chmiel et al. 2000). Because all females rebuilt a web after each manipulation, microhabitat quality may have been high enough to warrant the repeated investment into a web, even under high disturbance when spiders spun smaller webs (Fig. 4.1). Overall, the balance between the costs and benefits of remaining in a microhabitat depends on a combination of factors, such as feeding state and neighbour presence.

4.6.2 Microhabitat Residence Time in the Presence of Neighbours

The most significant finding from this field experiment is the longer residence time of *L. hesperus* females in microhabitats occupied by established conspecifics and their webs. Females introduced into occupied microhabitats stayed longer and had lower departure rates than those placed into unoccupied microhabitats (Fig. 4.2). Furthermore, most females (80.9%) leaving unoccupied microhabitats did so within the first 24 h, while only 58.3% of outgoing females housed with a conspecific left during this time. This suggests that microhabitat occupancy may be an indicator of good prospects to incoming individuals, causing them to prolong their stay and eventually settle in occupied microhabitats. The presence of established conspecifics in a microhabitat may provide accessible ‘public’ information about resource quality, which in turn may favour longer assessment times in occupied microhabitats and hence longer residence times, and thus increase the efficiency of site assessment (Smith et al. 1999; Dall et al. 2005). This type of information may be particularly useful for non-omniscient foragers such as *L. hesperus*

spiders. Furthermore, sharing a microhabitat with one or more conspecifics may be beneficial overall and promote group living (Krause & Ruxton 2002). For instance, living in a group may decrease per capita predation risk due to the 3-dimensional nature of *L. hesperus* cobwebs, provide access to more or better prey through the enhanced prey capture potential procured by clustering (see Chapter 6), or permit an economy of silk through partial or full web sharing (see also Whitehouse & Lubin 2005). This last point may be particularly important for *L. hesperus* spiders, because physical disturbance causes a reduction in web-building investment (see Fig. 4.1).

Inter-individual interactions are a leading cause of mortality and reduced fitness in territorial animals such as web-building spiders (Wise 2006). Despite the close proximity between *L. hesperus* females that shared microhabitats, no cannibalism took place and only 54.5% of spiders abandoned their microhabitats. Furthermore, previously-established females colonized almost all available space, forcing incoming spiders to share their web or add onto it, which has been shown to promote agonistic interactions and relocation (Hodge & Uetz 1995; Bilde & Lubin 2001). I controlled for major differences in body size, which may have influenced the likelihood of aggression and movement between microhabitats (Wise 2006). The context in which females were tested in this experiment favoured the expression of tolerance towards neighbouring conspecifics and longer residence times in occupied microhabitats. Therefore, the benefits of sharing a web or microhabitat with a conspecific (e.g. energy savings, information acquisition) may have outweighed the costs of partitioning a common resource (e.g. interference competition).

Why did spiders leave unoccupied microhabitats, considering that they had access to all available resources? One possible reason for leaving an unoccupied microhabitat is an animal's inherent tendency to move before establishment to sample various locations and only to exhibit site fidelity once established (as shown in Exp. 1). However, the finding that *L. hesperus* females kept with conspecifics displayed low rates of microhabitat relocation conflicts with this explanation. Instead, it appears that unestablished females are quite mobile unless they encounter specific microhabitat

conditions, such as other occupants and their webs. Furthermore, since most females left unoccupied microhabitats within 24 h, they had not yet built much webbing; hence, the cost of leaving (lost silk investment; Tanaka 1989) was probably small.

4.6.3 Combined Influence of Feeding State and Neighbours on Microhabitat Residence Time

As predicted by optimal foraging models (Janetos 1982; Nonacs 2001) and supported by other empirical data (Nakata & Ushimaru 1999; Jakob 2004; Hahn et al. 2006), the results of this experiment show that feeding state is positively correlated with overall microhabitat residence time. However, this effect was only apparent when spiders were housed alone. Furthermore, the rate and timing of microhabitat departures varied with microhabitat occupancy level: poorly fed spiders housed with conspecifics had lower departure rates and left later compared to those in unoccupied microhabitats. These results suggest that microhabitat residence time in *L. hesperus* is determined by the interaction between feeding state and microhabitat occupancy.

Why might feeding state affect microhabitat residence time? For a well-fed spider, remaining longer in a given microhabitat may be beneficial; firstly, because finding different or more resources may not be immediately required for sustenance (Nakamura 1987), and second, because moving is a costly endeavour (Lubin et al. 1993). Conversely, for a poorly fed individual that has a more pressing need to forage, the optimal decision may be to relocate rapidly or at a higher rate, because greater movement activity increases the likelihood of finding exploitable resources (Krebs & Kacelnik 1991). Furthermore, individuals in good condition, such as well-fed *L. hesperus* females, may be better able to afford a longer stay in a microhabitat to retrieve more information about it, while those in a poorer condition may have to make a rapid assessment of microhabitat quality before deciding whether to stay or leave. The movement behaviour of poorly fed spiders (Fig. 4.3a) was similar to that of spiders tested in the field (Fig. 4.2), suggesting that spiders in both situations may have experienced comparable levels of food limitation.

Why was there no effect of feeding state on movement behaviour when spiders were housed with conspecifics? A likely explanation invokes the informational value of resident conspecifics. The presence of established spiders and their webs may be used to assess microhabitat suitability because they are highly noticeable features (Danchin et al. 2004), which would thus reduce the overall influence of feeding state on movement decisions. Their presence could indicate that a location is favourable or worthy of further investigation, which is expected to favour longer residence times in occupied microhabitats irrespective of feeding state, as was observed in this study (Fig. 4.3). Another possibility is that neighbours may represent an alternative source of food (e.g. Wagner & Wise 1997), which would also lead to longer residence times in occupied microhabitats. However, this latter explanation is unlikely since there were very few instances of cannibalism (4.2%) and, if other microhabitat occupants were mainly perceived as prey, residence time in occupied sites would have been longer for poorly fed spiders who were likely experiencing a higher degree of hunger. Furthermore, because web ownership often determines the outcome of behavioural interactions between spiders (Hodge & Uetz 1995), incoming spiders would be at a disadvantage. An alternative explanation would be that most poorly-fed spiders have limited energy reserves available for web construction and can only afford to join the web of an established conspecific, whereas well-fed individuals can either build a new web or join an existing one. Despite the lack of an effect of feeding state on movement decisions in the presence of conspecifics at the time scale used in this experiment, it should be noted that state-dependent decisions may come into play after the initial microhabitat settlement phase. Further research will determine how this applies to *L. hesperus*.

4.6.4 Conclusion

The evidence put forward in this study indicates that a web-building animal, such as *L. hesperus*, may employ a movement strategy contingent on both its encounters with other co-occurring conspecifics within a habitat and its feeding state. By adjusting its level of activity according to both the proximity of neighbours and its feeding state, an individual can allocate its foraging and reproductive efforts effectively so as to maximize the net fitness returns from a habitat. It would be interesting to test whether such

movement strategies account for the patterns of habitat usage observed in natural communities. More generally, this study highlights the importance of using an experimental approach that considers the role of multiple factors on an animal's movement behaviour, without solely focusing on well-established ones, such as feeding rate.

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Table 4.1. Microhabitat tenacity of established *L. hesperus* females during a 5-day experiment. Manipulations were done on days 1-4. Values represent: number that left / number that stayed (percentage leaving)

	Treatment group		
	Unmanipulated	Half web removed	Whole web removed
Day 2	0/20 (0%)	0/20 (0%)	1/19 (5%)
Day 3	0/20 (0%)	0/20 (0%)	2/18 (10%)
Day 4	0/20 (0%)	1/19 (5%)	2/18 (10%)
Day 5	0/20 (0%)	1/19 (5%)	1/19 (5%)
Overall	0/20 (0%)	2/18 (10%) ^a	4/16 (20%) ^b

All pairwise comparisons of the proportion of spiders staying vs. leaving between treatment groups at each 24-h interval and overall were non-significant (all $P > 0.1$)

^a 2 different spiders relocated; ^b 2 spiders moved once each, and 2 other spiders moved twice on 2 consecutive nights

Table 4.2. Number of spiders in each treatment group that left their microhabitats during the first 24 h and over the whole 48 h, in Experiments 2 and 3. Values represent: number that left / number that stayed (percentage leaving)

	Microhabitat occupancy level	
	Alone (control)	With a conspecific
Experiment 2:		
0-24 h	16/6 (72.7%)	7/15 (31.8%)
0-48 h	18/4 (81.8%)	12/10 (54.6%)
Experiment 3:		
Poorly fed spiders		
0-24 h	13/11 (54.2%)	3/17 (15%)
0-48 h	15/9 (62.5%)	8/12 (40%)
Well fed spiders		
0-24 h	5/19 (20.8%)	2/16 (10%)
0-48 h	11/13 (45.8%)	7/13 (35%)

Figure 4.1. Mean daily web area (\pm SE) of established *L. hesperus* females whose webs were either left untouched or manipulated in one of two ways (N = 20 per group). Manipulations were implemented on days 1-4

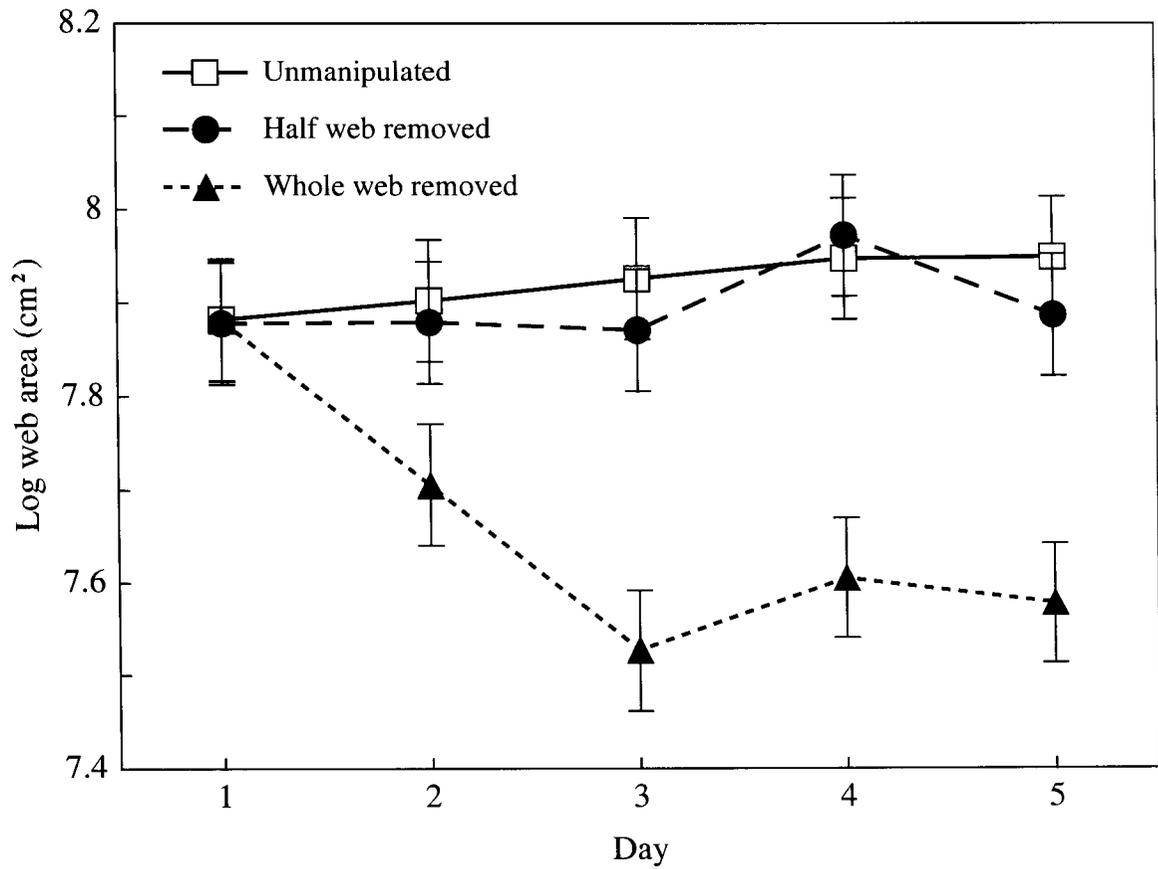


Figure 4.2. Rate of microhabitat departure of *L. hesperus* spiders tested in a field experiment. Each line corresponds to a different microhabitat occupancy treatment: alone (N = 22), or with a conspecific spider (N = 22)

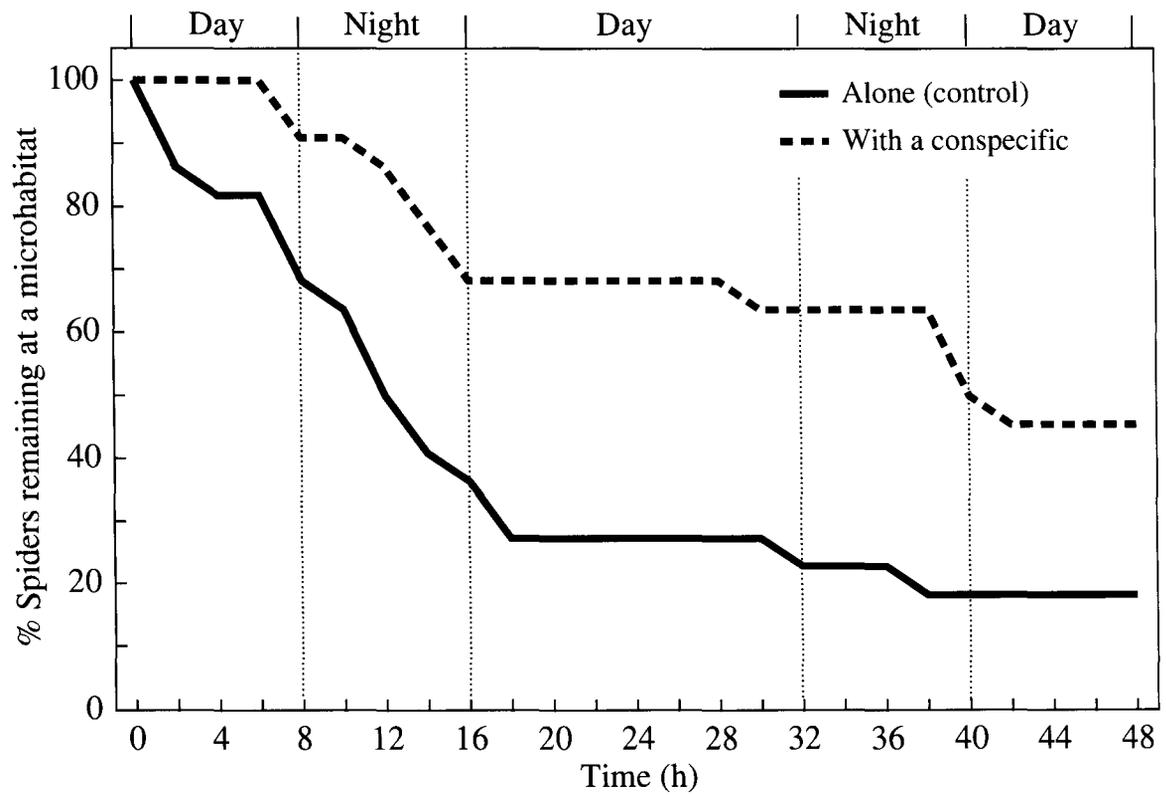
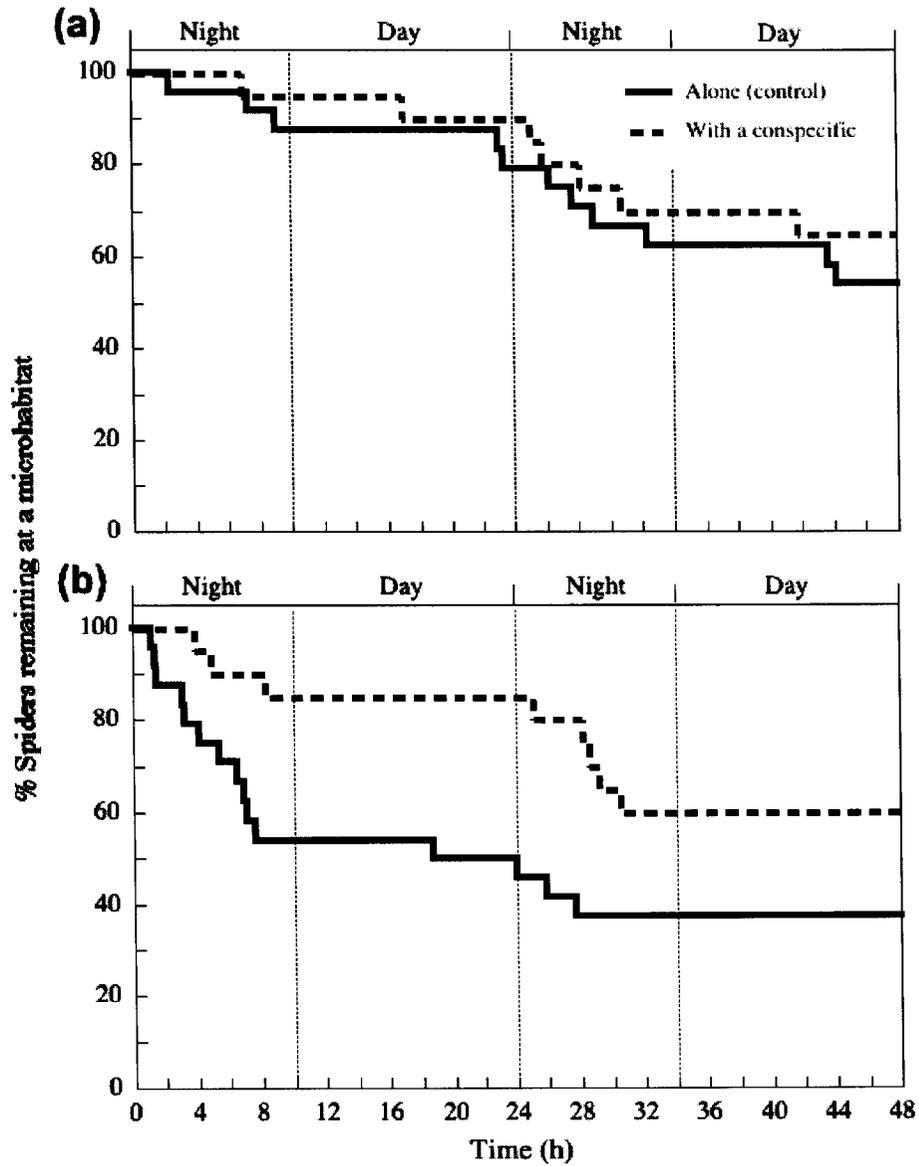


Figure 4.3. Rate of microhabitat departure by *L. hesperus* spiders tested in a laboratory experiment. Spiders were maintained on two different diets (well fed vs. poorly fed) and tested at one of two microhabitat occupancy levels (alone (N = 24), or with a conspecific spider (N = 20)). Each graph corresponds to a different diet group: (a) well fed, (b) poorly fed



Chapter 5: **WESTERN BLACK WIDOW SPIDERS EXPRESS
STATE-DEPENDENT WEB-BUILDING STRATEGIES
TAILORED TO THE PRESENCE OF NEIGHBOURS ***

* A version of this study appears as: **Salomon, M.** 2007. Western black widow spiders express state-dependent web-building strategies tailored to the presence of neighbours. *Animal Behaviour*, **73**, 865-875. Reprinted with permission from the Association for the Study of Animal Behaviour.

5.1 Abstract

Web-building spiders are territorial animals whose webs serve several purposes including foraging, reproduction and protection. Two factors are predicted to be of primary importance in determining a spider's web-building strategy: (1) current nutritional state (a function of prior feeding rate), which determines the net value of a web, and (2) the presence of co-occurring spiders with whom it may have to interact and partition resources. I conducted a laboratory experiment to test whether western black widow spiders, *Latrodectus hesperus*, express state-dependent web-building strategies that vary with the presence of conspecific or heterospecific (*Tegenaria agrestis* and *T. duellica*) spiders in a microhabitat. I maintained *L. hesperus* females on two different diets (high- versus low-food) and tested their web-building behaviour in the presence or absence of neighbours. When sharing a microhabitat with con- or heterospecific spiders, *L. hesperus* increased their web-building investment by producing higher-density webs containing more silk and by initiating web-building sooner. Web building was further influenced by nutritional state, such that well-fed spiders produced more silk and built denser webs than their poorly fed counterparts. Furthermore, microhabitat occupancy level and nutritional state showed a combined effect on the different components of web-building behaviour in *L. hesperus*. I discuss how this behavioural plasticity might optimize microhabitat settlement investments in the context of constraints on web-building activities imposed by nutritional state and cohabitation.

Keywords: behavioural plasticity; cohabitation; foraging; habitat selection; *Latrodectus hesperus*; spider web; state-dependent behaviour; trade-offs; web building; western black widow spider

5.2 Introduction

Behaviours involved in the discrimination and usage of habitat components are fundamental attributes of an animal's ecological niche. Habitats are often spatially

and temporally heterogeneous, so it is essential that an animal select a suitable microhabitat in which to settle. In fact, this choice can have a major effect on several factors involved in determining an individual's fitness, such as energy uptake, biotic interactions and reproductive output (Stamps 2001). The ability to distinguish and select among different microhabitats is contingent on the use of specific cues that provide information about the potential costs and benefits of a particular location, such as resource availability or the presence of other occupants. Use of such cues allows individuals to decide how much time and energy to invest when settling into a microhabitat. Assuming that individuals seek to maximize their fitness returns from residing in a microhabitat, they should also adjust settlement investments according to their current condition; an individual's condition may constrain the duration or intensity of its activities during the establishment process or influence its motivation to perform these activities (Carriere & Roitberg 1996; Cuthill & Houston 1997; Bilde et al. 2002). Settlement strategies should therefore reflect an integration of perceived microhabitat suitability and an individual's condition.

Web-building spiders are useful model organisms with which to investigate settlement decisions, because the structural properties of their webs provide a convenient measure of their investment into a microhabitat over a particular time period.

Many environmental factors influence web building, and by extension web structure, such as prey availability (e.g. Pasquet et al. 1994), prey type (Sandoval 1994; Schneider & Vollrath 1998), the nature of the substrate for web attachment (McNett & Rypstra 2000), temperature (Barghusen et al. 1997) and predation pressure (Li & Lee 2004; Gonzaga & Vasconcellos-Neto 2005). The presence of other microhabitat occupants may also affect a spider's web-building decisions. Incoming individuals may use the webs of resident spiders as anchor points or support threads, thus permitting an economy of silk (Lloyd & Elgar 1997; Jakob 1991), and, in some cases, enhancing prey detection and capture (Uetz 1989). However, sharing a microhabitat with other spiders may depress resource availability and cause territorial disputes involving agonistic behaviours, leading to web eviction or even cannibalism (e.g. Samu et al. 1996). The

presence of neighbours may thus serve as an indicator of net microhabitat profitability, and thereby greatly influence a spider's web-building investment (e.g. Schuck-Paim & Alonso 2001). Few studies have investigated whether the proximity of conspecifics has any effect on a spider's web-building behaviour, and those that have showed contrasting results: some failed to detect a relation between these two variables (Jakob et al. 1998; Thévenard et al. 2004), while others indicated that individuals living in aggregations with conspecifics modified web size or position, relative to those living in isolation (Leborgne & Pasquet 1987; Herberstein 1998; Harwood & Obrycki 2005). Furthermore, no study to date has explicitly examined the effect of sharing a microhabitat with other co-occurring web-building species on web construction. The balance between the costs and benefits of microhabitat sharing may vary depending on neighbour type. For example, conspecifics have overlapping foraging requirements that would cause them to be competitors, while heterospecifics may instead form predator-prey relationships.

Intrinsic individual parameters also influence web-building behaviour, such as foraging experience (Heiling & Herberstein 1999; Venner et al. 2000; Segoli et al. 2004), age (Opell 1990; Lubin & Kotzman 1991), size (Sherman 1994; Venner et al. 2003), mobility (Nakata & Ushimaru 2004) and nutritional state (Riechert 1981; Lubin & Henschel 1996; Pasquet et al. 1999; Watanabe 2000; Blackledge & Wenzel 2001). A spider's nutritional state (i.e. its energy level, which is a function of prior feeding rate) is of particular interest, because it is one of the major determinants of body condition. For example, well-fed spiders with large energy reserves reduce their web-building efforts or even refrain from this activity altogether, whereas individuals with low reserves allocate more energy into web construction because of increased hunger, often resulting in larger webs or greater thread densities (e.g. Lubin & Henschel 1996). Such behavioural plasticity is adaptive in cases in which the marginal value of a web varies according to a spider's nutritional state. However, certain types of webs involve significant building costs (Ford 1977; Prestwich 1977; Tanaka 1989), so a spider may be constrained in its ability to behave adaptively. Moreover, spider webs may serve several purposes, in which case the relation between nutritional state and web-building effort is not always clear.

I investigated microhabitat settlement strategies in the western black widow spider, *Latrodectus hesperus*, which builds spatially and temporally persistent cobwebs used concurrently for prey capture, protection and reproduction (personal observation). In particular, I examined the combined influence of nutritional state and the presence of neighbours on web-building behaviour. Because web building is a costly activity, an individual's investment into web construction is expected to be correlated with its nutritional state. Furthermore, if the presence or absence of established spiders in a microhabitat is perceived by *L. hesperus* as a critical indicator of its future fitness in that site, incoming individuals may adopt specific web building tactics that allow them to profit maximally from potential interactions with neighbours. To test the hypothesis that web-building strategies in *L. hesperus* depend on nutritional state and the presence of neighbours, I designed a laboratory experiment that examined whether females (1) showed state-dependent web-building strategies and (2) whether these strategies were affected by the presence of other microhabitat occupants (con- versus heterospecific spiders). I maintained individuals under two feeding regimes (high or low), introduced them into novel microhabitats that varied in their level of occupancy and the species of the occupants, and measured their subsequent investments into web construction (i.e. silk production, web architecture, weight loss and extent of building activity). I extend previous findings on state-dependent web-building strategies in spiders by characterizing the specific influence of neighbours in shaping web-building behaviours in *L. hesperus*, considering both con- and heterospecifics, and provide some insight into the ecology of cohabitation.

5.3 Materials and Methods

5.3.1 Study Organisms

Latrodectus hesperus Chamberlin & Ivie (Araneae: Theridiidae) is an orbicularian cobweb weaver found in dry habitats of western North America, from Mexico to southern Canada (Kaston 1970). Females build large, three dimensional webs close to the ground under pieces of wood or rocks, in rodent burrows or on rocky outcrops. These structurally

complex webs are composed of a main tangled component in the centre, attached to the substrate on all sides by long radiating anchor threads. Threads anchored to the ground are supplemented with viscid glue droplets, and serve as prey capture devices ('gumfooted lines'; see Benjamin & Zschokke 2003). These intricate webs are built over several nights and are used to intercept ground-active arthropods (M. Salomon & S. Vibert, unpublished data). Unlike some orbicularian spiders, *L. hesperus* females do not recycle and usually do not replace their webs, but instead repair or expand them as necessary. Cobwebs are thus enduring structures, on which adult spiders remain to forage and reproduce. Coastal British Columbia populations of *L. hesperus* often co-occur with two abundant nonorbicularian web building species: *Tegenaria agrestis* Walckenaer, the hobo spider, and *T. duellica* Simon, the giant house spider (Araneae: Agelenidae). These non-native spiders build funnel-webs close to the ground on the underside of objects. In areas where all three species co-occur, cobwebs and funnel-webs are often found in close proximity or in contact with one another (personal observation). In particular, *L. hesperus* cobwebs may share frame threads and even form complexes of interconnected individual webs. While all three species are cannibalistic, *L. hesperus* is the top predator that preys upon individuals of both *Tegenaria* species.

5.3.2 Spider Collection and Rearing

For this experiment, *L. hesperus* females were reared from egg sacs produced in the laboratory by 17 mated adult females collected from a beach close to Cordova Spit, Saanichton, on Vancouver Island, British Columbia, Canada. All egg sacs produced (2-4 per female) were individually transferred to new dishes to allow spiderlings to emerge in isolation from their mothers. Upon hatching, spiderlings were kept together and fed *Drosophila melanogaster* prey ad libitum. After their third or fourth moult, surviving spiderlings were housed individually and fed one blow fly (*Phaenicia sericata*) twice weekly. Once females reached the penultimate stage, they were fed four blow flies per week until their final moult to maturity, after which they were fed according to the experimental diets described below (see Feeding Regimes).

Adult female *T. agrestis* and *T. duellica* were collected from the same field location, kept in Plexiglas cages (14 × 14 × 14 cm) and fed twice weekly with blow flies. For the purpose of this experiment, *T. duellica* and *T. agrestis* were used indiscriminately because they form similar associations with *L. hesperus*. Where all three species co-occur, field observations suggest that both species build structurally undistinguishable funnel-webs in similar locations and that adult females of either *Tegenaria* species are found during the period when female adult *L. hesperus* are most active (May-October; M. Salomon & S. Vibert, unpublished data). All spiders were maintained on a reversed 16:8 h light:dark cycle at $29 \pm 1^\circ\text{C}$ and $40 \pm 5\%$ RH.

5.3.3 Feeding Regimes

To determine whether nutritional state influences web building behaviour in *L. hesperus*, I randomly assigned adult virgin females to one of two feeding regimes: high or low food. Females on the low-food diet (N = 36) received one blow fly every 12 days and those on the high-food diet (N = 33) received two blow flies every other day (mean blow fly weight \pm SE = 30.797 ± 1.258 mg, N = 112). Thus, there was a seven-fold difference in feeding rate between diet groups; spiders on the high-food diet were close to satiation, whereas those on the low-food diet were food limited but not starving. All spiders were provided with water ad libitum. Prey were placed directly onto the spiders' webs to be consumed. I verified that all spiders had captured their prey items within 6 h; any prey that was still alive was grasped with tweezers and carefully presented to the spider until it started to wrap it in silk. Prey wrapping always led to prey capture and consumption. Spiders were maintained for 3 weeks on one of the feeding regimes before initial testing. Experimental trials using poorly fed spiders were run 12 days postfeeding and those using well-fed spiders were run 1 day postfeeding. There was no significant difference in size between spiders from the two feeding regimes (mean \pm SD tibiapatellar length for the first pair of legs: well fed: 6.461 ± 0.371 mm; poorly fed: 6.426 ± 0.433 mm; Student's t test: $t_{67} = -0.366$, $P = 0.716$). All spiders used as cues in the experiment (both *Tegenaria* spp. and *L. hesperus*; see Experimental trials) were well fed (i.e. two blow flies every second day) except when in the experimental units. Some test spiders within each diet group shared the same mother, but all spiders were from different egg

sacs. *Latrodectus hesperus* test and cue spiders housed together in an experimental unit (see Experimental trials) always had different mothers.

5.3.4 Experimental Procedure

5.3.4.1 Apparatus

Each experimental unit consisted of a 75-cm-long section of black PVC tubing (inner diameter: 9 cm) cut in half longitudinally, and divided into three chambers (length: 25 cm) by means of rigid metal meshing (mesh size: 2 mm). Each unit thus had one central chamber surrounded by two side chambers. The meshing prevented spiders from moving between chambers, while still allowing spiders to reach inside and contact any silk webbing or individuals present in the adjacent chambers. The sides and base of the half-tubes were closed off with black synthetic meshing, and construction paper was fitted onto the inside walls of each chamber to provide a rough surface for web attachment (I used black paper to achieve contrast with the silk). To allow monitoring of web-building behaviours, the experimental units were placed on railings at eye level and all observations were taken from below, through the synthetic meshing covering the base. Preliminary trials confirmed that spiders readily settled and built webs in these chambers, which I was able to observe.

5.3.4.2 Experimental trials

To investigate web-building behaviours in *L. hesperus*, I conducted a 2×3 factorial experiment testing the relative influence of microhabitat occupancy and nutritional state. Test spiders kept on one of the two diets were introduced into the central chambers of PVC units whose adjoining chambers were either: (1) empty (control treatment), (2) occupied by one female conspecific, or (3) occupied by one female *Tegenaria* spider. Each spider was used three times, once for each occupancy treatment, and the order of treatments was randomly chosen for each spider. Consecutive trials using the same spider were separated by at least 12 days, during which time the test spider was kept on its original web in the feeding dish. ‘Cue’ spiders were introduced to the side

chambers 5 days before a trial to allow settlement and the construction of a web, which I humidified every 2 days by spraying water through the meshing. These spiders were only used once. Furthermore, I used only those experimental units in which cue spiders had established a web in both of the side chambers, and whose silk threads were anchored to the metal partition separating them from the middle chamber. Test spiders were introduced into the units at 1200 hours, corresponding to the beginning of the dark cycle when they are most active, and allowed to settle and lay silk for 24 h. Trials were run under the same lighting, temperature and humidity conditions as for rearing (see Spider collection and rearing). Spiders were not fed while kept in the experimental units, to avoid the potentially confounding effects of prey presence on their web-building behaviours.

To establish a baseline value of weight loss for both well fed and poorly fed *L. hesperus* females, laboratory-reared adult females were individually housed in petri dishes for 25 days and their body weight was compared on two consecutive days (days 25 and 26). Twenty-nine females were tested under each of the two feeding regimes outlined above (see Feeding regimes), for a total of 58 spiders. There was no significant difference in spider size between the two groups (Student's *t* test; $t_{56} = -0.163$, $P = 0.871$). Spiders were placed inside new dishes and allowed to settle and build a web (humidified every second day) for 25 days. On day 25, I delicately removed spiders from their webs and weighed them to the nearest 0.1 mg, placed them back onto their webs for 24 h and reweighed them. In these dishes, *L. hesperus* females usually attach most of their webbing to the underside of the lid and build only a few gumfooted lines, which they anchor to the bottom. To minimize web damage, I used only those females that had built most of their web on the underside of a lid; thus, when removing spiders for weighing purposes, most if not all of their webs stayed intact, owing to the extensibility and high tensile strength of their capture threads (Blackledge et al. 2005). Spiders generally did not lay any silk within 2 h of the first weighing. Changes in weight result from either losses due to movement and metabolic maintenance or gains due to fluid absorption.

5.3.5 Data Recording

5.3.5.1 Web-building activity

To assess differences between treatments in spiders' time to onset of web construction, I conducted hourly observations during the entire dark phase of the experiment and the first 2 h of the light phase. Preliminary trials confirmed that spiders laid silk almost exclusively during the dark phase of their cycle. The central chamber of each experimental unit was marked off into three equally sized subdivisions (8.3×11 cm) along its length. Every hour I watched each unit for 2 min under red light (monochromatic red filters were fitted onto desk lamps with red light bulbs; white light disrupts the normal web-building process; personal observation), and rated the amount of silk present in each subdivision on a categorical scale: 0 = no silk present; 1 = spun fewer than 10 threads; 2 = spun at least 10 threads (these categories were chosen based on preliminary testing). Spiders were considered to have started building a web when one of the subdivisions contained at least 10 threads (i.e. category 2). When fewer threads were present, they were generally laid at random, without forming a web-like structure, and were used as support strands for resting. Therefore, these threads may not be considered indicative of the onset of web construction.

5.3.5.2 Material investment and web design

To examine whether test spiders modified their web building investment (in terms of silk production and web design) under different feeding regimes and levels of microhabitat occupancy, I measured both the thread density and weight of each silken structure at the end of the trials (i.e. after test spiders had been removed). Thread density was determined by fitting a fine metal wire, three to six times, through a web in each of three orthogonal directions, and counting the number of silk strands that touched the wire, following the method of Rypstra (1982). I first sprayed each web with water to increase its visibility, and then ran wires in each of three directions: first, longitudinally (down the length of a chamber at mid-height), by introducing a 25-cm wire through the gaps in the metal meshing (three readings: one at the 1/4, 1/2 and 3/4 marks along the

chamber's width); second, vertically, in each of the three subdivisions using a 5.5-cm wire (six readings: one at each 1/4 and 3/4 mark of each subdivision along the longitudinal midline); third, through the cross section, by placing a 9-cm wire on the bottom of the web (five readings: one in the centre of each subdivision and one adjacent to each metal partition). The mean number of threads/cm was calculated for each of the three directions, and these were then multiplied together to obtain a global density value, expressed as the number of threads/cm³. Subsequently, the silk was harvested by carefully winding silk threads onto a glass rod, which were then dried in an oven at 60°C for 72 h, and weighed to the nearest 0.001 mg on a microbalance. Because of the physical constraints imposed by the walls of the chambers, this study did not allow for an exact assessment of the effect of the treatments on web size. However, I was able to examine gross differences in colonization of the available space (i.e. web size) between treatment groups by counting the number of chamber subdivisions containing silk at the end of a trial.

5.3.5.3 Energetic cost of web construction

To assess the energetic costs associated with web building, I calculated changes in spider weight and body condition (using an index; see below) and compared them across treatment groups. Before their introduction into the central chambers, I weighed all test spiders to the nearest 0.1 mg, and measured the combined length of the tibia and patella of their first pair of legs using callipers (precise to 0.01 mm), as an index of size. Spiders were then reweighed after the trials to determine the amount of weight lost during the experiment. Weight loss values were used as indicators of individual investment into web building, both in terms of silk production and web construction. Body condition was represented by an index value defined as a test spider's residual from a regression of weight over size (both variables log-transformed) using data for all test spiders; two regressions were performed, with weight values from before and after the experiment, respectively. Differences between initial and final body condition were compared between treatment groups.

5.3.6 Data Analysis

Parametric tests were used when the distribution of the data did not deviate significantly from normality (Shapiro-Wilk's test: $P > 0.05$), and nonparametric tests were used otherwise; raw data were transformed where appropriate. With respect to web-building activity, I assessed the influence of diet and microhabitat occupancy level on the time to onset of web construction by means of survival analysis, using the Cox regression method (Hosmer & Lemeshow 1999). I also assessed differences in the proportion of spiders with webs at different time points using Cochran's Q test when comparing between microhabitat occupancy treatments and log-likelihood ratio tests (with William's correction; Sokal & Rohlf 1995) when comparing between feeding regimes. To analyse the data on web-building investment (total and net) and its associated energetic costs, I used general linear mixed models (GLMM) with spider identity and mother identity as random factors to account for the lack of independence. I chose the best models using Akaike's information criterion (see Burnham & Anderson 2002), starting with all factors and interactions. To examine the effect of each treatment on web-building investment (silk production and web design), I used two GLMMs, one with silk mass and another with thread density as response variables. Each model had the following predictors: diet as the between-subject factor, microhabitat occupancy level as the within-subject factor and initial body condition as the covariate. Another GLMM was then applied to evaluate the relationship between thread density and silk mass, using the same factors as in the above models, but including silk mass as a covariate. I also compared the number of subdivisions containing silk between treatments using Mann-Whitney U and Friedman tests. I used two separate GLMMs to test whether web-building costs differed between treatment groups: one with body condition (initial and final) and another with percentage weight loss as the response variable. Each model had diet as a between-subject factor and microhabitat occupancy as a within-subject factor. The body condition models included spider size (tibia-patella length of the first pair of legs) as a covariate, and the weight loss model included initial weight as a covariate. In the control experiment, the baseline values of weight change were compared between diet groups using a t test, and I examined relationships between weight loss and initial weight using linear regression. Finally, I calculated the ratio between silk mass and weight loss as a

means of indexing an individual's relative web-building investment. These ratio values were used as response variables in a GLMM to compare the relative investment between treatment groups, using diet as a between-subject factor, microhabitat occupancy as a within-subject factor and initial condition as a covariate. All statistical analyses were completed with SPSS v. 11 (SPSS, Chicago, Illinois, U.S.A.) following methods from Sokal & Rohlf (1995).

5.4 Results

5.4.1 Web-building Activity

The time at which *L. hesperus* spiders started building a web (i.e. their latency to web construction) differed across microhabitat occupancy treatments but not between the two diet groups, and there was no interaction between these two factors (Table 1). In both diet groups, spiders in empty microhabitats delayed web building relative to when they were kept with con- or heterospecifics, but this delay was longer for well-fed spiders (Fig. 5.1). However, within each diet group, there was no difference in latency between spiders in the con- and heterospecific treatments. Most web-spinning activity took place during the first 8 h, when the lights were off and spiders are most active; yet a few individuals started building webs afterwards, especially when housed alone in a microhabitat.

At the end of the dark phase (after 8 h), the proportion of well-fed spiders with webs varied with the level of microhabitat occupancy (Cochran's Q test: $Q_2 = 19.200$, $N = 33$, $P < 0.0001$; Fig. 5.1a): 93.9% of spiders that were sharing microhabitats with either con- or heterospecifics had started spinning webs, while only 57.6% of them had webs in the empty treatment. This difference was also apparent after 24 h ($Q_2 = 12.000$, $N = 33$, $P = 0.002$), as all spiders in the shared treatments had built a web by then, compared to only 81.8% when housed alone. Pairwise contrasts between the empty treatment and each of the two shared treatments were all significant (McNemar's tests: after 8 h: both $P < 0.01$; after 24 h: both $P < 0.05$), but not those between the con- and heterospecific treatments (P

= 1.000 after 8 h and 24 h). In the poorly fed group, the proportion of spiders with webs was not significantly different between occupancy treatments after 8 h ($Q_2 = 3.231$, $N = 36$, $P = 0.199$; 77.8% versus 88.9% versus 91.7%) or after 24 h ($Q_2 = 1.600$, $N = 36$, $P = 0.449$; 91.7% versus 97.2% versus 97.2%). At the end of the trials a few poorly fed spiders in each of the treatment groups had failed to build a web, whereas some well-fed spiders failed to build a web only when housed alone. However, within each microhabitat occupancy treatment, there was no difference between diet groups in the fraction of spiders with webs after 8 h (adjusted log-likelihood tests: all $P > 0.05$) or after 24 h (all $P > 0.1$).

5.4.2 Material Investment and Web Design

There was an interaction between diet and microhabitat occupancy level on the mass of silk produced (GLMM with square-root transformed response variable; $F_{2,133.7} = 4.703$, $P = 0.011$). Spiders spun more silk when sharing a microhabitat with con- or heterospecifics than when alone, and this difference was more pronounced in the well-fed treatment (Fig. 5.2a). In occupied microhabitats, well-fed spiders produced more silk than did poorly fed spiders. Furthermore, individuals with a higher initial body condition produced more silk relative to others ($F_{1,149.0} = 11.724$, $P = 0.001$). Likewise, the silken structures built by well-fed spiders were denser than those of poorly fed spiders (GLMM with square-root transformed data; $F_{1,79.1} = 4.902$, $P = 0.030$; Fig. 5.2b), which was also the case for spiders in occupied microhabitats compared to those housed alone ($F_{2,133.0} = 13.258$, $P < 0.0001$). There was no interaction between these two factors ($F_{2,132.4} = 0.520$, $P = 0.596$), nor was there any effect of initial body condition ($F_{1,105.2} = 0.027$, $P = 0.869$). Moreover, there was no difference in either silk mass or thread density between webs spun by spiders housed with con versus heterospecifics.

As expected, spiders that produced more silk usually built denser web structures, as shown by a positive relationship between thread density and silk mass (GLMM: $F_{1,142.8} = 73.794$, $P < 0.0001$), which was equivalent across diet groups ($F_{1,73.5} = 0.852$, $P = 0.359$) and occupancy treatments ($F_{2,109.7} = 0.403$, $P = 0.669$). This relationship was also

greater (with a steeper slope) for spiders with higher initial body condition (condition: $F_{1,125.1} = 4.764$, $P = 0.031$; condition x silk mass: $F_{1,141.1} = 10.366$, $P = 0.002$).

Within microhabitat occupancy treatments, the number of chamber subdivisions containing silk at the end of the experiment did not differ between diet groups (Mann-Whitney U test: alone: $U = 505.5$, $N_1 = 33$, $N_2 = 36$, $P = 0.188$; with conspecifics: $U = 575.5$, $N_1 = 33$, $N_2 = 36$, $P = 0.679$; with heterospecifics: $U = 538.5$, $N_1 = 33$, $N_2 = 36$, $P = 0.254$). However, spiders sharing microhabitats with con- or heterospecifics had a tendency to cover the entire available space with webbing, while they laid silk in fewer subdivisions when housed alone; this difference was especially pronounced for well-fed spiders (Friedman tests: well-fed spiders: $\chi^2_2 = 19.579$, $P = 0.0001$; poorly fed spiders: $\chi^2_2 = 7.750$, $P = 0.021$).

5.4.3 Energetic Cost of Web Construction

I compared spider body condition between treatment groups by examining the relationship between spider weight and size (both log-transformed). At the time of introduction, well-fed spiders were in better condition than poorly fed ones (GLMM: $F_{1,66.0} = 74.405$, $P < 0.0001$), regardless of their microhabitat occupancy treatment ($F_{2,136.0} = 0.336$, $P = 0.715$). Furthermore, spider weight covaried with size ($F_{1,66.0} = 19.949$, $P < 0.0001$). At the end of the trials, well-fed spiders remained in better condition than those that had been food-deprived (GLMM: $F_{1,66.0} = 71.827$, $P < 0.0001$), but there were no differences in condition across microhabitat occupancy levels ($F_{2,136.0} = 0.438$, $P = 0.646$); there was also a positive effect of size ($F_{2,66.0} = 20.513$, $P < 0.0001$). All spiders experienced a drop in condition over the course of the experiment (paired t tests: $P < 0.0001$ for all treatment groups). Well-fed spiders lost a greater percentage of weight than did poorly fed ones (GLMM with log-transformed response variable: $F_{1,78.7} = 12.932$, $P = 0.001$; Fig. 3), and spiders in both feeding regimes lost a greater percentage of weight when introduced into occupied microhabitats than when housed alone ($F_{2,107.1} = 3.509$, $P = 0.033$), an effect inversely correlated with initial weight ($F_{1,98.0} = 15.429$, $P = 0.0002$). However, there was no interaction between diet and microhabitat occupancy level in determining the percentage weight loss ($F_{2,106.8} = 0.773$, $P = 0.464$).

In the control trials, where spiders were kept in petri dishes, individuals in both diet groups lost weight over the 24-h period (paired t tests: well fed: $t_{28} = -8.950$, $P < 0.0001$; poorly fed: $t_{28} = -16.907$, $P < 0.0001$). However, well-fed spiders lost a larger proportion of their initial weight than did their poorly fed counterparts (t test: $t_{37.451} = -10.036$, $P < 0.0001$); poorly fed spiders only lost, on average, $0.409 \pm 0.157\%$ (mean \pm SD; range 0.2 - 0.7%) of their initial weight, whereas well-fed spiders lost $1.456 \pm 0.648\%$ (range 0.3 - 2.7%). For poorly fed spiders, there was an inverse relationship between percentage weight loss and initial weight (linear regression: $F_{1,28} = 10.728$, $P = 0.003$, $R^2 = 0.284$), because all spiders lost a similar amount of weight regardless of their initial weight ($F_{1,28} = 0.278$, $P = 0.603$, $R^2 = 0.010$). In contrast, there was a positive relationship between percentage weight loss and initial weight in well-fed spiders ($F_{1,28} = 10.588$, $P = 0.003$, $R^2 = 0.282$), because larger individuals lost relatively more weight ($F_{1,28} = 30.522$, $P < 0.0001$, $R^2 = 0.531$).

5.4.4 Ratio of Investment to Cost

A comparison of the ratio between the mass of silk produced and the weight loss associated with web-building activities between experimental treatment groups established that the level of microhabitat occupancy was the sole factor that had an effect on this variable (GLMM: $F_{2,134.6} = 31.309$, $P < 0.0001$). Spiders introduced into microhabitats with established con- or heterospecifics produced more silk per unit loss of body weight than those in empty microhabitats (Fig. 5.4). Neither feeding regime ($P = 0.669$), the interaction between occupancy level and feeding regime ($P = 0.156$), nor initial body condition ($P = 0.803$) influenced this relationship.

5.5 Discussion

The results of this experiment support the hypothesis that *L. hesperus* females adopt state-dependent web-building strategies when settling into novel microhabitats, and that these strategies are further determined by the presence of con- and heterospecific

spiders. Both nutritional state and the presence of neighbours influenced the timing of web construction, as demonstrated by the clear differences between treatments in the latency in onset to web spinning (Fig. 5.1). Likewise, the diet manipulations had a direct effect on web-building behaviour, causing noticeable variation in web architecture between treatments. Overall, webs of well-fed spiders contained more silk and higher thread densities than those of poorly fed spiders (Fig. 5.2). These differences between diet groups were greatest for individuals that shared a microhabitat with other occupants, suggesting that *L. hesperus* perceived the presence of both con- and heterospecifics and adjusted their web-building efforts accordingly. However, I found no effect of diet on relative web-building investment (measured as the ratio between silk production and weight loss), but there was an obvious occupancy effect: individuals allocated a larger fraction of their total energy expenditure to silk production when sharing a microhabitat with other spiders (Fig. 5.4). The web-building behaviour of *L. hesperus* females did not differ when in the presence of con- or heterospecifics. Together, these results allow me to address one of the fundamental questions pertaining to the plasticity in web-building behaviour, which is that of its functional significance. Below, I consider how conflicting demands are managed in *L. hesperus*, and how this translates into strategic web-building behaviours, focusing on the effects of nutritional state and neighbour presence.

5.5.1 State-dependent Web-building Decisions

The classical view of optimization theory predicts an inverse relationship between an individual spider's condition and its web-building effort (viewed as a foraging activity), which has found some support in previous research on the web-building behaviour of a diverse array of spiders (e.g. Araneidae: Sherman 1994; Venner et al. 2000; Agelenidae: Riechert 1981; Eresidae: Lubin & Henschel 1996; Pasquet et al. 1999). Hence, one would expect a spider's web-building investment, represented here as the structural design of its web (i.e. silk mass, thread density, web size), to be proportional to the balance between the immediacy of its need for a web and the cost of web construction, weighed against its perception of habitat profitability. Contrary to this hypothesis, the results of the present experiment showed that well-fed *L. hesperus* spiders produced heavier and denser webs than their poorly fed counterparts. Two main lines of

reasoning may be invoked to account for this positive correlation between feeding status and web-building investment.

First, in natural settings, *L. hesperus* spiders that build webs on the underside of logs (a microhabitat mimicked in this experiment) do not commonly construct a separate retreat, but instead use webs as both a retreat site and a foraging platform (personal observation). In fact, a recent study by Blackledge et al. (2003) provides compelling evidence in support of the hypothesis that three-dimensional webs (such as the cobwebs of *L. hesperus*) have evolved as structural adaptations to predation pressure. The presence of a web may therefore be essential for protective purposes, which may explain why well-fed individuals spent more energy building a web even though their body condition was high. Thus, when a particular structure built by an animal (e.g. a spider's web) is tied to satisfying multiple needs (e.g. protection versus prey capture), a clear relationship between feeding status and investment into the structure is not necessarily expected. Although the return on investment for each of the possible uses of a web may be state dependent, the relationship describing each of them is likely to follow a different optimization criterion at a given state. For example, a poorly fed spider may be able to maximize its immediate foraging returns at the expense of a small and loosely woven web, whereas well fed spiders in good condition receive optimal short-term benefits from further web-building investment that contributes primarily to protection through an improved structural design. This multifunctionality argument is consistent with my observation that all of the spiders tested spun some silk threads during the experiment, regardless of their feeding status.

Second, because cobweb weavers usually build their webs over several consecutive nights, and my study only investigated settlement behaviours during the first 24 h, the differences in web-building effort detected at this particular timescale may not necessarily reflect that of an individual's entire web-building investment. Segoli et al. (2004) found similar results in a study with the sheet web-weaving spider *Frontinella* cf. *frutetorum*, where experimentally fed spiders maintained a larger web than starved ones over several days. It is likely then that in both *L. hesperus* and *F. cf. frutetorum*, for

which web construction is energetically costly and web persistence is high, an adaptive strategy would be to seek a close match between building investment and current nutritional state. However, the reason underlying each of these web-building strategies may differ, because cobwebs and sheet-webs vary in their ability to capture prey or provide concealment. *Latrodectus hesperus* spiders may initially start building a web for protective purposes and progressively expand it to enhance its prey capture potential, while *F. cf. frutetorum* may directly invest into a foraging structure.

The increase in web-building activity of well-fed *L. hesperus* spiders was characterized by the production of more silk and greater thread densities, leading to the enhancement of a web's three-dimensionality. Previous research has shown that strand density is positively correlated with prey capture rate in other cobweb-weaving spiders (Rypstra 1982; Barghusen et al. 1997). A high-food diet could thus enable a spider to maintain the integrity and prey capture potential of its web, while poorly fed spiders have to trade off a web's design efficiency against the building costs. However, another very important feature of a *L. hesperus* cobweb that is necessary to achieve prey capture success is the presence of sticky anchor threads (gumfooted lines) at the bottom of a web used to intercept passing prey (Benjamin & Zschokke 2003). Thus, in *L. hesperus*, an overall increase in the strand density of a cobweb may contribute more to structural resilience and protection against disturbance than to prey capture per se. Although I did not directly quantify the occurrence of gumfooted lines, viscid silk lines were commonly observed on webs spun by both well-fed and poorly fed *L. hesperus* spiders, suggesting that the production of sticky silk is unlikely to be limited by individual condition, at least not on the short term.

Rypstra (1982) measured the thread density of cobwebs spun by several species of Theridiidae (including *L. mactans*) in seminatural settings, and found values that were for the most part several orders of magnitude higher than the ones reported here. As mentioned above, *L. hesperus* spiders, like other theridiids, build their webs over several nights during which they progressively add more silk to the main structure, thereby increasing the density of threads and also web size. In the present study, *L. hesperus*

females were confined to a small microhabitat and were only allowed to build a web for 24 h, which is why strand densities were low. However, strand density measurements of cobwebs spun by *L. hesperus* were similar to those reported for *Achaeranea tepidariorum* (Barghusen et al. 1997).

5.5.2 Influence of Neighbours on Web Building

An important finding of this experiment is that *L. hesperus* spiders modified their web-building behaviour in the presence of neighbours. In both diet groups, the presence of con- and heterospecifics caused spiders to build webs sooner (within the first few hours); by the end of the dark phase the majority of individuals were in the process of establishing a web. In contrast, spiders delayed web construction when housed alone relative to when they shared microhabitats. However, this delay was much greater for well-fed spiders, suggesting that their requirements for a web were lower than those of poorly fed spiders. Similarly, individuals in the shared treatments increased their silk production and built denser webs covering a larger area relative to the control groups. Although my experimental design did not allow for a precise assessment of the effects of the various manipulations on web size, the size differences observed here may reflect the interdependence of size and strand density in *Lactrodectus* cobwebs. The confinement experienced by spiders in this experiment may also have biased their web-building behaviour, since they were not free to abandon a microhabitat if the conditions were deemed unsatisfactory. For instance, the greater delay in web construction shown by spiders that were housed alone, along with their lower material investment, may have been an indication of their willingness to leave. However, this alternative behaviour would not have altered the general conclusion drawn from these data, which is that the presence of neighbours increases a spider's web-building efforts.

The ability to gather information about the distribution of previously established microhabitat occupants might influence web construction in *L. hesperus* for several reasons. First, their presence may reflect the quality of a particular microhabitat, which could preclude the need for costly habitat sampling and encourage co-settlement by conspecifics (e.g. Stamps 1988; Schuck-Paim & Alonso 2001) or even heterospecifics

(e.g. Forsman et al. 2002). Second, because neighbour presence may render interactions and resource partitioning unavoidable, incoming foragers may benefit from rapidly colonizing the available space before it is taken up by others. Furthermore, spiders may build more webbing in occupied microhabitats to compensate for the potential decrease in resource availability caused by the presence of neighbours. In the orb weaver *Zygiella x-notata*, constraints on space occupation associated with group living have been shown to lead to the reduction of web size, which in turn may affect foraging success (Leborgne & Pasquet 1987). *Latrodectus hesperus* spiders may also have increased their web-building efforts in the presence of neighbours as a means of limiting potentially aggressive web intrusions from conspecific neighbours. However, field observations of females sharing microhabitats do not provide strong support for this explanation, because females readily move from web to web, and the rate of cannibalism is low (personal observation). Finally, if sharing some of the microhabitat space with other spiders confers a net payoff in terms of energy return or survival, a spider may be more inclined to build a web in an occupied microhabitat. This has typically been observed in colonial spiders that form communal assemblages of individual territories, where spiders benefit from living in aggregations because of the protective, energetic or feeding advantages involved in this form of living (reviewed in Uetz & Hieber 1997). In my experiment, the presence of other spiders close to the openings of the microhabitats may have induced earlier web construction in the shared treatments because of their shielding role against potential predators, as seen in colonial orb-weaving spiders of the genus *Metepira* (Rayor & Uetz 1990). However, further research is necessary to determine whether the presence of neighbours in a microhabitat provides any fitness benefits to *L. hesperus* females, such as facilitated prey detection, enhanced web resilience or improved protection.

My experimental design was not intended to determine whether *L. hesperus* spiders are able to distinguish between neighbouring individuals and their webs; however, the finding that spiders showed similar web construction behaviours (i.e. timing, silk production and thread densities) in the presence of conspecifics and heterospecifics (*Tegenaria* spp.) suggests that they were cued by the presence of silk in the surrounding chambers rather than by the identity of their occupants per se. The

physical barriers between chambers made it difficult for individuals to interact in a ‘normal’ fashion; however, since I used only cue spiders that had attached some silk to the partitions, test spiders were able to make contact with neighbouring webs very easily (i.e. individuals were frequently observed extending their legs through the meshing to reach the other side and touch some webbing). These observations agree with the results of a previous study in an orbweaving species suggesting that spiders are attracted to the presence of silk (‘sericophily’) and settle more readily in microhabitats that contain some silk (Schuck-Paim & Alonso 2001). However, long-term settlement decisions in *L. hesperus* living in natural settings may rely on both the interaction with neighbouring individuals (which was restricted in the experiment) and their webs.

5.5.3 Net Energy Investment into Silk Production

In contrast to the lack of difference in energy allocation across diet groups, the presence of microhabitat occupants caused *L. hesperus* spiders to channel their energy into silk production: spiders housed with con- and heterospecifics increased the fraction of energy allocated to silk production relative to spiders housed alone. The lower investment by spiders that were housed alone is consistent with their longer delay in initiating web construction, because they may have spent a greater share of their energy moving around and exploring the microhabitat before starting to spin a web. This provides further evidence that the presence of neighbours serves as an indicator of microhabitat quality, allowing individuals to rapidly and directly invest their energy into web building, rather than spending it on preliminary related activities such as site exploration. Despite the absence of an effect of diet on energy allocation, well-fed spiders lost a greater percentage of their initial weight during web construction. In the control trials, where spider weight loss reflects the basic metabolic rate under each of the two feeding regimes, weight loss due to basic metabolism averaged 0.4 and 1.5% for poorly fed and well-fed spiders, respectively. However, in the main experiment, spiders in both diet groups lost 2 – 2.5% of their initial weight. Relative to the values of spiders in the control trials, poorly fed spiders lost six to eight times more weight during the main experiment, whereas well-fed spiders only lost two to three times more weight. Moreover, the amount of weight lost by well-fed spiders in the experimental units was

positively correlated with their initial weight, which probably reflects a higher basal metabolic rate for spiders in good condition. Overall, these results suggest that a low-food diet increases the energetic costs of web building, relative to a high-food diet.

In summary, this study provides some of the first empirical evidence showing that a cobweb weaver is capable of modifying its investment into web construction in response to the presence of other spiders, both con- and heterospecifics, when settling into a microhabitat. Moreover, these results highlight the interplay between external environmental factors and intrinsic physiological state in determining an individual's microhabitat settlement decisions. This plasticity in web-building behaviour allows *L. hesperus* to strategically adjust its web-building efforts according to the associated state-dependent costs and benefits. Further research is needed to determine whether these strategic behaviours confer net fitness advantages to those that express them (i.e. whether they are adaptive), as well as to characterize the specific nature of these benefits.

5.6 Acknowledgments

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Table 5.1. Effect of different predictors on the time to onset of web construction during the 24-h experiment, determined by survival analysis, using the Cox regression method

Source	df	χ^2	<i>P</i>
Whole model	5	36.903	<0.0001
Feeding regime (FR)	1	0.189	0.664
Microhabitat occupancy (MO)	2	31.117	<0.0001
FR × MO	2	4.790	0.091

Figure 5.1. Percentage of (a) well-fed (N = 33) and (b) poorly fed (N = 36) *L. hesperus* spiders that had constructed a silken structure (with ≥ 10 threads) within a subdivision at each time step. The different lines correspond to different microhabitat occupancy treatments: alone (broken line, circles), with conspecifics (full line, squares) and with heterospecifics (full line, triangles). The horizon bar below the X axis denotes the duration of each lighting phase: dark and light. The vertical lines indicate the end of the dark phase (the 9th hour), at which time the lights came on and stayed on until the end of the experiment

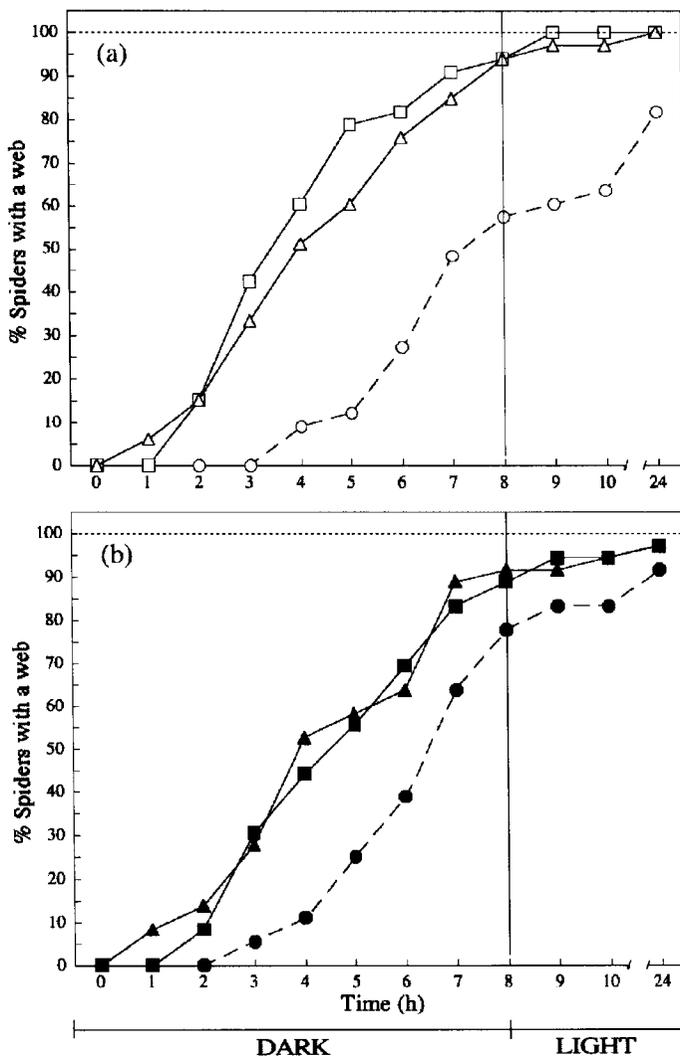


Figure 5.2. (a) Mass of silk and (b) density of silk webbing produced by well-fed (\square , $N = 33$) and poorly fed (\blacksquare , $N = 36$) *L. hesperus* females housed for 24 h under three different microhabitat occupancy treatments (alone, with conspecifics, or with heterospecifics). Data are represented as box plots, with the mean (square symbols), the median (central lines), the 25th and 75th percentiles (top and bottom of boxes), and the 5th and 95th percentiles (cap of lower and upper whiskers)

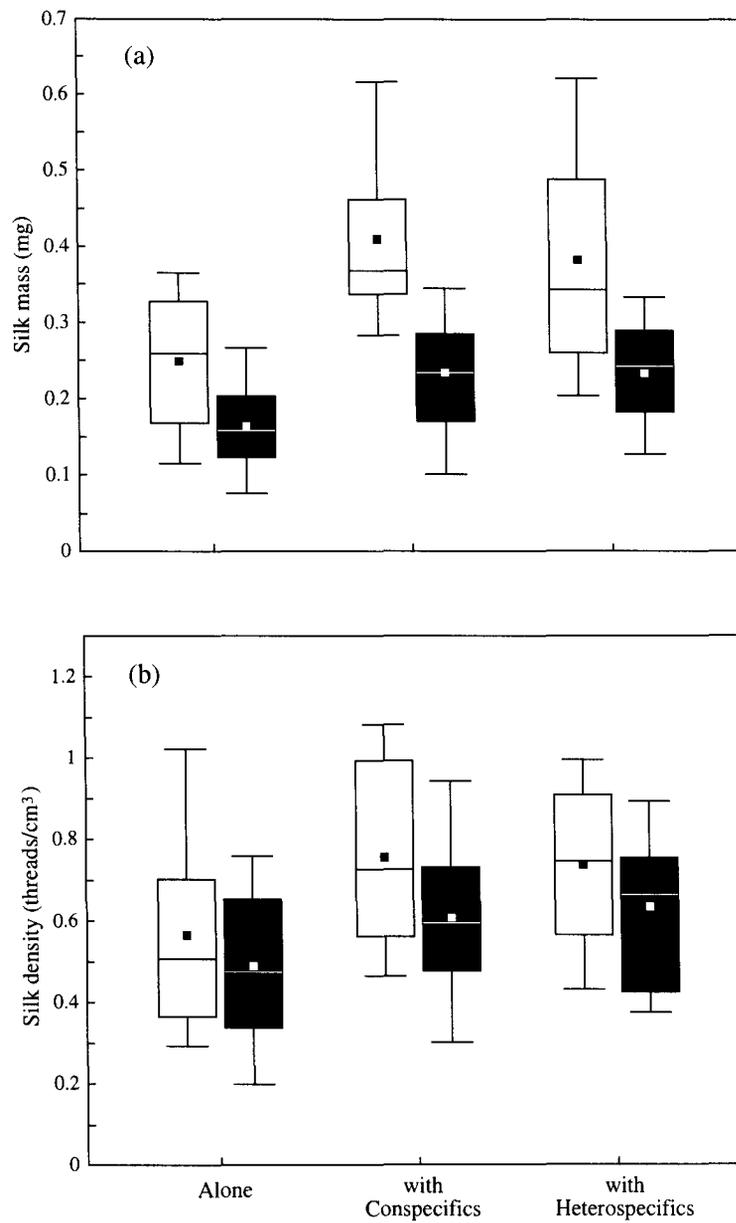


Figure 5.3. Percentage weight loss (least square means + 95% CI) in well-fed (□) and poorly fed (■) *L. hesperus* females, after residing in the experimental units for 24 h at three microhabitat occupancy levels

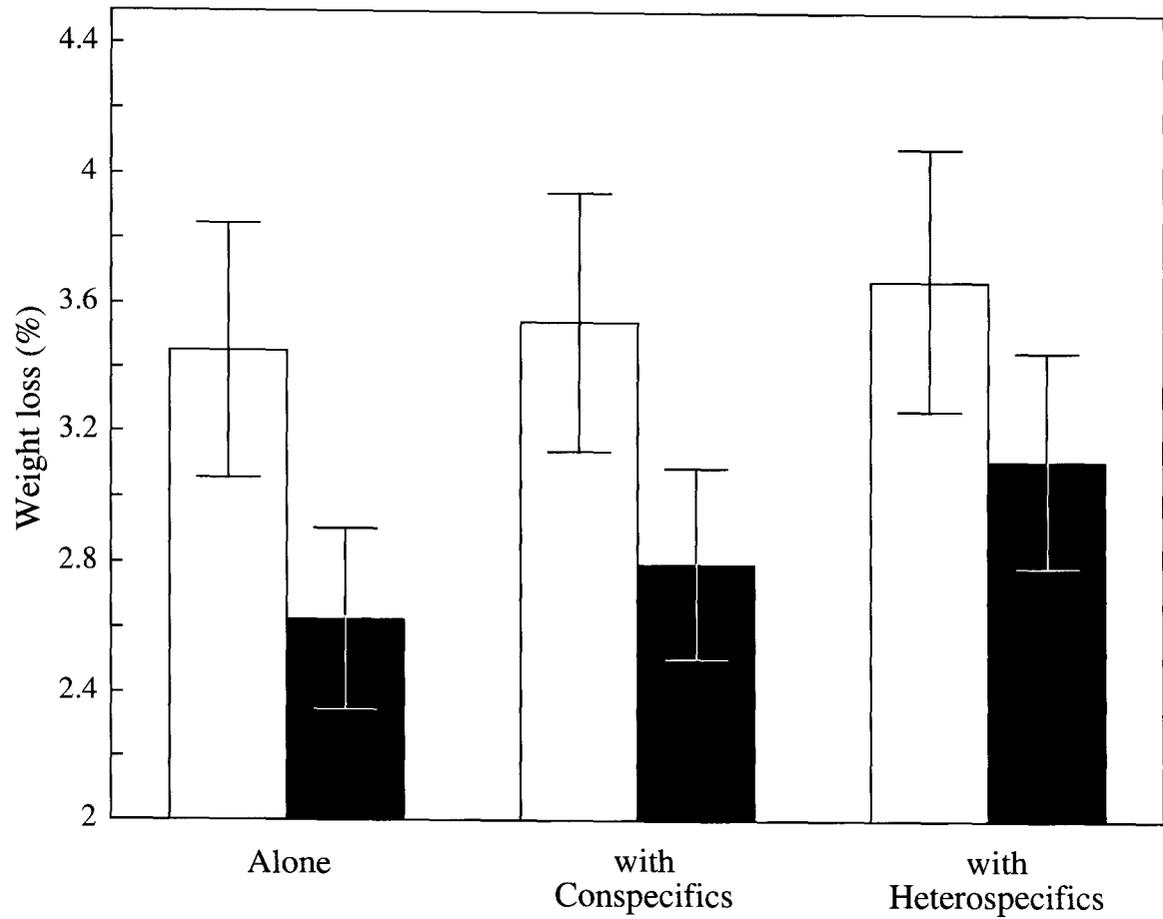
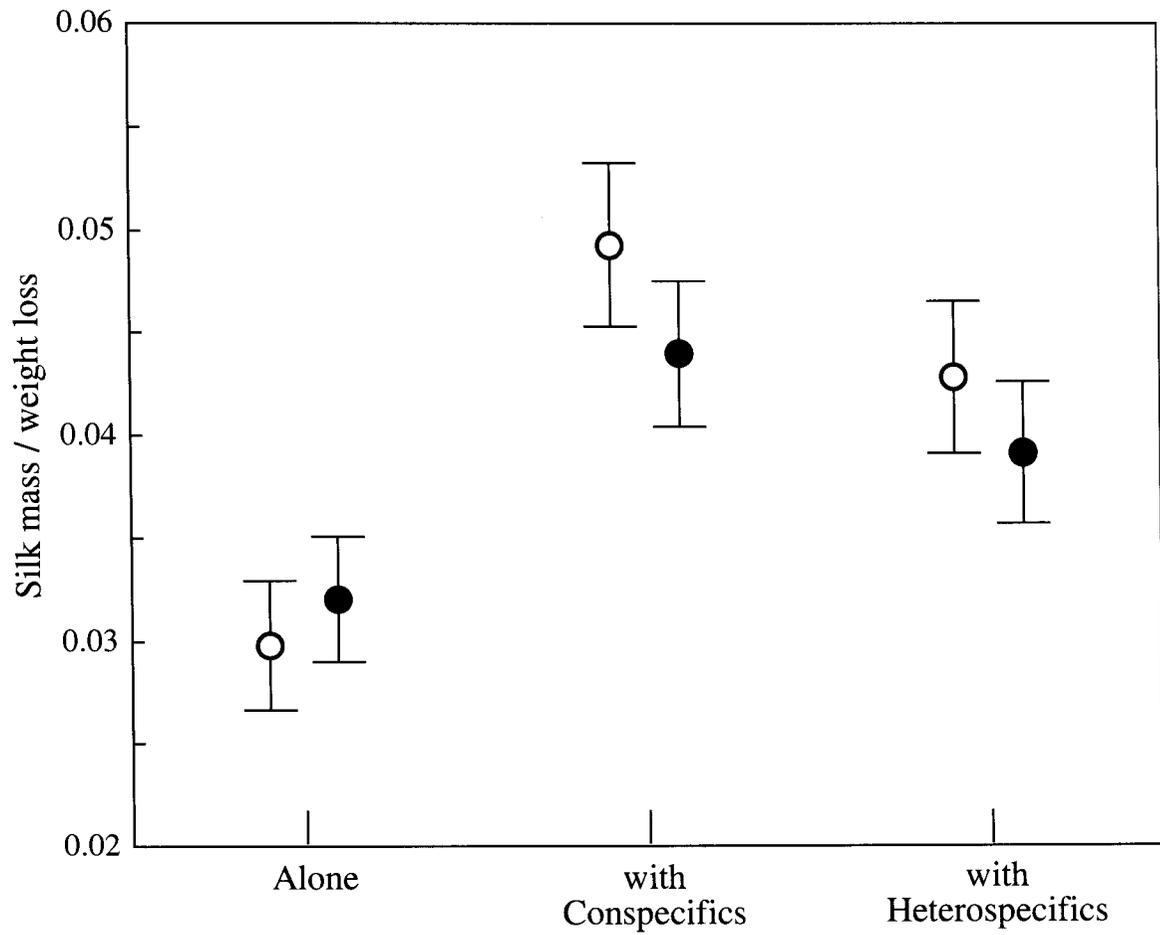


Figure 5.4. Least square means (\pm SE) of the ratio between the quantity of silk mass produced (mg) and the associated loss in body weight (mg) in well-fed (\circ) and poorly fed (\bullet) *L. hesperus* females subjected to three different microhabitat occupancy treatments



**Chapter 6: GROUP SIZE INFLUENCES PREY CAPTURE
SUCCESS IN A FACULTATIVELY GROUP-LIVING
SPIDER ***

* This study is co-authored by Maxence Salomon & Bernard D. Roitberg

6.1 Abstract

To understand the social structure of a species, one has to investigate the costs and benefits associated with group versus solitary living. Here, we experimentally examined the influence of group living, and in particular group size, on foraging success in *Latrodectus hesperus*, a web-building spider that facultatively lives in groups. Females were housed either alone or in small or large groups, and we recorded different components of their foraging behaviours at various prey densities. We tested two different situations: food abundance and food limitation. All cohabitating spiders shared a common web, but they did not cooperate in prey capture, and there was no cannibalism among them. When food was abundant, females in large groups captured more prey per capita than those housed alone or in pairs, but when food was limited, spiders living in small groups experienced greater foraging success. Furthermore, the variance in prey capture decreased with increasing group size. High foraging success lead to corresponding increases in individual body condition, an index of fitness. At low prey densities group-living spiders caught prey sooner relative to those housed alone, suggesting that the proximity of conspecifics enhances prey detection. Foraging investments varied with group size, such that spiders living in large groups had the greatest foraging returns per unit of silk invested when food was abundant, whereas under food limitation those in small groups seemed to do best. These results demonstrate the net foraging benefits associated with group living in this spider at different group sizes. We discuss the group size-dependent trade-offs involved in grouping associations and how they may influence group-living dynamics.

6.2 Introduction

Animal societies vary dramatically in social structure according to the local environment, the persistence of a social unit, and the types of activities that individuals

engage in as a group versus solitarily. Group living is an adaptive strategy in many selective environments, and has been shown to increase individual fitness by providing net foraging, reproductive and/or survival benefits in various species (see Krause & Ruxton 2002 for a review). For example, in taxa as wide-ranging as birds, fish and arthropods, individuals living in groups may have lower risks of predation, gain access to more profitable food, or reduce their energy expenditures relative to solitary individuals (e.g. Herskin & Steffensen 1998; Prokopy & Roitberg 2001; Fernández et al. 2003). Studies that examine trade-offs between the costs and benefits of group living provide valuable insight into the evolution of sociality.

The nature and intensity of these trade-offs often depend on the size of a group (e.g. Packer et al. 1990). Indeed, group size is a determining factor in the formation, organization, and persistence of a group entity. Many lines of evidence suggest that the primary function of group living may differ according to the size of a group, and that trade-offs arising at different group sizes determine the stability of grouping associations. In damselfish, for instance, individuals living in small groups (<3 individuals) have a higher feeding success than those in larger groups, suggesting that conflict arises over foraging when groups are too large (Kent et al. 2006). These size-dependent differences in foraging outcome favour the formation of small damselfish groups. In social insects, group size (or in this case colony size) is correlated with per capita productivity and several behavioural, morphological and life-history traits that determine social complexity, such as reproductive potential and behavioural plasticity (Karsai & Wenzel 1998; Bourke 1999). An increase in group size can modify within-group interactions, causing stronger competition over resources such as food, which may result in lower per capita food intake rates (e.g. Schmidt & Mech 1997), greater levels of aggression and even cannibalism (e.g. Sirot 2000; Bilde & Lubin 2001), decreased growth rates (e.g. Lubin et al. 2001), and a decline in survival rates (e.g. Brouwer et al. 2006). Conversely, species forming large social groups may experience an increase in per capita feeding rate with group size, until an optimum is reached (e.g. fish, Milinski 1979; colonial spiders, Uetz 1988; group-foraging birds, reviewed in Beauchamp 1998; wild dogs, Creel 1997). This is explained by the fact that the presence of many group members may facilitate

prey detection by means of information sharing (Valone & Templeton 2002), or favour cooperation in prey capture, which may lead to greater foraging efficiency and access to more profitable prey (e.g. Powers & Avilés 2007). The occurrence of large animal groups has also been attributed to decreased variance in prey capture depending on prey availability (Caraco et al. 1995). Likewise, group size has been shown to affect other components of fitness such as reproductive success or clutch size (e.g. Avilés & Tufino 1998; Hatchwell & Komdeur 2000). Thus, what constitutes an optimal group size is contextual in nature, as several potentially conflicting factors may influence social organization (Slobodchikoff & Schulz 1988; Higashi & Yamamura 1993).

Species that express both solitary and social tendencies are particularly suitable to examine the interplay between group size and social dynamics, because they show natural variation in their social behaviour. However, few studies of group living have focused on non-social species. Here, we investigate the effects of group size on foraging behaviour in a sedentary web-building spider, *Latrodectus hesperus* Chamberlin & Ivie (Araneae: Theridiidae). Individuals of this species establish territories (i.e. webs) for foraging and reproductive purposes and facultatively live in groups at certain times of the year, either by forming clusters of webs or more commonly by sharing webs (see Chapter 2). Group living is rare among spiders, and social behaviour follows a continuum from purely territorial and solitary populations to permanently social and cooperative ones (Avilés 1997; Whitehouse & Lubin 2005). Species such as *L. hesperus* that exhibit intermediate social strategies, and live either alone or in groups, represent excellent study systems to examine grouping dynamics in the context of sociality. Furthermore, the fact that individuals live in groups of different sizes allows for a direct test of the relative benefits and costs of group living.

For this study, we hypothesized that per capita foraging success would vary between group- and solitarily-living spiders, and that the magnitude of this difference would depend on group size. Furthermore, the foraging outcome of a spider living in a group or alone should differ at low versus high prey density, given that foraging trade-offs associated with group living depend on prey availability (e.g. Rypstra 1989). To test

this hypothesis we designed two laboratory experiments in which we manipulated the size of groups of *L. hesperus* spiders and recorded different components of their foraging and social behaviours (prey capture, web-building investment, movement, territoriality, spatial distribution) at various prey densities. In one experiment, we manipulated the number of prey per capita to create a situation of food abundance, and in the other we manipulated the number of prey per microhabitat to cause food limitation. When food is abundant, spiders have equal chances of capturing a given number of prey, whereas when food is limited not all spiders sharing a microhabitat have access to the same number of prey, and as a result some may starve if prey are captured by other microhabitat occupants. Overall, this study offers a quantification of the fitness consequences of group living in a non-social animal by characterizing the effect of group size on foraging behaviour in an ecological context.

6.3 Methods

6.3.1 Study animals

The western black widow spider, *Latrodectus hesperus*, is a cobweb-weaving spider that is indigenous to western North America (Kaston 1970). In natural habitats of southern British Columbia it lives close to the ground on the underside of driftwood logs, on rocky outcrops, or at the entrance of small mammal burrows (M. Salomon, pers. obs.). Web building and prey capture generally take place at night, and during the day spiders are generally inactive.

Only mature *L. hesperus* females were used in the experiment because males generally do not forage after reaching adulthood (M. Salomon, pers. obs.). Spiders used in Experiment 1 were reared from egg sacs produced in the laboratory by wild-caught females from a coastal beach habitat of southern Vancouver Island, British Columbia, Canada (48°35' N, 123°22' W). Each spider was provided insect prey at 3-day intervals through maturation and reared at 28°C ± 2°C and 40 ± 5% RH, under a reversed 8D: 16L light cycle (progressively switched to a 10D: 14L cycle in late summer). An assortment

of prey was used to feed spiders, including, in order of provision from early to late instar, fruit flies (*Drosophila melanogaster*), house flies (*Musca domestica*), blow flies (*Phaenicia sericata*), and house crickets (*Acheta domesticus*). Spiderlings were kept together during their first 3 instars and subsequently transferred to individual Petri dishes. Mature females were maintained on a generous diet and fed medium-sized crickets twice weekly until the start of an experimental trial.

In Experiment 2, we used *L. hesperus* females collected from the above-mentioned field location in November. These females were kept in the laboratory for one week prior to the experiment under the same conditions as for laboratory-reared females, and fed one medium-sized cricket each. Females used in both experiments were all marked for individual identification with dots of whiteout paint on their front and/or back legs. Furthermore, these females were last fed 48 h prior to the start of an experiment, which means that by the time they were exposed to prey in the experiment (see below) they had been food-deprived for 7 days. Experiment 1 was conducted in September-October, and Experiment 2 at the end of November.

6.3.2 Experimental setup

6.3.2.1 Test apparatus

We tested the effects of spider group size and prey density on the foraging behaviour of *L. hesperus* spiders in a laboratory setting, using wooden sheds as microhabitats (see Fig. 6.1). The sheds were designed to mimic pieces of driftwood under which *L. hesperus* spiders naturally occur in coastal beach habitats of southern British Columbia. The length and width of a shed corresponded to the mean dimensions of driftwood logs measured in a natural habitat (see Chapter 2). Sheds were placed on a wooden base that was covered with a layer of clear plastic (for ease of cleaning between trials) over a layer of white paper (to facilitate observations of spiders). Spiders readily settled under the sheds and attached their cobwebs to all surfaces of the underside, with prey capture threads extending down to the plastic substrate. The experiment was run under the same temperature, humidity and lighting regimes as for rearing (lighting: 10D:

14L cycle). Full-spectrum white lights were turned on during the light phase, and lamps fitted with low-intensity red filters were used during observation periods in the dark phase, so as not to disturb spiders.

6.3.2.2 Prey

We used 4-week old house crickets as prey in the experiments (*A. domesticus*; mean weight \pm SD = 219.376 \pm 58.155 mg, N = 200), purchased from a local cricket farm. Crickets were housed in a large Plexiglas tank (50 L \times 26 W \times 32 H cm), fed cricket food pellets and apple pieces and provided water ad libitum. Crickets used as experimental prey were marked on the dorsum for individual identification with different patterns of acrylic paint dots (4 colours). Because theridiid spiders such as *L. hesperus* hunt using primarily vibratory and odour cues from prey and not visual information, it is highly unlikely that the colour of the markings had any effect on their prey capture behaviours (Barth 2001). Prey were marked 16 h prior to the start of a trial and individually housed in solo plastic cups (4 cm in diameter, 2-cm height). They were then weighed to the nearest 0.1 mg 2-3 h before a trial, and transferred either individually or in groups of 2-8 to plastic vials used for prey introduction under experimental sheds. These vials were either 8 or 16 cm long (depending on the number of crickets), with a diameter of 16 mm, and open ended with a cap at one end and a plunger at the other that was used to gently introduce crickets to the sheds through the shed openings (see Fig. 6.1).

6.3.3 Experimental procedure

6.3.3.1 General

In each experiment, we manipulated the following independent factors and conducted a full-factorial design: (1) the number of *L. hesperus* spiders per shed (3 levels: 1, 2, and 4); and (2) prey density. The group sizes tested correspond to common sizes of *L. hesperus* groups found in their natural habitat (see Chapter 2). In Experiment 1, a situation of food abundance, prey density corresponded to the number of prey provided per capita (4 levels: 1, 2, 4, and 8), whereas in Experiment 2, a situation of food

limitation, it corresponded to the number of prey per shed (3 levels: 1, 2, and 4). Spiders were introduced under a shed 5 days prior to the start of the experiment to allow for acclimation and web construction. Each spider was used only once and randomly assigned to one of the treatment combinations. The prey capture experiment was initiated at the onset of the dark phase, at 1200 hours on day 5, and lasted 24 h. At the start of each experiment, the appropriate number of prey was introduced to each shed through the 2 openings (side of introduction determined by coin flip). In Experiment 1, we ran 3 trials at 10-day intervals, and tested 3 or 4 replicates (1 per shed; 40 sheds per trial) of each spider group size \times prey density combination in each trial, for a total of 10 replicates per treatment combination. In Experiment 2, we ran 1 trial with 7 replicates per treatment combination. All behavioural observations were done from above the sheds by turning over the lids, causing minimal disturbance to spiders and no damage to their webs.

At the start of a trial, when spiders were introduced under the sheds, there were no detectable differences in spider body condition across group sizes, prey densities and trials (GLM on log-transformed response: Exp. 1: group size: $F_{2, 272} = 1.848$, $P = 0.159$, power = 0.484; prey density: $F_{3, 272} = 1.259$, $P = 0.289$, power = 0.435; trial: $F_{2, 272} = 1.902$, $P = 0.151$, power = 0.494; Exp. 2: group size: $F_{2, 144} = 0.126$, $P = 0.882$, power = 0.069; prey density: $F_{2, 144} = 2.326$, $P = 0.101$, power = 0.465). Body condition was calculated as the residuals of a linear regression of weight over size (tibia-patellar length of first pair of legs; both variables log-transformed; Exp. 1: $R^2 = 0.053$, $P < 0.0001$; Exp. 2: $R^2 = 0.334$, $P < 0.0001$) including data for all spiders used in the experiment, which is a reliable method of indexing condition in spiders (Jakob et al. 1996).

Two supplementary ‘Control’ trials were run after Experiment 1, where spiders were placed either alone, in pairs, or in groups of 4 under a shed for 5 consecutive days without any prey (26 replicates of each treatment). During this time, we recorded spider movement, spacing under the sheds, changes in body weight, and the mass of silk produced using the same protocols as in the main experiment (see below). The purpose of these data was to compare differences across group sizes between the acclimation phase and the prey capture phase, since spiders were not weighed immediately before the

feeding trials to avoid disturbing them, and silk production was not assessed before prey introduction.

6.3.3.2 Prey capture

To assess prey capture behaviours, we surveyed sheds every 2 h during the dark phase and every 4 h during the light phase of each feeding trial, and counted the number of prey captured by each spider and their identities based on their markings. In *L. hesperus*, prey capture involves silk wrapping and prey attachment to the web for consumption; once consumed, prey are usually dropped to the ground (M. Salomon, pers. obs.). All consumed prey were collected after the trials, dried in an oven at 60°C for 96 h, and weighed to the nearest 0.1 mg. To determine the mass of prey consumed by each spider during a feeding trial, we subtracted a prey's dry weight after consumption to its initial dry weight before the trial. The latter measure was derived from a prey item's initial wet weight using a regression equation. To obtain this equation we weighed 4-week-old crickets to the nearest 0.1 mg (N = 200), froze them for 24 h to kill them, then dried them at 60°C for 96 h, and re-weighed them once fully dry. The following second-order regression equation was derived from these data and used for the calculations: $\text{dry weight} = 0.184 * \text{wet weight} + 0.000254 * (\text{wet weight})^2$, ($R^2 = 0.994$, $P < 0.0001$).

6.3.3.3 Weight changes

All spiders were weighed before and after the experiment and we measured weight change as: final weight – initial weight. Because spiders were not weighed immediately before a feeding trial (i.e. after the acclimation phase), changes in weight reflect both web building and movement activities during the acclimation phase and foraging activities during the feeding trial. We also calculated spider weight changes during the supplementary trials and compared these values to that of the experiments to assess the influence of primarily web building (acclimation phase) versus web building and prey capture (feeding trial) on weight change.

6.3.3.4 Web building

At the end of the trials, silk was carefully collected from under each shed by rolling it onto a glass rod. It was then dried at 60°C for 72 h, and weighed on a microbalance to the nearest 0.001 mg. This allowed for a comparison of the mean per capita web-building investment across treatment groups. Silk was also collected and processed in the same fashion after the supplementary trials.

6.3.3.5 Movement and spatial distribution

We recorded the position of each spider on a daily basis during the acclimation phase (in the first hour of the dark phase), at the start of a feeding trial, 8 h into the trial, and at the end of a trial (i.e. after 24 h). To do so, we divided each shed into 4 equally sized zones and assigned a zone number to each individual during observations. Therefore, the dependent variable represents the mean number of zones travelled per time step. In treatments where spiders were kept in groups of 2 or 4, we also measured nearest-neighbour distances at each census time as a measure of spacing between individuals. Together, these data provided a means of quantifying the influence of group size and prey density on movement dynamics.

6.3.4 Data analysis

All analyses were performed with SPSS v. 13 (SPSS, Chicago, U.S.A.). Data were tested for normality and homoscedasticity and transformations were applied where appropriate. We used general linear models (GLM) to assess the influence of spider group size and prey density (fixed factors), and their interaction, on the different response variables relating to spider foraging behaviours (i.e. number of prey captured, latency to first prey capture, mass of prey consumed, mass of silk produced, ratio of prey capture to silk production), with trial number as a random factor for Experiment 1. Each response variable accounted for per capita values. To avoid pseudo-replication (data for spiders housed together in groups of 2 or 4 are not independent) the mean of a given response variable for each group was taken as a single replicate, and used for analysis. We compared differences across group sizes, prey densities, and trials in the proportion of

spiders that caught prey using a generalized linear model (GZLM) with a Poisson distribution, a log-link function and an overdispersion parameter. We used two separate GLMs to assess the effects of group size and prey density on changes in body weight and body condition, with initial weight and initial condition as the respective covariates, and final weight and condition as the respective response variables (both log-transformed), and trial as a random factor (in Experiment 1). Finally, we analysed differences in the amount of movement and nearest-neighbour distances using general linear mixed models (GLMM) with a first-order autoregressive covariance structure, day/time as the within-subject factor, spider group size and prey density as between-subject factors, microhabitat as a random subject factor, and trial as a random factor (in Experiment 1). The same models were applied to the data from the supplementary trials.

6.4 Results

6.4.1 Interactions between Spiders

In both experiments, there was no cannibalism between females sharing microhabitats in groups of 2 or 4, either during the acclimation period or the prey capture phase. Spiders moved freely within a microhabitat and two or more spiders were often seen resting in close proximity to one another (1-3 units of body length apart) without any signs of aggression. After prey introduction, once females started detecting and hunting prey, we observed two instances of territorial displays between two females that were close to each other. During these encounters, one of the females performed “push-ups” on the web while the other stayed immobile; however, it did not escalate.

6.4.2 Prey Capture Success

All *L. hesperus* females captured and consumed prey individually; there was no cooperation in prey capture and no prey sharing. Furthermore, females did not suffer any injuries from the prey.

6.4.2.1 Experiment 1

Both spider group size and prey density had a positive effect on the number of prey captured per capita, but there was no interaction between these factors (Table 6.1a; Fig. 6.2a). Mean prey mass per microhabitat had no effect on prey capture success (as a covariate), so it was removed from the final model. At each spider group size, the number of prey captured per capita increased with prey density (number per spider). For spiders housed alone or in groups of 2, prey capture rate stabilized at high prey densities, whereas it kept increasing for spiders in groups of 4 (Fig. 6.2a). Overall, the number of prey capture per capita was greater in groups of 4 relative to groups of 2 and spiders living alone, but there was no detectable difference between the latter two groups (Tukey's HSD: $P = 0.016$, $P < 0.0001$, and $P = 0.088$, respectively). Likewise, spiders captured more prey per capita at high prey densities than at low prey densities (i.e. 1 and 2 vs. 4 and 8 prey spider⁻¹; all $P < 0.05$), but there was no difference among the high and low densities (both $P > 0.1$). The variance in the number of prey captured per capita decreased with increasing spider group size (group size 1: CV = 129.288; group size 2: CV = 71.017; group size 4: CV = 57.579) and prey density (1 prey: CV = 110.922; 2 prey: CV = 85.837; 4 prey: CV = 55.220; 8 prey: CV = 60.336). Furthermore, the proportion of spiders that caught prey increased with prey density (GZLM: $\chi^2_3 = 22.488$, $P < 0.0001$) but there was no effect of spider group size ($\chi^2_2 = 4.774$, $P = 0.092$) or trial ($\chi^2_2 = 0.668$, $P = 0.716$); yet, a greater percentage of spiders in groups of 2 and 4 caught prey relative to those living alone.

6.4.2.2 Experiment 2

Both spider group size and prey density influenced prey capture success, but there was no interaction between these factors (Table 6.1a; Fig. 6.2b). The number of prey captured per capita was greater in groups of 2 than for spiders living alone (Tukey's HSD: $P = 0.006$), but there was no detectable difference between groups of 4 and groups of 2 ($P = 0.224$) and between groups 4 and spiders living alone ($P = 0.274$). At each spider group size, the number of prey captured per capita increased with the number of prey per microhabitat, but the only significant difference was between 1 and 4 prey

microhabitat⁻¹ (Tukey's HSD: $P = 0.001$). Mean prey mass per microhabitat had no effect on prey capture success and was removed from the final model. The variance in the number of prey captured per capita decreased with increasing spider group size (group size 1: CV = 144.914; group size 2: CV = 64.226; group size 4: CV = 56.486) and prey density (1 prey: CV = 106.620; 2 prey: CV = 84.931; 4 prey: CV = 61.492). The proportion of spiders that caught prey was not different across prey densities (GZLM: $\chi^2_2 = 2.956$, $P = 0.228$) and spider group sizes ($\chi^2_2 = 2.747$, $P = 0.253$), although there was an increasing trend with prey density.

6.4.3 Latency to Prey Capture

6.4.3.1 Experiment 1

Spiders in groups of 4 captured their first prey sooner than those in smaller groups, but this effect was only present at low prey densities (i.e. 1 and 2 prey spider⁻¹; Table 6.1b; Fig. 6.3a). At high prey densities (>2 prey spider⁻¹) the latency to the first prey capture was similar across spider group sizes. In groups of 2 and in solitary spiders, the latency to prey capture decreased with prey density, and this effect was especially strong for spiders living alone. However, there was no difference across prey densities for spiders in groups of 4.

6.4.3.2 Experiment 2

There was a positive effect of spider group size on the latency to first prey capture, but no effect of prey density and no interaction between these factors (Table 6.1b; Fig. 6.3b). Spiders in groups of 2 and 4 captured their first prey sooner than those living alone (Tukey's HSD: $P = 0.027$, $P = 0.024$, respectively), but there was no difference between groups of 2 and 4 ($P = 1.000$). Furthermore, there was a decreasing trend with increasing prey density.

6.4.4 Prey Consumption

6.4.4.1 Experiment 1

In groups where spiders caught prey, there was no correlation between the average mass of prey consumed and spider group size (GLM: $F_{2,79} = 0.932$, $P = 0.398$), prey density ($F_{3,79} = 0.691$, $P = 0.560$), and the average number of prey captured per capita ($F_{1,79} = 2.965$, $P = 0.089$). The only positive correlate was the average initial prey mass ($F_{1,79} = 225.380$, $P < 0.0001$). Furthermore, there were no interactions between these factors. On average, spiders at all group sizes and prey densities that caught at least one prey item consumed 65-85% of it during the experiment.

6.4.4.2 Experiment 2

As in Experiment 1, there was no correlation between the average mass of prey consumed and spider group size (GLM: $F_{2,36} = 1.600$, $P = 0.216$), prey density ($F_{2,36} = 1.801$, $P = 0.180$), and the average number of prey captured per capita ($F_{1,36} = 0.942$, $P = 0.338$), except for the average initial prey mass ($F_{1,36} = 34.883$, $P < 0.0001$). Furthermore, there were no interactions between these factors. Most spiders that caught a prey item consumed 60-80% of it during the experiment.

6.4.5 Changes in Body Weight and Condition

Spiders either gained or lost weight overall by producing silk, moving, interacting with neighbours, capturing prey, and consuming prey. The variation in the number of prey captured per capita across treatment groups was consistent with the changes in spider body weight and condition, indicating that captured prey were consumed.

6.4.5.1 Experiment 1

Spiders in groups of 2 and 4 gained more weight relative to those living alone (Table 6.2a; Bonferroni-adjusted pairwise comparisons: $P = 0.004$, $P < 0.0001$, respectively), but there was no difference between the two treatment groups ($P = 0.546$).

As prey density increased, spiders captured more prey and thus experienced a net gain in weight: spiders kept at 4 and 8 prey spider⁻¹ gained more weight relative to those kept at 1 and 2 prey spider⁻¹ (all $P < 0.05$), but there were no differences within these two groups. These changes in body weight lead to corresponding changes in body condition (Table 6.2b). Overall, spiders in groups of 2 and 4 experienced a positive change in body condition relative to those living alone (Bonferroni-adjusted pairwise comparisons: $P = 0.003$, $P < 0.0001$, respectively), but there was no difference between groups of 2 and 4 ($P = 1.000$). At high prey densities (4 and 8 prey spider⁻¹), the overall changes in condition across group sizes were positive, whereas they were negative at low prey densities (1 and 2 prey spider⁻¹), and pairwise differences between each high and low prey density combination were significant (all $P < 0.05$).

6.4.5.2 Experiment 2

Both spider group size and prey density influenced changes in spider weight during the experiment (Table 6.2a). Overall, spiders in groups of 2 gained more weight than those living alone (Bonferroni-adjusted pairwise comparisons: $P = 0.013$), but there was no difference between groups of 2 and groups of 4 ($P = 0.429$) or between groups of 4 and spiders living alone ($P = 0.428$). As prey density increased, spiders gained more weight from prey capture, but this difference was only significant between spiders living alone and those in groups of 4 ($P = 0.027$). These changes in body weight lead to corresponding changes in body condition (Table 6.2b). Spiders in groups of 2 experienced less change in body condition relative to those living alone (Bonferroni-adjusted pairwise comparisons: $P = 0.013$), but there was no difference between groups of 2 and 4 ($P = 0.198$), and between groups of 4 and spiders living alone ($P = 0.816$). These differences increased with prey density: at high prey density (4 prey microhabitat⁻¹), mean final body condition was higher than at the lowest prey density (1 prey microhabitat⁻¹; $P = 0.025$), but there was no difference between all other paired treatment groups (both $P > 0.1$).

6.4.5.3 Control trials

There was no effect of spider group size on weight change when spiders were tested in a 5-day acclimation phase without subsequent exposure to prey, but initial weight had a strong effect (GLM on log-transformed variables: group size: $F_{2, 73} = 1.305$, $P = 0.277$; initial weight: $F_{1, 73} = 610.861$, $P < 0.0001$). An analysis of the changes in body condition generated the same relationships. The results of this control trial thus indicate that the differences in weight change and condition change across group sizes in the prey capture experiment were primarily due to the differential prey capture success, and not differential web building investment.

6.4.6 Web Building

6.4.6.1 Experiment 1

There was a clear effect of spider group size on the mass of silk produced per capita, but no effect of prey density, and there was no interaction between these two factors (Table 6.1c; Fig. 6.4a). Spiders in groups of 2 laid more silk relative to those living in groups of 4 and those living alone (Tukey's HSD: $P = 0.0002$, $P = 0.028$, respectively), but there was no difference between the latter 2 groups ($P = 0.289$), even though spiders in groups of 4 produced less silk relative to those living alone. Furthermore, the magnitude of this difference was greater at high prey densities.

The percentage web cover per microhabitat varied with spider group size. Spiders in groups of 4 colonized the entire space available to them and those in groups of 2 covered practically all of it (mean cover \pm SD = $97.918 \pm 9.386\%$), whereas those living alone built webs that did not cover all the available space ($76.876 \pm 27.445\%$). However, web cover did not vary across prey densities within each group size treatment. There was a similar increase in the total mass of silk per web with spider group size (mean \pm SD; 1 spider: 2.163 ± 0.686 mg; 2 spiders: 5.019 ± 1.246 mg; 4 spiders: 7.851 ± 1.754 mg).

6.4.6.2 Experiment 2

Unlike in Experiment 1, there was no effect of spider group size and prey density on the per capita mass of silk produced (Table 6.1c; Fig. 6.4b). However, spiders in groups of 2 had a tendency to build more webbing than those in the other 2 groups. The percentage web cover per microhabitat varied with group size, but not prey density; spiders in groups of 4 covered the whole space available with silk and those in groups of 2 covered practically all of it (mean cover \pm SD = $98.095 \pm 6.016\%$), whereas those housed alone built webs that covered less space ($88.619 \pm 16.824\%$). Furthermore, the total mass of silk per web increased with spider group size (mean \pm SD; 1 spider: 1.837 ± 0.424 mg; 2 spiders: 4.140 ± 1.158 mg; 4 spiders: 7.039 ± 2.094 mg).

6.4.6.3 Control trials

A similar effect of group size on the mass of silk produced as in Exp. 1 was found during the acclimation period, when spiders were housed in groups of 1, 2 or 4 for 5 days without being tested for prey capture (GLM: $F_{2, 74} = 7.235$, $P = 0.001$). Spiders in groups of 2 laid more silk compared to those in groups of 4 or living alone (Tukey's HSD: $P = 0.024$, $P = 0.001$, respectively), but there was no difference between those in groups of 4 versus housed alone ($P = 0.537$). This means that the differences in per capita silk production between spider group sizes during the prey capture experiment reflect differential web building efforts during the acclimation (i.e. settlement) phase. Nevertheless, there was an overall increase in the amount of silk mass produced after the prey capture experiment due to prey wrapping with silk.

6.4.7 Ratio of Foraging Returns to Foraging Investment

6.4.7.1 Experiment 1

The main foraging investment for a web-building spider is the production of silk for prey capture. The per capita ratio between the number of prey captured (foraging returns) and the mass of silk produced (foraging investment) increased with spider group size and prey density, but there was no interaction between these two factors (Table

6.1d). Spiders in groups of 4 captured more prey per unit of silk mass than those in groups of 2 or alone (Tukey's HSD: $P = 0.003$, $P = 0.0001$, respectively; Fig. 6.5b), while there was no difference between spiders in groups of 2 and alone ($P = 0.925$). Depending on the prey density, spiders in groups of 4 captured on average 1.8-2.4 more prey per unit silk mass than those housed alone, and there was a 1.3-2.0 \times difference compared to those in groups of 2 (Fig. 6.5b).

6.4.7.2 Experiment 2

As in Experiment 1, the ratio between the number of prey captured and the mass of silk produced varied with spider group size and prey density (Table 6.1d). Overall, spiders in groups of 2 captured more prey per unit of silk mass than those living alone (Tukey's HSD: $P = 0.027$), but there was no difference between those in groups of 2 and 4 ($P = 1.000$) and between those in groups of 4 and alone ($P = 0.257$). Furthermore, this ratio of foraging return to foraging investment increased with prey density, with a significant difference between the lowest and highest prey densities ($P = 0.004$). At the lowest prey density (1 prey microhabitat⁻¹), spiders in groups of 2 captured more prey per unit of silk than those in the other 2 groups, while at the highest prey density (4 prey microhabitat⁻¹) spiders in groups of 2 and 4 experienced similar net foraging returns that were greater than that of spiders living alone (Fig 6.5b).

6.4.8 Movement and Spatial Distribution

6.4.8.1 Experiment 1

The average daily distance moved per capita decreased over time (Table 6.3a; Fig. 6.6a): many spiders travelled from one side of a microhabitat to the other at the beginning of the acclimation phase, but they progressively moved less. There was no significant difference between spider group sizes or prey density treatments. However, during the prey capture phase that followed the acclimation period, spiders in groups of 4 showed a peak of activity during the first 8 h following prey introduction, while there was no major change in the amount of movement for spiders in groups of 2 and living alone.

Overall, spiders in groups of 4 stayed closer to each other (mean nearest-neighbour distance \pm SD = 30.375 ± 5.660 cm; range: 3-91 cm) than did those in groups of 2 (66.750 ± 28.639 cm; range: 8-115 cm), both during the acclimation period and the prey capture phase (Table 6.3b). These distances approximate 25% and 50% of the total length of a microhabitat used in the experiment, respectively (see Fig. 6.1). Thus, spiders in groups of 2 and 4 were evenly spaced out. There were no changes in average nearest-neighbour distances over time and across prey density treatments.

6.4.8.2 Experiment 2

Spiders in this experiment had a tendency to move more than those tested in Experiment 1 during the acclimation phase (Fig. 6.6b). The average distance moved by each spider decreased over time between the acclimation phase and the prey capture phase, and there were no differences across spider group sizes and prey densities (Table 6.3a). Spiders in groups of 4 stayed closer to each other (mean nearest-neighbour distance \pm SD = 34.727 ± 4.321 cm; range: 3-101 cm) than did those in groups of 2 (78.135 ± 24.691 cm; range: 7-111 cm), both during the acclimation period and the prey capture phase (Table 6.3b). There were no differences over time nor across prey densities. These distances approximate 25% and 60% of the total length of a microhabitat used in the experiment, respectively, which again suggest that spiders were evenly spaced out.

6.5 Discussion

The results of this study clearly demonstrate the fitness value of group living in terms of foraging for a facultatively group-living animal. Using an experimental approach, we showed that both prey availability and spider group size determine prey capture success and corresponding changes in body condition associated with group living in *L. hesperus* spiders. When prey were abundant (Experiment 1), individuals in large groups experienced greater prey capture success than those in small groups or living alone, but when prey were limited (Experiment 2), spiders living in small groups

captured more prey, even though the differences between group sizes were small. Group living did not promote agonistic interactions, regardless of group size, and spiders living in groups captured prey individually. Furthermore, the foraging return on investment covaried with group size and prey availability, such that spiders in large groups caught up to twice as many prey per unit of silk produced than those in small groups or living alone when prey were abundant, whereas the return on investment was maximized by spiders in small groups when prey were limited. Collectively, these findings provide support for the hypothesis that foraging performance varies with the social context (i.e. group versus solitary living) and that the size of a group determines the foraging payoffs. A summary of the main results combining data from Exp. 1 and 2 is presented on Fig. 6.7.

Group size influenced the prey capture behaviour of *L. hesperus* spiders in two ways. First, the number of prey captured per capita varied with group size: when prey were abundant, spiders in groups of four captured more prey than those living alone, while there was no difference between groups of two and solitary individuals; when prey were scarce, spiders in groups of two caught more prey than those living alone, and spiders in groups of 4 experienced intermediate prey capture success. A representation of these data on the same scale of prey density (Fig. 6.7a) shows that spiders in small groups have the highest prey capture success at low and intermediate prey densities. Second, spiders foraging in groups experienced lower variance in prey capture success relative to solitary ones, and the variance further decreased with increasing group size. Together, these data suggest that prey availability determines whether living in large vs. small groups is the preferred foraging strategy. When prey is limited, spiders living in large groups have a higher chance of catching prey compared to those living alone, although they also have to compete with other group members to secure a meal, which is why they have low individual foraging success. However, foraging success is higher overall for spiders living in small groups, as they are more likely to obtain prey due to a low variance in prey capture and their having to compete for limited prey with fewer individuals. Conversely, when prey are very abundant, spiders in large groups do best overall, since they have access to more food and can catch prey more readily than those in small groups or living alone. These results agree with a prediction of risk-sensitive

foraging theory, which states that group foraging should lead to an increase in prey capture success and reduce the variance in prey capture (Mangel 1990; Caraco et al. 1995; Bateson & Kacelnik 1998). This prediction has been verified in other species of spiders, such as colonial spiders of the genus *Metepeira* and the cobweb-weaving spider *Achaearanea tepidariorum*, where individuals gain foraging benefits from group living when prey are abundant and thus form groups under these conditions (Uetz 1988; Rypstra 1989).

In general, spiders more commonly experience low prey densities (Wise 1993), and many species do not live in groups under these conditions because it promotes competitive interactions (Whitehouse & Lubin 2005). In fact, some of the prey densities tested in the prey abundance scenario are probably rarely or never experienced by *L. hesperus* spiders in nature. However, our results show that even when prey is limited, group-living *L. hesperus* spiders have higher foraging success, or at least comparable success, than those living alone (see Fig. 6.7). The positive effects of group size on foraging success are likely to reach an optimum at a particular size, since foraging interactions in very large groups may involve antagonism between group members, which would cause individual foraging benefits to sharply decline. The group sizes tested in this experiment correspond to common sizes of *L. hesperus* groups found in nature (see Chapter 2), which represent moderate densities.

Of course, other factors that were not considered in this study may influence the likelihood of group formation in *L. hesperus* spiders, such as the degree of relatedness among group members or the physical attributes of a habitat (Lubin 1974; Higashi & Yamamura 1993; Rannala & Brown 1994). Furthermore, nutritional state impacts foraging and group-living decisions in spiders and other animals (Bilde et al. 2002; Hensor et al. 2003; Salomon 2007), which implies that foraging payoffs may vary in different ways between group- and solitarily-living spiders according to prey density when spiders are food-deprived and in poor condition (unlike those tested in this study whose access to prey had only been restricted for a few days). Clearly, our results invite

further research on the propensity to form groups at different prey densities and feeding states.

An important finding of this study is the greater net foraging gains of individuals living in small and large groups relative to those living alone at low prey densities (Fig. 6.7d). When prey were limited, spiders in groups of 2 had higher net foraging gains overall, and spiders in groups of 4 and living alone had overlapping net foraging gains. When prey were plentiful (Exp. 1), the ratio between the number of prey captured per capita and the amount of silk produced was significantly greater for spiders in large groups compared to those in small groups or living solitarily. Furthermore, these differences increased with prey density because spiders did not produce more silk at higher prey densities (Fig. 6.7c). These results are consistent with previous studies showing that group living confers net benefits by reducing energy expenditures associated with movement or the construction of foraging and protective structures (e.g. shoaling fish, Herskin & Steffensen 1998; spiders, Lloyd & Elgar 1997; insect larvae, Axén & Pierce 1998). Web-building spiders are sedentary predators whose primary and most costly foraging investment involves the construction and maintenance of a web (Ford 1977). *Latrodectus hesperus* spiders in both small and large groups shared a common web that spanned the entire space available to them instead of building individual webs, which for those in large groups reduced per capita web-building costs. This web sharing strategy may improve the sensory perception of prey via interconnected framework threads, and thus lead to an increase in individual foraging success, as was seen in this study. We were unable to assess whether each group member invested equally into web building, due to the difficulty of measuring this type of variation. Such differences in foraging investment would create an imbalance in individual foraging payoffs and cause within-group conflict, with a possible dissolution of the group and/or an increase in the level of agonism (Komdeur 2006). However, our results suggest that even if there were any disparities between group members, there were no noticeable signs of conflict.

Group living in *L. hesperus* did not promote aggression or cannibalism, even at low prey abundance or in large groups. Spiders shared webs and tolerated the close proximity of conspecifics over several days, suggesting that the experimental conditions were conducive to group living. Intra-sexual cannibalism is widespread among invertebrate predators such as spiders, and it is influenced by a variety of factors, including food availability, size asymmetries, feeding history, age and habitat structure (Polis 1981; Elgar & Crespi 1992; Wise 2006). The degree of relatedness between individuals may also affect the level of cannibalism through kin recognition, and lead to the formation of groups of related individuals (Reeve 1989; Evans 1999; Bilde & Lubin 2001). In our study, however, spiders living together were not related, and we controlled for differences in size, age, feeding history, and habitat structure. The only factors that we manipulated were prey availability and group size, and neither of these influenced the level of cannibalism. This result contrasts with previous studies in spiders where the likelihood of cannibalism increased with group size due to higher encounter rates between individuals (Bilde & Lubin 2001), and at low prey abundance to compensate for the lack of an alternative food source (Wagner & Wise 1997). Therefore, the absence of aggression between *L. hesperus* group members indicates an aptitude to behave socially. The foraging benefits obtained from group living might strengthen mutual tolerance and favour group cohesion.

There are several reasons why foraging in a group may be advantageous and lead to an increase in foraging efficiency. The availability of social information from other group members may facilitate prey detection and capture (Valone & Templeton 2002), and in the case of web-building spiders, web clustering may increase an individual's chances of prey capture via the "ricochet effect", where prey are deflected between neighbouring webs or between different areas of a large web and thus more likely to be caught (Uetz 1989). These foraging benefits are expected to vary with group size, and one might predict greater efficacy in larger groups (until a given size threshold is reached). Three lines of evidence suggest that living in a group enhances prey detection and interception for *L. hesperus* spiders: first, at low prey densities, spiders in small and large groups caught prey sooner than those living alone (Fig. 6.7b); second, the presence

of abundant prey caused spiders in large groups to move more, which may result from improved prey detection; and third, the amount of silk per web and microhabitat web coverage both increased for group-living spiders and also with group size, which may facilitate prey interception. Overall, these changes in foraging activity lead to greater prey capture success. Similar effects of group living on the timing and likelihood of prey capture were found in cooperatively foraging spiders (Jones & Parker 2000; Kim et al. 2005); however these studies focused on groups of juvenile spiders, while our results pertain to adult females, in which territoriality is often more pronounced. Another important foraging benefit of living in large groups is access to larger prey (Nentwig 1985; Pasquet & Krafft 1992; Powers & Avilés 2007), which may increase growth rates and reproductive output (Rypstra 1993). However, this is a characteristic of social species that generally cooperate in prey capture (but see Pekár et al. 2005), unlike *L. hesperus* spiders that forage individually.

The function of group living is not only tied to foraging, which is why it is necessary to consider the interplay between different fitness currencies to fully understand how group size influences social organization. For instance, living in a large versus small group may affect individual survival rates due to size-dependent differences in anti-predator protection (Clutton-Brock et al. 1999; Uetz et al. 2002; Fernández et al. 2003), nest structure resilience (Evans 1998), or level of egg parasitism (Hieber & Uetz 1990), and also affect reproductive fitness through differential offspring survival or reproductive output (Emlen 1991; Avilés & Tufino 1998; Hatchwell & Komdeur 2000). It would be interesting to compare the relative importance of the group-size related foraging benefits uncovered in the study to that of the potential protective role conferred by large versus small webs, or the reproductive performance of individuals at various group sizes.

In conclusion, we have shown that group size is a key determinant of foraging interactions between facultatively group-living spiders, and that it affects individual fitness through differential foraging success. Group living among *L. hesperus* spiders is tied to accruing foraging benefits, especially when food is abundant, which could favour

and maintain grouping relationships. These findings contribute to our understanding of how sociality may have evolved in spiders by providing empirical evidence for the role of foraging associations as promoters of group living. The use of an experimental approach such as ours to address questions pertaining to the adaptive value of group living often yields clear relationships between the factors involved, and should thus be used more widely. It would be interesting to examine the effects of group size on foraging behaviour in a natural setting, to determine whether it reflects the results of our experiment. In this study, we focused on group living in a foraging context. However, the dynamics of grouping behaviours depend on the ecological context in which these behaviours are expressed. Further research is needed to examine how several components of fitness (e.g. growth rate versus survival) are traded-off and contribute to the formation and maintenance of groups of different sizes.

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Table 6.1. GLM analyses of the effects of spider group size and prey density on: (a) the number of prey captured per capita (log-transformed); (b) the latency to first prey capture (log-transformed); (c) the per capita mass of silk produced; and (d) the per capita ratio between the number of prey captured and the mass of silk produced, by *L. hesperus* spiders

Source	Experiment 1			Experiment 2		
	df	F	P	df	F	P
(a) Number of prey captured per capita						
Group size	2, 106	12.988	<0.0001	2, 54	5.217	0.008
Prey density	3, 106	11.851	<0.0001	2, 54	7.660	0.001
Group size × Prey density	6, 106	0.308	0.932	4, 54	0.051	0.995
(b) Latency to first prey capture						
Group size	2, 75	3.969	0.023	2, 34	4.519	0.018
Prey density	3, 75	3.712	0.015	2, 34	1.459	0.247
Group size × Prey density	6, 75	1.875	0.096	4, 34	0.164	0.955
(c) Silk mass per capita						
Group size	2, 106	8.701	0.0003	2, 54	2.769	0.072
Prey density	3, 106	2.123	0.100	2, 54	2.102	0.132
Group size × Prey density	6, 106	0.447	0.846	4, 54	0.242	0.913
(d) Ratio of prey capture to silk production						
Group size	2, 106	12.425	<0.0001	2, 54	3.789	0.029
Prey density	3, 106	7.675	0.0001	2, 54	5.732	0.006
Group size × Prey density	6, 106	0.901	0.497	4, 54	0.113	0.978

Table 6.2. GLM analyses of the effects of spider group size and prey density on (a) per capita weight change (log-transformed final weight), and (b) per capita changes in body condition (log-transformed final condition), among *L. hesperus* spiders

Source	Experiment 1			Experiment 2		
	df	F	P	df	F	P
(a) Change in body weight						
Group size	2, 105	11.441	<0.0001	2, 53	4.430	0.017
Prey density	3, 105	10.356	<0.0001	2, 53	3.839	0.028
Initial weight	1, 105	165.710	<0.0001	1, 53	71.813	<0.0001
Group size × Prey density	6, 105	0.304	0.934	4, 53	0.152	0.961
(b) Change in body condition						
Group size	2, 105	9.454	0.0002	2, 53	4.562	0.015
Prey density	3, 105	8.076	<0.0001	2, 53	3.828	0.028
Initial condition	1, 105	120.606	<0.0001	1, 53	41.574	<0.0001
Group size × Prey density	6, 105	0.401	0.877	4, 53	0.230	0.920

Table 6.3. GLMM analyses of the effects of different factors on (a) the average per capita distance moved by *L. hesperus* spiders, and (b) the average nearest-neighbour distances in spider group sizes 2 and 4 (log-transformed)

Source	Experiment 1			Experiment 2		
	df	F	P	df	F	P
(a) Distance moved						
Group size	2, 113.9	2.646	0.075	2, 133.9	1.633	0.199
Prey density	3, 113.9	0.380	0.768	2, 133.9	0.275	0.760
Day/time	5, 349.0	4.007	0.002	5, 233.1	3.814	0.002
(b) Nearest-neighbour distances						
Group size	1, 75.0	94.790	<0.0001	1, 71.9	144.357	<0.0001
Prey density	3, 75.0	1.038	0.381	2, 71.9	2.208	0.117
Day/time	6, 270.0	0.950	0.460	6, 183.2	1.891	0.085

In each analysis, non-significant interaction terms were removed from the final model to increase the fit based on Akaike Information Criterion (AIC) scores (see Burnham & Anderson 2002)

Figure 6.1. Wooden sheds (i.e. spider microhabitats) used in both experiments (dimensions: 125 cm L \times 15 cm W \times 8 cm H). The sheds had a removable lid with underneath a sheet of metal meshing (mesh size: 2 mm) that was stapled onto the sides, and under which *L. hesperus* females built their webs. The lid and metal meshing were 1 cm apart to prevent females from attaching silk to the underside of the lid. Both openings were closed off with synthetic meshing (mesh size: 1 mm), and in the centre of each sheet of meshing was glued a circular piece of plastic with a hole in the middle (hole diameter: 16 mm) that was capped with a rubber cork. These holes were used to introduce prey under the sheds

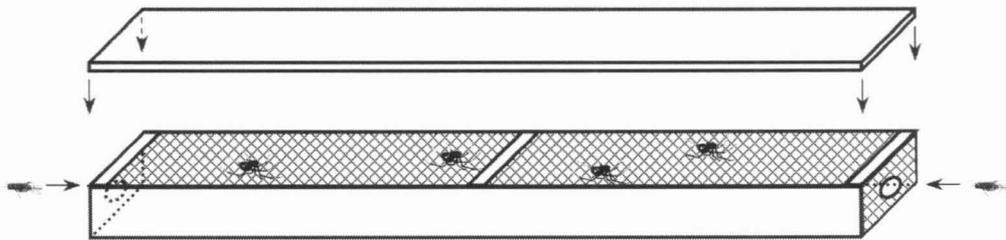


Figure 6.2. Mean (\pm SE) number of prey captured per capita by *L. hesperus* females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2

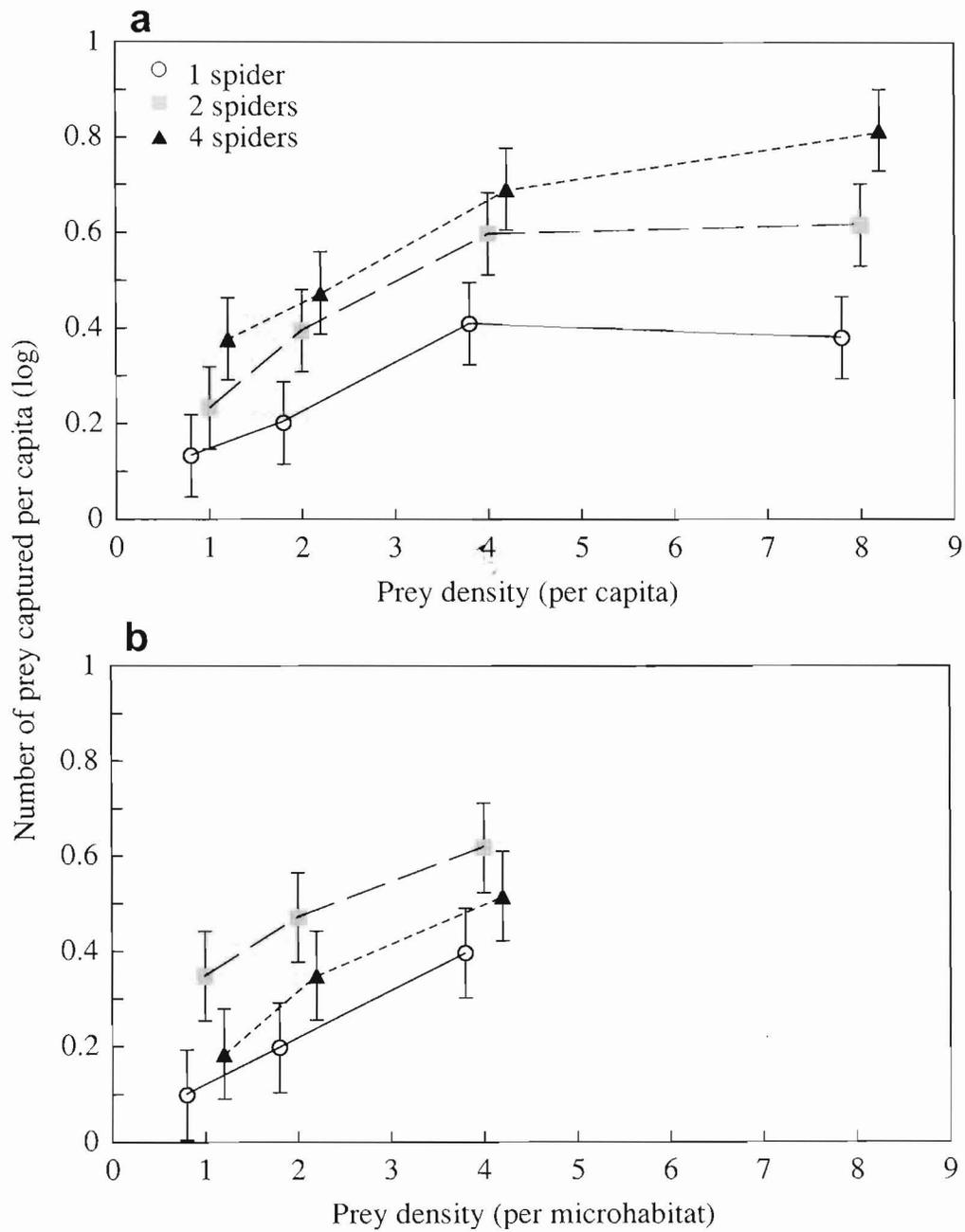


Figure 6.3. Mean (\pm SE) latency to first prey capture (min) by *L. hesperus* females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2

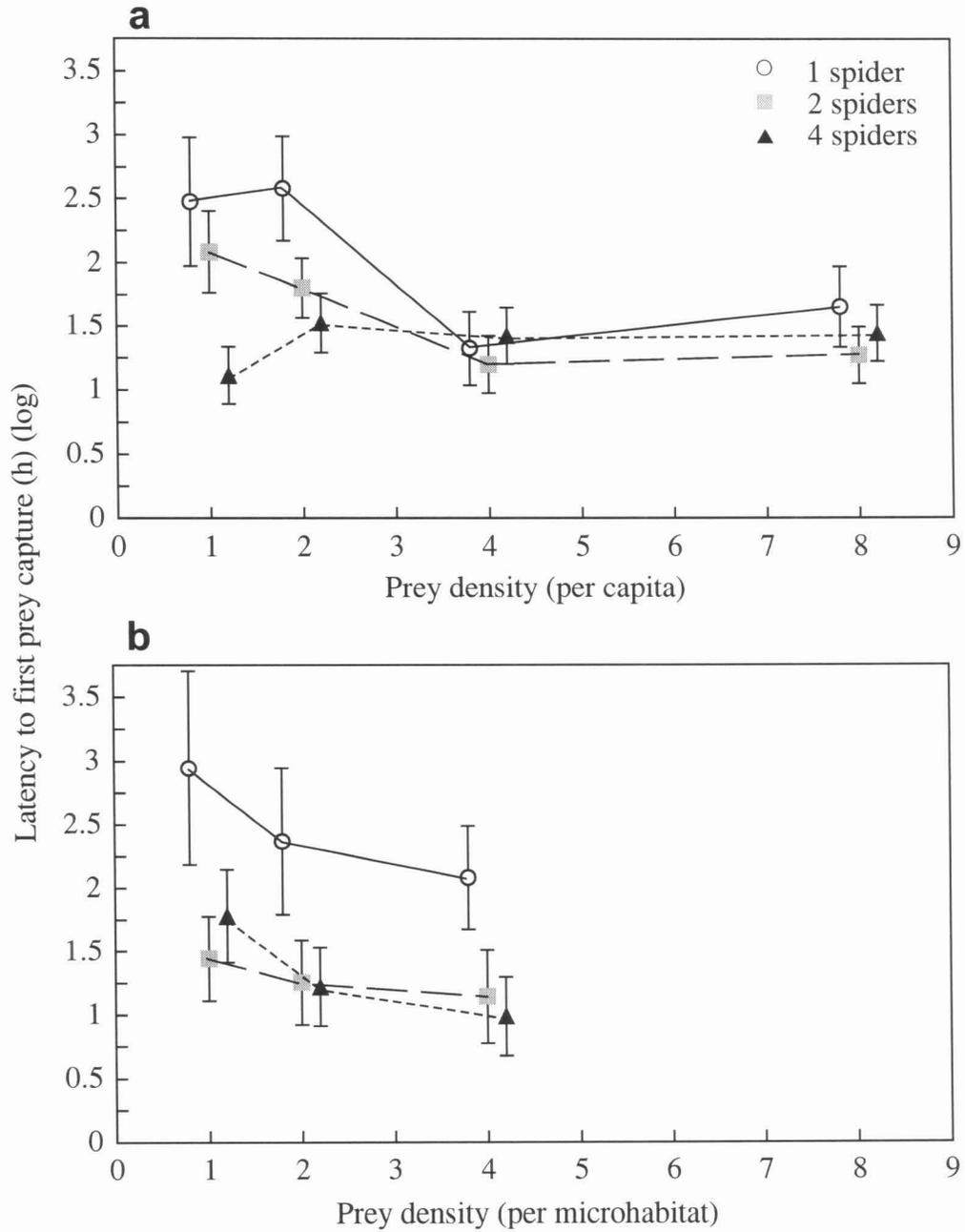


Figure 6.4. Mean (\pm SE) mass of silk (mg) produced by *L. hesperus* females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2

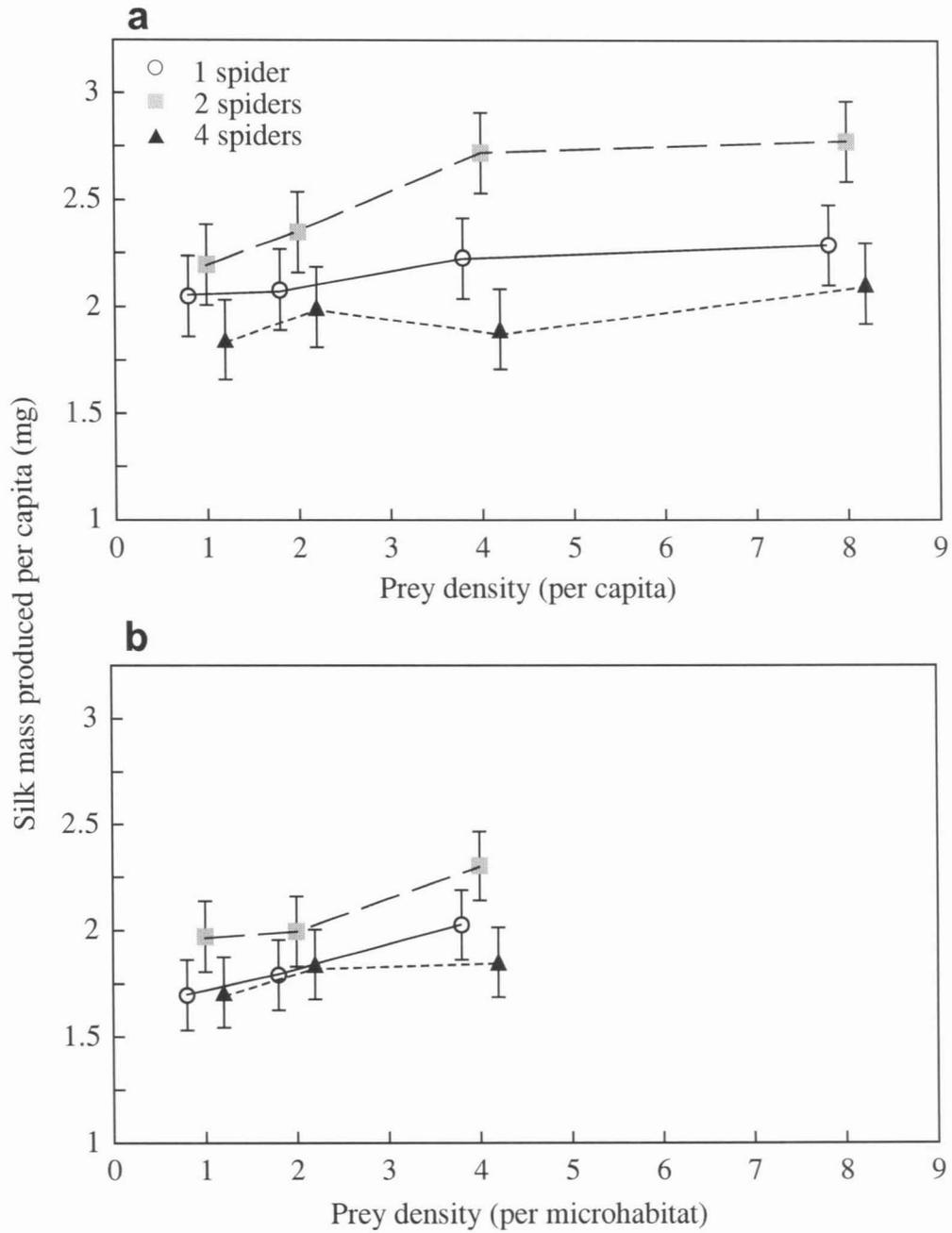


Figure 6.5. Mean (\pm SE) ratio between the number of prey captured and the mass of silk produced by *L. hesperus* females at different group sizes and prey densities in (a) Experiment 1, and (b) Experiment 2

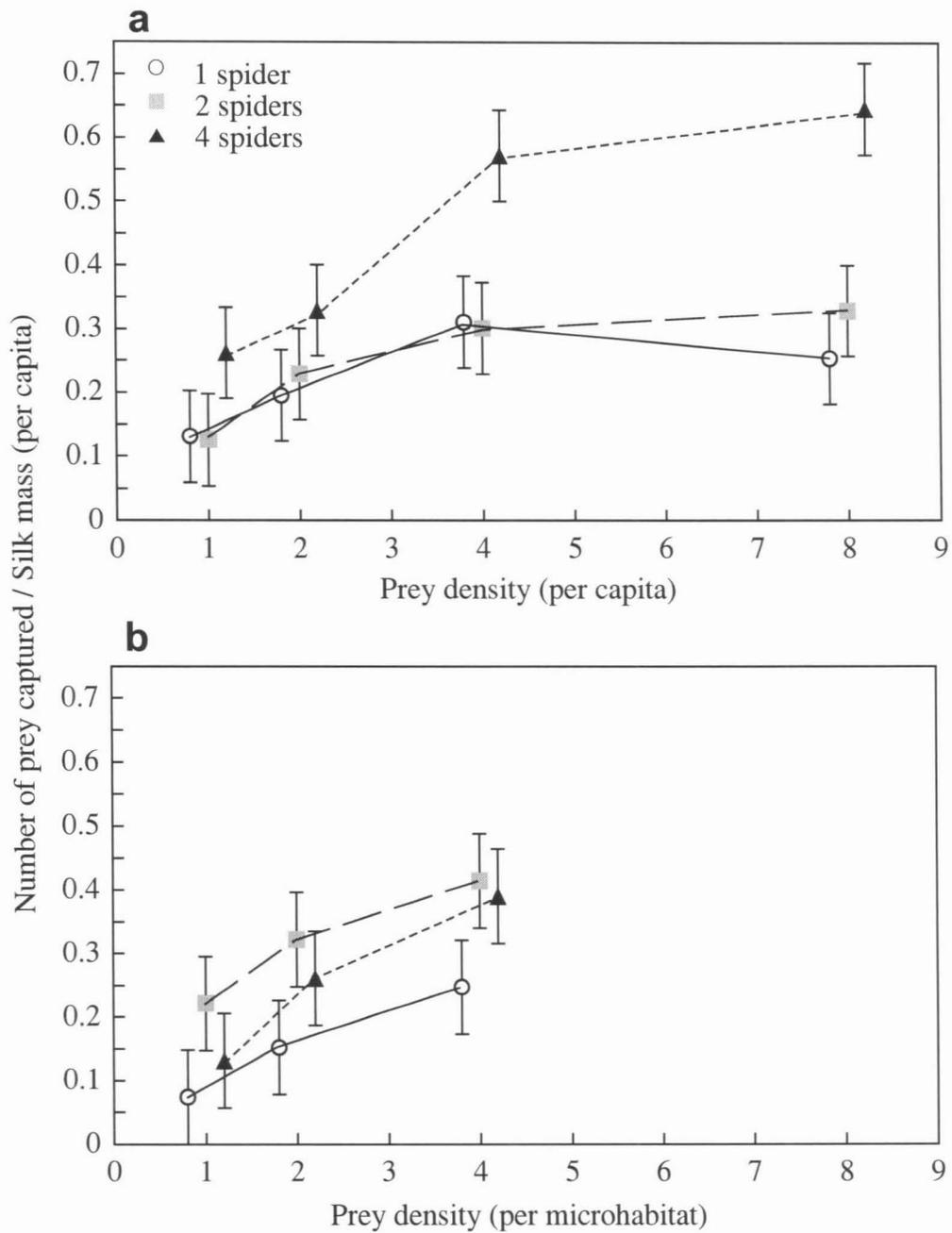


Figure 6.6. Mean (\pm SE) distance moved by *L. hesperus* females at different group sizes and prey densities over the course of the acclimation period and prey capture (experimental) phase in (a) Experiment 1, and (b) Experiment 2. Distances on the y-axis represent the mean number of microhabitat zones travelled over 2 consecutive census times

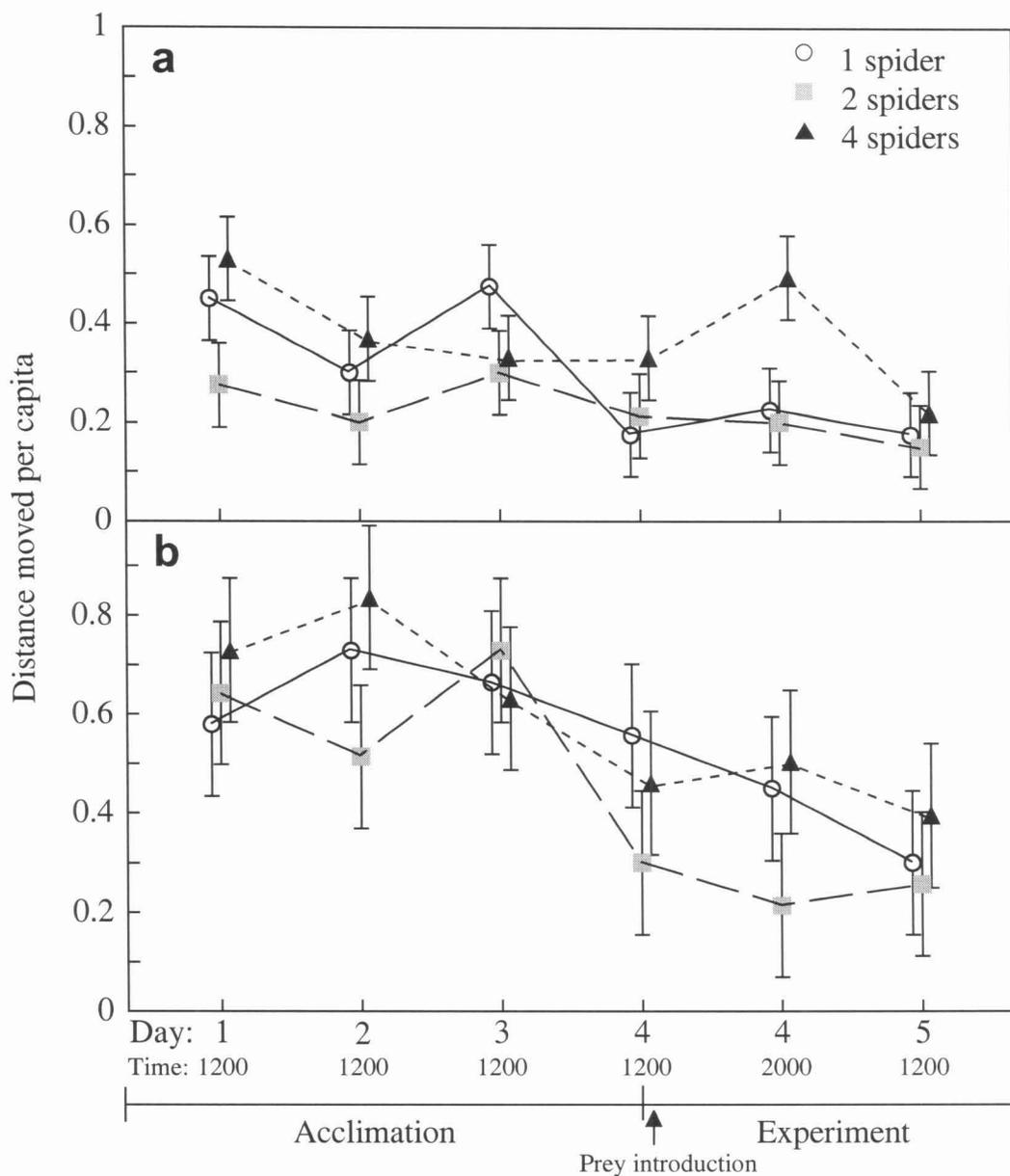
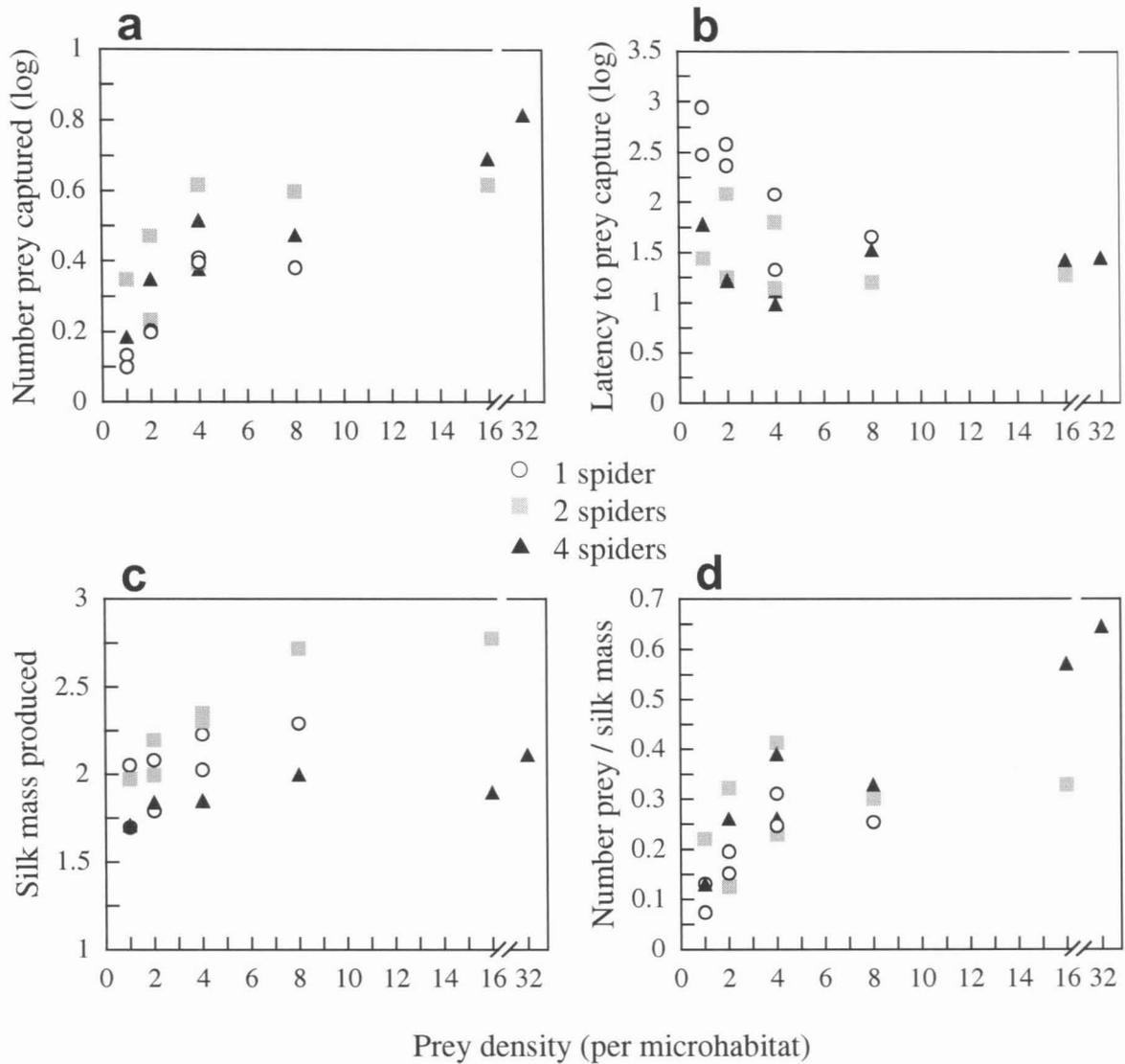


Figure 6.7. Summary of data from Exp. 1 (prey abundance) and Exp. 2 (prey limitation) for relationships between prey density and (a) the number of prey captured per capita (log-transformed), (b) the latency to first prey capture (log-transformed), (c) the mass of silk produced per capita, and (d) the ratio between the number of prey captured and the mass of silk produced per capita. Results of both experiments are plotted on the same scale for the x-axis (number of prey per microhabitat), and datapoints of each experiment are represented with the same symbol within each spider group size treatment. Each datapoint represents a mean value of a given response variable



Chapter 7: **GENERAL CONCLUSION**

7.1 Summary of Main Findings, Implications and Perspective

Decisions by individuals about where to live and what resources to exploit are strongly influenced by the distribution of other co-occurring individuals. Their presence or proximity may on the one hand be used to assess resource quality or accessibility, while it may also serve to improve resource acquisition and thus accrue individual fitness. An individual's social behaviour determines the nature of its associations with other conspecifics and the types of interactions involved.

The results of this study show that *Latrodectus hesperus* spiders facultatively live in groups and that their group-living strategy depends on environmental conditions such as prey availability and spider density, as well as individual nutritional state and group size. This constitutes the first evidence of group-living behaviour in the genus *Latrodectus*. Subadult and adult females spontaneously join and form groups by sharing webs at certain times of the year (late summer, fall and winter), while they live alone at other times (late spring and summer). Furthermore, juveniles form groups after emergence from the egg sacs in the summer. These associations are not based upon microhabitat shortage and they were observed over different years. Furthermore, I show that *L. hesperus* females are able to perceive the presence of neighbours and their webs and adjust their web-building and microhabitat settlement behaviours accordingly. Both prey availability and the nutritional state of a spider (which are linked) play an important role in determining the social dynamics, i.e. the likelihood of cannibalism, group formation, and group persistence. In addition, females experience different levels of foraging success depending on the size of the group in which they are living and the availability of prey, such that living in small or large groups may provide net foraging benefits under certain conditions. Finally, the fact that *L. hesperus* spiders coexist and partition resources with *Tegenaria* spp. spiders has little effect on their social behaviour.

Animals such as *L. hesperus* spiders that show intermediate forms of social behaviour, in which either solitary or group living tendencies are expressed depending on the ecological context, could be model study organisms to provide insight into the

selective pressures and individual traits involved in the evolution of different social strategies. The general hypothesis about the origin of sociality in spiders is that solitary living is the plesiomorphic state from which various types of social systems have evolved across different lineages (Agnarsson et al. 2006). Intermediately social spiders such as *L. hesperus* offer some perspective on the transitions involved in a particular evolutionary pathway, by showing how ecology and behaviour may interplay to produce naturally selected phenotypes. The plasticity in their social behaviour may be used to study potential adaptations to changing environments.

The extent of group living among *L. hesperus* spiders is unexpected, first because it involves associations among adult and subadult females, which is unlike many examples of group living among juveniles in intermediately social spiders (e.g. Avilés & Gelsey 1998; Kim et al. 2005); and second because it contrasts with the usual pattern of lower levels of sociality at higher latitudes (such as the temperate region in which this study was conducted) for spiders and other arthropods (Wilson 1975; Richards 2000; Avilés et al. 2007), even though exceptions and other patterns also exist (Furey 1998; Cronin & Schwarz 2001; Jones et al. 2007). This again illustrates the overall plasticity of social behaviours that allows individuals to form groups under unusual circumstances. The net energetic, protective and/or foraging advantages gained from group living may cause subadult and adult females to join or form groups in the fall and winter, while they other selective pressures may cause them to live solitarily during the egg-laying season.

These results raise interesting questions concerning the nature of group-living relationships in *L. hesperus*. More research is needed to further characterize individual social strategies in different contexts and the factors that modulate them. For example, one unresolved question is whether closely related individuals are more likely to associate and form groups. The degree of relatedness between co-occurring individuals has been shown to affect the likelihood of group formation and agonism in other spider species, which in some cases may result in high levels of inbreeding (Riechert & Roeloffs 1993; Evans 1999; Bilde et al. 2005). Such a strategy makes sense from an evolutionary perspective, as closely related individuals that live in groups and cooperate in various

activities will accrue indirect fitness benefits through kin selection, and are less likely to suffer the costs involved in asymmetric relationships. It is unlikely that only closely related *L. hesperus* spiders would associate, given the tendency for juveniles to disperse (pers. obs.) and the fact that I was able to maintain groups of unrelated females in the laboratory; however, it remains to be elucidated and constitutes a goal of my future research.

It would also be interesting to compare the conditions that influence group formation vs. group maintenance. Group living may lead to different outcomes depending on the duration of inter-individual associations; for example, spiders that form groups to exploit profitable patches of food resources (Whitehouse & Lubin 2005) may rapidly experience the consequences of associating with conspecifics, whereas groups involving parent-offspring interactions may persist if vertical relationships influence growth and/or survival. Furthermore, since group living often involves associations between different age-classes, one should investigate social dynamics in these different contexts. In *L. hesperus*, most of the group living is observed from late summer to winter; yet, my results show that most of the foraging takes place from late spring to late summer, which is when females lay eggs and juveniles emerge. This begs the question of what causes these spiders to be solitary and territorial during the reproductive season? Further research is needed to explore group-living interactions at different times of year when reproductive, foraging, or other activities predominate. Finally, the results presented here provide evidence that *L. hesperus* spiders form heterospecific associations with *Teegenaria* spp. spiders. We are currently examining these associations in more detail, and it would be interesting to contrast social interactions involved in intraspecific vs. interspecific associations, to determine the directionality of each and the factors that influence their dynamics.

7.2 Future Directions: Building a Theory of Group Living ¹

A further step into the study of the evolution of group living in spiders, which represents an extension of the research presented in this thesis, is the development of a theoretical model of group living that explores the adaptive value of behaving socially under different ecological scenarios. Few attempts have been made to build a theory that makes predictions about the formation and maintenance of group living in spiders (Caraco et al. 1995; Ulbrich & Henschel 1999; Avilés 2002; Jones et al. 2007). Group living, and by extension sociality, is rare among spiders and the few species that express social tendencies live either colonially or cooperatively (reviewed in Avilés 1997; Hieber & Uetz 1997; Whitehouse & Lubin 2005). The function of group living varies widely between species, and includes reproductive, protective and/or foraging associations. Given this variation, it would be useful to establish a general theoretical framework that characterizes the dynamics of group living in this taxon.

Here, we develop a dynamic game model of group living in spiders. This theory specifically addresses the question of what is the evolutionary stable microhabitat selection strategy for a spider that can either live solitarily or in a group. In our model, we consider individuals that live in a heterogeneous environment characterized by patchily distributed microhabitats in which they can forage and reproduce, and by doing so may interact with other individuals. Microhabitats contain food resources (i.e. prey), which are fixed and non-depletable, and also provide space for settlement. The general assumption is that individuals seek to maximize lifetime reproductive success, which depends on their foraging and reproductive decisions. We hypothesize that two factors will impact a spider's microhabitat selection decisions, and thus its group living behaviour: (1) current nutritional state, which is based on an individual's foraging history and energy reserves, and (2) the size of a group of conspecifics within a given microhabitat. Previous studies have shown that both of these factors may individually affect foraging and reproductive behaviours in various spider species (Pasquet et al. 1999; Bilde et al. 2002; Uetz et al.

¹ This work is co-authored by Maxence Salomon and Bernard D. Roitberg

2002), but none has examined what effects they have when considered together. We evaluate the impact of different ecological scenarios by varying parameters relating to the type of spider considered (e.g. web-building vs. cursorial, aerial vs. ground forager) and its social tendencies (e.g. territorial vs. cooperative). This allows us to make predictions about group-living behaviours for a range of spiders for which different microhabitat selection rules apply.

We combine two modelling approaches: dynamic state-variable programming and evolutionary game theory. The first approach is an optimization method that has been used to predict the behavioural strategies of a wide range of animals in various contexts, such as foraging, habitat selection, and mating (e.g. Roitberg & Mangel 1997; Clark & Mangel 2000; Wajnberg et al. 2006). Dynamic-state variable models differ from other models in that they explicitly consider the different states experienced by an individual, such as its level of energy reserves or reproductive state, and treat them as dynamic variables that may influence the decisions involved in a particular biological problem, and in turn their fitness outcomes (see Mangel & Clark 1988 for details). This modelling method computes the optimal decisions for all combinations of state values based on the maximization of the expected fitness associated with each possible outcome, and thus provides a flexible framework with which to analyze tradeoffs under different scenarios. This is therefore a deterministic approach that solves a single optimum for each behavioural decision in a stochastic context, where events (e.g. cannibalism, prey capture) happen with given probabilities.

A shortcoming of this modelling technique for solving some evolutionary problems is that it assumes that an individual's fitness payoff is independent of the actions of other individuals, and thus it does not take into account the different types of interactions that take place between individuals or species (e.g. competition), and how other individuals' behaviours may influence behavioural decisions. To take this into account in our model, we concurrently apply evolutionary game theory, which is used to examine the impact of frequency-dependent interactions on behavioural strategies (see Maynard Smith 1982). In any biological situation, the interests of individuals involved do not necessarily coincide,

and game theory provides a method to specifically consider the fitness payoffs associated with all possible outcomes of all possible interactions between players participating in the game. Within this frequency-dependent framework, individuals make decisions based on the most profitable outcome, which in itself is based on the decisions made by other individuals. In other words, individuals behave strategically, i.e. they adopt a set of decision rules that applies to the various interactions involved in a particular game. The solution of an evolutionary game is an evolutionary stable strategy (ESS), which is defined as a strategy, which, if adopted by all members of a population, cannot be invaded under natural selection by any other “mutant” strategy (*sensu* Maynard Smith 1982; Vincent & Brown 1988). Evolutionary game theory has widely been used to model biological problems involving conflicts of interest such as mating, habitat selection, cannibalism, competition, and social foraging, to name but a few (Brown 1990; Mangel 1990a, b; Hugie & Dill 1995; Perry & Roitberg 2005). Our overall modelling approach therefore generates predictions about group living behaviour in spiders through the analysis of state-dependent and frequency-dependent microhabitat selection decisions using dynamic games (e.g. Mangel 1990a).

7.2.1 The Model

7.2.1.1 Basic Structure of the Algorithm

We model microhabitat selection behaviour in spiders using a dynamic game approach where individuals make state-dependent decisions that are influenced by the behaviours of co-occurring individuals, i.e. we consider frequency-dependent strategies. Spiders are all assumed to be of the same age and sex and we model the behaviour of adult females, which perform various activities associated with foraging and reproduction, and are further assumed to forage and reproduce throughout their lifetime (an assumption that holds true for some species). The model has four different state variables: (1) time (t) represented as a series of discrete time units (in this case days), (2) the current nutritional state of a spider (x), (3) the size of a group of spiders (g) within a given microhabitat (note that group size does not include the focal individual), and (4) the web state (w), which refers to the presence or absence of at least one web within a

microhabitat. This last state can be set to 0 when non-web building spiders are considered.

In each time step (t) and for each possible value of a state variable (x, g, w), a spider is faced with two consecutive decisions: (1) upon encountering a microhabitat, whether to accept it and stay or reject it and leave, and (2) if the microhabitat is accepted, whether to forage or reproduce (i.e. lay eggs) in it. We assume that individuals always seek to forage or reproduce upon entering a microhabitat. For each decision, the two alternatives are mutually exclusive, and at each time step, a spider can make at most one decision of each type. The basic sequence of events is depicted in Fig. 7.1. Our approach assumes that an individual seeks the optimal set of decisions that maximizes fitness. The optimal decisions are computed for each combination of (x, g, w, t) using a backward iteration procedure that solves backwards in time starting at the end of time (T), which in this model represents the end of the foraging and reproductive season, down to the first day of the season (see Mangel & Clark 1988). This deterministic approach solves a single optimum for each behavioural decision. This conditional policy is then implemented in a forward simulation procedure, which calculates the frequency of behaviours and distribution of individuals across microhabitats.

7.2.1.2 Parameterization

The purpose of this model is to make predictions about the microhabitat selection behaviours of spiders under different ecological scenarios and for different types of spiders, and to examine how this influences grouping dynamics. It is therefore important to use empirically derived data, when possible, to parameterize the model and make it more realistic. When this is not possible, we must make reasonable assumptions based on our knowledge of the study system. Sensitivity analysis is then applied to verify the validity of our parameter values by testing a wide range of possible values. For this model, we refer to data from various field and laboratory studies to characterize spiders' foraging behaviours (i.e. web building, prey capture, prey consumption), interactions with other spiders in a group, and reproductive behaviours (i.e. extent and timing of egg

laying, duration of egg sac guarding). Since the model investigates different types of spiders, we use our own data for scenarios pertaining to *Latrodectus hesperus*, *Tegenaria agrestis* and *T. duellica* spiders, and obtain data on other types of spiders from the literature.

7.2.1.3 State Variables and Conditional Decisions

Following the algorithm depicted in Fig. 7.1, we now describe state-dependent decisions in greater detail. The model parameters are listed in Table 7.1. A spider that searches for a microhabitat is subject to a baseline daily survival rate ρ_0 . It has a probability λ_i of encountering a microhabitat i , which is either unoccupied or occupied. Occupied microhabitats contain one or more webs on which other spiders may or may not be present, and unoccupied microhabitats do not contain any webs or occupants (note that in the case of non-web-building species, microhabitat occupancy is only described in terms of spider presence/absence and number, i.e. the state g_i). If the focal spider does not encounter a microhabitat, its new energy state in the next time step $t + 1$ will be

$$x' = x - \alpha - \chi, \quad (1)$$

where α represents the fixed energetic cost of being active during one time unit, and χ is the fixed energetic cost of moving between microhabitats (note that all energy increments and decrements are expressed in the same unit). In this model, spider group size and web state assume the values g_0 and w_0 , respectively, which correspond to a state where no microhabitat is found. If on the other hand, the spider finds a microhabitat or is already in one, it is faced with a decision: whether to accept or reject the microhabitat in the case of a new encounter, or whether to stay or leave it if it is already in one, provided that it survives in it, which is expressed as a probability ρ_i . This decision will depend on time (t), the current energy state of the individual $x_i(t)$, the size of the spider group $g_i(t)$, and the occurrence of a web $w_i(t)$ in microhabitat i , all of which are associated with specific fitness values (see below). If a spider decides to leave the microhabitat without exploiting it in that time step, its new energy state in the next time step will be x'_i , which follows equation 1. (Note that we assume (1) no energy cost of rejecting a microhabitat, and (2)

that it takes one time unit to reject or leave a microhabitat). In this scenario, spider group size and microhabitat web state are expressed as g_i' and w_i' , respectively, which assume different values depending on the microhabitat conditions encountered by the spider in the next time step. Conversely, if the spider decides to accept the microhabitat and settle in it or stay at its current location, spider group size stays the same, and web state is updated accordingly to w'' : it stays the same if there is already ≥ 1 web in that location, or it gets an increment of 1 if that location is devoid of webs (we assume that settlement always involves some web building activity in the case of web-building species, whether it be associated with foraging or reproduction).

Upon settling or staying in a microhabitat, the spider is faced with a second decision: whether to forage or reproduce. These are mutually exclusive activities, at least within a given time step, which can last for more than one time unit depending on the type of spider and the microhabitat conditions (see Appendix). If the spider decides to forage, its foraging outcome will depend on the probability of finding prey (κ_i) and catching prey (δ_i), the latter of which varies with spider group size (see Appendix). In the case of web-building spiders, foraging (and to a large extent reproduction) requires the use of a web, and therefore also involves a cost of web building $\omega_i(x, g, w)$ (i.e. silk production, web construction and web maintenance), which depends on individual energy level, spider group size and web state (see Appendix; note that the term $\omega_i(x, g, w)$ is dropped in the case of non web-building species). A spider that does not find prey (with probability $1 - \kappa_i$) will have a new energy state

$$x_i'' = x - \alpha - \gamma_i(g) - \omega_i(x, g, w) , \quad (2)$$

where $\gamma_i(g)$ is the group-size dependent cost of searching for prey during one unit of time. A spider that finds prey without catching any (with probabilities κ_i and $1 - \delta_i$, respectively) will have a new energy state determined by

$$x_i''' = x - \alpha - \gamma_i(g) - \omega_i(x, g, w) - \mu_0 , \quad (3)$$

where the parameter μ_0 corresponds to the fixed energetic cost of trying to catch prey without success over one unit of time. However, if a spider finds and catches prey (with probabilities κ_i and δ_i , respectively), it will consume part of it, and its new energy state will be

$$x_i^{''''} = x - \tau_C(g)[\alpha - \gamma_i(g) - \omega_i(x, g, w) - \mu_1] + \varepsilon_i(g) , \quad (4)$$

where $\varepsilon_i(g)$ is the group-size dependent energy return from eating one prey, μ_1 is the fixed energetic cost of catching one prey, and $\tau_C(g)$ is the amount of time required to catch and consume prey, which depends on spider group size (see Appendix). We assume that each spider can only catch and consume up to one prey item per time step. The amount of energy return $\varepsilon_i(g)$ varies with spider group size, and is weighed according to the level of territoriality between group members, θ , which determines the extent of prey ownership and sharing (see Appendix). If, on the other hand, the spider decides to reproduce and lay an egg sac (spiders generally lay eggs in a silken sac), its new energy state becomes

$$x_i^{''''} = x - \tau_E(g)[\alpha - \omega_i(x, g, w) - \sigma] , \quad (5)$$

where σ is the energetic cost per time unit of producing one egg sac (which involves both egg and egg sac production costs), $\omega_i(x, g, w)$ is the cost of web building, and $\tau_E(g)$ is the amount of time required to lay an egg sac, which depends on spider group size (see Appendix). For the sake of simplicity, we assume that (1) the cost of egg sac production (σ) is fixed, (2) each individual produces one egg sac at a time (which to the best of our knowledge is generally true), and (3) each egg sac contains the same number of eggs.

A spider's energy state $x_i(t)$ ranges from x_{crit} to x_{max} ; if $x < x_{crit}$, the spider dies (e.g. from starvation), and there is a maximum amount of energy that can be stored, x_{max} , due to physical constraints associated with body size and gut capacity. We assume that a spider with an energy state $x_{crit} \leq x \leq x_{max}$ has sufficient energy to forage and reproduce. Continuous values of the energy state variable are dealt with using linear interpolation (see Clark & Mangel 2000). We choose a range of values for the energy state $x_i(t)$ that

reflects the actual variation in energy level observed in each particular type of spider considered in the model. Likewise, we test a realistic range of spider group sizes $g_i(t)$ that reflect the natural distributions of different types of spiders across microhabitats (in simulations of *Latrodectus hesperus* spiders, $g_i(t) = [0; 7]$).

7.2.1.4 The Fitness Equations

Fitness is related to the overall state of an individual and is characterized in terms of the four state variables: x , g , w , and t . We model fitness maximization strategies in the context of group living, where individuals seek to avoid starvation and cannibalism associated with particular state-dependent foraging and reproductive decisions. The stochastic dynamic programming equation is expressed by the following fitness function

$$F(x, g, w, t, T) = \{ \text{maximum expected reproductive success from} \quad (6) \\ \text{time } t \text{ to } T \mid x(t) = x, g(t) = g, w(t) = w \}$$

At the end of time T , which corresponds to end of the foraging and reproductive season when individuals enter the overwintering phase, the terminal fitness depends on an individual's energy state, x , and group size, g , according to the following equation

$$F(x, g, T, T) = \begin{cases} 0 & \text{if } x < x_{crit} \\ s(g)(w_{max} - \exp(x_{crit} - x)) & \text{if } x \geq x_{crit} \end{cases}, \quad (7)$$

where w_{max} is the maximum amount of future fitness that an individual can attain (i.e. the asymptote), x_{crit} represents the critical energy level for survival, and $s(g)$ is the effect of group size on fitness, which is described as

$$s(g) = \exp(1 - g_i^\theta), \quad (8)$$

where θ is the species-specific coefficient of territoriality, ranging from 0 (social and tolerant of group members) to 1 (highly territorial and agonistic towards group members).

Therefore, at time T , a spider's future fitness increases with energy state x_i (above the critical threshold) according to an asymptotic gain function with diminishing returns at high values of x_i . The shape and slope of this function is determined by the parameter $s(g)$, such that spiders overwintering in large groups will have reduced fitness if they are highly territorial species, whereas fitness will stay constant as group size increases in the case of social species.

7.2.1.5 The Full Stochastic Dynamic Programming Equation

$$F(x, g, w, t, T) = \max \left[\begin{array}{l} \sum_{i=0}^{i_{\max}} \lambda_i \rho_0 F(x_i, g_i, w_i, t+1, T); \\ \max \left[\begin{array}{l} (1 - \kappa_j) \rho_{g', w'} F(x_j'', g, w_j'', t+1, T) + \\ \kappa_j (1 - \delta_k) \rho_{g', w'} F(x_{j,k}''', g, w_{j,k}'', t+1, T) + \\ \kappa_j \delta_k \rho_{g', w'} F(x_{j,k}''''', g, w_{j,k}'', t + \tau_{C_{j,k}}, T) \end{array} \right]; \\ \rho_{g', w'} [f_i + F(x''''', g, w'', t + \tau_E, T)] \end{array} \right] \quad (9)$$

7.2.1.6 Optimal Decisions and Game Implementation

The frequency-dependent method used to solve this dynamic game model is borrowed from previous theoretical studies (see Houston & McNamara 1987; Alonzo & Warner 2000; Alonzo 2002). What follows is a brief description of the method. We assume that individuals are randomly distributed across microhabitats at the beginning of time (note that simulations can be run with different initial distributions and the results compared). At each time step, from $t = T-1$ to $t = 1$, an optimal decision matrix is calculated by backward iteration for all values of (x, g, w) , based on the maximum fitness outcomes. In this model, a decision represents the probability of performing a particular behaviour. Based on a given decision matrix at time t , a forward simulation then calculates the number of individuals in each microhabitat (N_i), and the frequencies of optimal decisions represented as (1) the probability of leaving vs. staying in a given microhabitat and (2) the probability of foraging vs. reproducing in that location. These

values are then used as starting densities to compute the decision matrix for the next time step $t + 1$ using backward iteration. Each new decision matrix is compared to the previous one, and this cycle of forward-backward iteration procedures is repeated until a stable solution is achieved. This technique is known as the “best response” method (see e.g. McNamara et al. 1997), where the iteration cycle continues until the best response to a given strategy (π_{n+1}) in the following iteration ($n + 1$) is equivalent to the strategy itself (π_n), within a pre-defined margin of error, e.g. when two consecutive decision matrices overlap by more than 95% (other confidence levels can be used depending on the context). From a game-theoretical perspective, the stable decision matrix represents an evolutionary stable strategy (ESS), which is stable against invasion by any other strategy (Maynard Smith 1982). However, it is possible that a dynamic game model fails to converge on a stable solution, in which case we use the stabilization methods proposed by McNamara et al. (1997) and Clark & Mangel (2000), and extended by Alonzo (2002).

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7.4 Appendix

7.4.1 Mathematical Functions

7.4.1.1 Probability of Survival

The probability that a spider survives to the next time step (ρ_i) is determined both by its energy state x_i and the size of group of spiders g_i in microhabitat i . The relationship is described by the following equation

$$\rho_i(x, g) = \rho_0(1 - \beta_i(g)) \frac{(x_i - x_{crit})}{(x_{max} - x_{crit})} ; \quad (a1)$$

where survival increases linearly with energy state, ρ_0 is the baseline probability of survival, and $\beta_i(g)$ is the group-size dependent probability of cannibalism within a microhabitat. The baseline probability of survival ρ_0 is determined by the habitat-specific risks of predation, parasitism, and climatic stress, which we assume to be independent of spider group size. The parameter β_i is described as

$$\beta_i(g) = \begin{cases} 0 & \text{if } g_i \leq 1 \\ \frac{\theta}{1 + \exp(2 - g_i)} & \text{if } g_i > 1 \end{cases} ; \quad (a2)$$

where θ is the coefficient of territoriality that ranges from 0 to 1, with values close to 0 indicating a low level of territoriality (i.e. high levels of tolerance towards other group members) and values close to 1 being indicative of high levels of territoriality (i.e. a great likelihood of aggression towards other group members).

7.4.1.2 Probability of Catching Prey

The probability that an individual at energy level x_i in a group of size g_i at time t will catch a prey item is described by the following equation

$$\delta_i(x, g) = \begin{cases} \delta_0 + \frac{(1 - \delta_0)}{1 + \exp\left(1 - g_i^{(0.5-\theta)}\right)} - \frac{\delta_0(x_i - x_{\max})}{\eta(x_{\text{crit}} - x_{\max})} & \text{if } 0 < \theta < 0.5 \\ \delta_0 - \frac{\delta_0(x_i - x_{\max})}{\eta(x_{\text{crit}} - x_{\max})} & \text{if } \theta = 0.5 \\ \delta_0 \exp\left(1 - g_i^{v(\theta)}\right) - \frac{\delta_0(x_i - x_{\max})}{\eta(x_{\text{crit}} - x_{\max})} & \text{if } 0.5 < \theta \leq 1 \end{cases}, \text{ (a3)}$$

where δ_0 is the baseline probability of prey capture determined by the level of food resources in a particular microhabitat (high vs. low), η is a shape parameter in the function describing the effect of energy level x_i , θ is the coefficient of territoriality that ranges from 0 to 1 depending on the social structure of a given species, and v is a shape parameter determining the influence of θ at high values. The probability of catching prey may either increase with group size, as in some group-living spiders, or decrease, such as in many solitary territorial species or some facultatively group-living species, although this may depend on environmental condition (Rypstra 1989; Uetz 1989; Jakob 1991; Rypstra & Tirey 1991; Lloyd & Elgar 1997).

7.4.1.3 Prey Consumption

The amount of energy gained from a prey item in microhabitat i , ε_i , depends on spider group size g_i and the coefficient of territoriality of a particular species, θ , and is described as

$$\varepsilon_i(g) = \frac{\varepsilon_0}{g_i^{(1-\theta)}}, \quad (\text{a4})$$

where ε_0 represents the fixed amount of energy contained in one prey item. Spider group size g_i is weighed according to θ , which determines the extent of prey ownership and sharing. When θ is close to 0, individuals in a group tend to share prey, and when it approaches 1, individuals are highly territorial and consume prey individually. For the sake of simplicity, we assume that (1) prey are shared equally between group members, and (2) the conversion rate of prey into useable energy is 100% (while alternatives would easily be included in the model, they would not provide any major contribution to the purpose of this study).

7.4.1.4 Web-building Cost

Web-building spiders have to spend energy producing silk and constructing a web prior to foraging. The function describing the cost of web building is

$$\omega_i(x, g, w) = \begin{cases} \omega_0 + \frac{\psi}{x_i} & \text{if microhabitat } i \text{ has no web } (w_i = 1) \\ \frac{\omega_0}{\exp(g_i^\phi - 1)} + \frac{\psi}{x_i} & \text{if microhabitat } i \text{ has } \geq 1 \text{ web } (w_i = 2) \end{cases}, \quad (\text{a5})$$

where ω_0 is the baseline cost of web building, x_i is an individual's energy state, g_i is the size of a group of spiders and w_i the web state in microhabitat i , and ϕ is the species-specific propensity to share webs when living in a group (this parameter is directly related to the level of territoriality θ). Unoccupied microhabitats have a web state of 1, and occupied microhabitats a value of 2. The parameter ϕ ranges from 0 and 0.5, and is based on empirical evidence that the cost of web building decreases with group size in species that can share silk threads (i.e. ϕ approaches 0.5), while in others it stays constant (i.e. ϕ approaches 0) (Whitehouse & Lubin 2005). We also assume that the cost of web building decreases with increasing energy reserves x_i by a factor ψ , which assumes different values depending on the type of web-building species under consideration. This

is again based on empirical evidence from different studies (e.g. Pasquet et al. 1999; Salomon 2007).

7.4.1.5 Cost of Searching for Prey

The energetic cost of searching for prey in microhabitat i , γ_i , is determined by the size of the group of spiders g_i and the coefficient of territoriality of the focal species θ such that

$$\gamma_i(g) = \gamma_0 \theta g_i, \quad (\text{a6})$$

where γ_0 is the baseline energetic cost of searching for prey. This means that this cost will either increase or decrease with group size depending on whether the species shows territorial or social tendencies, respectively.

7.4.1.6 Duration of Activities

The type of activity performed by an individual in a microhabitat, which may last for more than one unit of time (i.e. catch and consume prey, and produce an egg sac) is determined by the decisions it makes (i.e. leave or stay and forage or reproduce), the probabilities λ_i , κ_i and δ_i (see Table 1), and the state variables x , g , and w . We assume that rejecting or leaving a microhabitat takes one unit of time, and that not finding or not catching prey are events that happen over one time step. The amount of time required to catch and consume prey, τ_C , and to produce an egg sac, τ_E , may assume different values depending on the state of the microhabitat (i.e. unoccupied, occupied by 1 or more webs, occupied by 1 or more spiders and their webs), and thus yields three possible values for each parameter. These values are chosen based on the type of spider being modelled and its associated level of territoriality, θ .

7.4.2 References

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Table 7.1. List of parameters used in the dynamic game model

Parameter	Description
i	General microhabitat status
j	Microhabitat status with respect to prey encounter
k	Microhabitat status with respect to prey capture
α	Energetic cost of being active during 1 time unit
β	Probability of cannibalism within a microhabitat
γ	Energetic cost of searching for prey in a microhabitat
γ_0	Baseline energetic cost of searching for prey
δ	Probability of catching a prey item in a microhabitat
δ_0	Baseline probability of prey capture
ε	Energy return from eating 1 prey
η	Shape parameter describing the effect of x on δ
θ	Species-specific coefficient of territoriality
κ	Probability of finding prey in a microhabitat
λ	Probability of finding a microhabitat
μ_0	Energetic cost of trying to catch prey without success
μ_1	Energetic cost of successful prey capture
ν	Shape parameter describing the effect of θ on δ
ρ	Probability of survival in a microhabitat
σ	Energetic cost of making an egg sac
τ_C	Time required to catch and consume a prey item
τ_E	Time required to produce an egg sac
ϕ	Species-specific propensity to share webs in a group
χ	Energetic cost of moving between microhabitats
ψ	Strength of energy reserve-dependent decrease in web-building cost
ω	Energetic cost of web building
ω_0	Baseline cost of web building
f	Fitness increment from producing 1 egg sac
s	Effect of spider group size on fitness

x_{crit}	Critical level of energy for survival
x_{max}	Maximum amount of energy
w_{max}	Maximum future fitness
N_i	Number of individuals alive in microhabitat i
P_i	Number of prey in microhabitat i
T	Terminal time

Figure 7.1. Basic model algorithm: sequence of events taking place within a given lapse of time. Each transitional step is associated with a specific set of probabilities for the occurrence of stochastic events, and each conditional decision is associated with a particular fitness return (see text for details)

