SPIDER WEB DESIGN AND RISK SENSITIVITY IN THE BANDED SPIDER, ARGIOPE TRIFASCIATA.

by

Jill Erin Cotter
B.Sc. (Hons), University of Windsor 1994

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the Department

of

Biological Sciences

© Jill E. Cotter 1996

SIMON FRASER UNIVERSITY

December 1996

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Title of Thesis/Project/Extended Essay

Spider Web Design and Risk Sensitivity in the banded spider, ARGIOPE TRIFASCIATA.

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December 11, 1996
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ABSTRACT

This thesis examines the webs of orb-weaving spiders as risk sensitive foraging devices. Prey capture by spider webs has long been recognized to be a highly variable process, but the idea that web design considers both the mean and variance in energy return is a new concept. Theoretically, a risk sensitive forager's preference for webs giving higher or lower variance in energy return depends on the relation of energy reserves to fitness, and the current state of reserves. I suggest that webs constructed by poor condition spiders give more variable energy return than those made by good condition spiders. This concept may explain a commonly reported inverse relationship between spider condition and web size. The idea of webs as risk sensitive devices was modelled using a dynamic programming algorithm. The assumption of the model that webs of poor condition spiders give more variable return was tested and supported in observations with the banded spider, *Argiope trifasciata*, in Tsawwassen, British Columbia, during the summer of 1995. A supplemental feeding experiment shifted web pattern with a change in condition in the expected direction. Expected trends of prey capture type with web design were not observed. Web design differences between adults and juveniles were attributed to age class constraints and not different foraging strategies. An alternative hypothesis of web design as a function of a foraging - growth tradeoff is also considered.
Acknowledgements

There are many people who assisted in my academic progress. Thanks to Ron Ydenberg for supporting my ideas for this thesis. Discussions over some type of beverage, my participation in the American Arachnology Conference, and especially Ron's aid in the modelling chapter were essential to the development of this thesis. Thanks to Bernie Roitberg and Larry Dill for thoughts on thesis structure and direction. Don Hugie, Yolanda Morbey, Tamara Grand and Greg Robertson were crucial to the completion of the dynamic program. My lab mates: Al Jaramillo, Andrea MacCharles, Dave Moore, Bill Hunt and Yolanda helped me clarify my ideas and field methods through critical comments at lab meetings or with one-on-one help. Thanks to Greg for SAS lessons and infinite patience with statistics questions. Greg also suggested and aided with the presentation of the figures in the modelling chapter. Alex Fraser was always available to enthusiastically answer practical questions and assist with lab and field problems- from videos to cameras to the anethetization of spiders etc. etc. I would like to thank the Tsawwassen Native Band for allowing me to study Argiope trifasciata on their land. Lara Webster and Fintan Maguire were excellent field and lab help.

Many more people helped with "the personal growth" aspect of the thesis experience (ask Ron for details). Some noteworthy people/events in no particular order... Raconteur Tom Chapman taught me that, with imagination and style, any mundane occurrence can be transformed into a story which gives new and hilarious pee-in-your-pants insight into the human condition. Thanks also to Tom for organizing Darwin's birthday at Valdez. The time to think and relax in that setting with all my friends helped me avoid a big life decision mistake. Speaking of wonderful week-ends, thanks to the PEC crews of 1994 and 1995, especially Dave for providing the awesome musical atmosphere in the big bad van and at all important functions, and Fred Sharpe for
showing us the way to sand dune hijinks and San Juan Island sunsets. Thanks to Fred for erasing all incriminating video tapes (nyark). Thanks to Don, the pub and red wine for providing inspiration for said videotapes. Thanks especially to Don and Alex, my co-conspirators in indulging our inner children and general silliness. You kept me sane.

Thank you, Alex, Bill, Stephanie Hazlitt and Tasha Smith for being at SFU on most weekends so that the lab was never silent or dull. Thanks to all slide fight participants. Three cheers for all hockey hackers and Gougers, particularly Larry Dill and Tom.

Yolanda initiated me to grad school life, including my first BC hike. Thanks for always listening Yo. Thanks to Michelle Harrison for her excellent musical taste during Christmas party mayhem and for her advocacy of my abilities; Stephanie - her humour was life support at the bitter end; Brett Sandeckock for his witty, biting comments and his infamous slides, Eric Reed and Joanne Dussureault for always being the host(es)s with the mostest. Thanks to Megan Hanacek, Holly Williams, Jen Clark, Mike Hayward, Scott Finley and the Lump (not), my roomies and friends who helped me escape from too much of a good thing. Thanks to my parents, and to my sister Meredith who kept me grounded. Thanks to everyone else who I have rudely missed who contributed to making my everyday social life in grad school something special.

Thanks Greg for everything.
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Chapter 1

Introduction

Foraging options are considered risk sensitive if choice of an option depends on variance as well as mean net rate of energy return (Stephens and Krebs 1986). Risk sensitivity is expected in any situation where the relationship between energy accumulation and expected fitness is non-linear (McNamara et al. 1991). An accelerating relationship of energy accumulation to expected fitness results in a preference for larger variance or risk proneness. A decelerating relationship of energy accumulation to expected fitness results in preference of smaller variance or risk aversion.

Risk sensitive foraging has been observed in a large number controlled laboratory settings in a wide variety of taxa, including birds (see summary by Bednekoff and Houston 1994), mammals (shrews: e.g. Barnard and Brown 1985), fish (bitterlings: Young et al. 1990), insects (bees: e.g. Real 1981). The validity of some of these studies has since been questioned as potential confounding effects have been recognized such as confusion about variance in time effects versus variance in reward, differences in net rate of gain between constant and variable choices (Harder and Real 1987, Banschbach and Waddington 1994) and lack of control for alternative explanations (Bednekoff and Houston 1994). Increasing awareness of these problems has lead to more rigourous studies which unequivocally support risk sensitivity e.g. Caraco et al. 1990. Far fewer studies have examined risk sensitive behaviour in natural populations (Gillespie and Caraco 1987, Uetz 1988, Guillemette et al. 1992, Barkan 1990, Cartar 1991).

Risk sensitivity is harder to support in the field. As Cartar (1991) suggests, foragers under laboratory conditions have a constrained set of choices given by the range
of foraging options made available by the experimental design, compared to foragers under natural conditions which might vary other aspects of their behaviour rather than responding in a risk sensitive manner. For example, a forager in poor condition might continue in the same behaviour but work harder or work longer, rather than switching to a more variable option. Foragers might tradeoff foraging options with other considerations such as predation risk, for example decreasing time spent scanning and increasing time spent foraging or using more risky habitats to obtain higher energy food sources. In addition, the range of alternative causation of observed behaviour is greater under field conditions, and this has emerged as a problem for a number of studies.

Cartar (1991) suggested that wild bumble bees behaved in a risk sensitive manner to depletion of colony level reserves by switching from flower types with constant returns to more variable flower types and vice versa. Cartar and Dill (1990) had first tested this effect of colony energy reserves on foraging behaviour in a controlled laboratory experiment and observed changes in flower type use. This experiment was repeated by Banschbach and Waddington (1994) with honey bees, controlling for nectar volume differences between foraging options. They found that bees responded to volume of nectar rather than variance in nectar return and suggest that the studies by Cartar and Dill (1990) and Cartar (1991) are confounded by this volume effect.

A paradox in web relocation by tetragnathid spiders was explored by Gillespie and Caraco (1987). They determined that two strategies of web relocation differed in variance in return and showed that poor condition spiders chose the risk prone option. However, a critical test by Smallwood (1993) in which poor condition spiders were food supplemented did not result in the expected shift to risk averse web relocation behaviour.

Uetz (1988) has suggested risk sensitivity as an explanation for rareness of colonality in spiders. In prey rich areas where spiders can meet their minimum
requirement to reproduce, spiders form communal webs as this behaviour reduces variance in prey capture. Conversely, in prey-poor areas, the common condition for most spiders, spiders forage singly as this increased variance may allow them to meet threshold requirements for reproduction. Recent work, while not contradicting the assertion that risk sensitivity has been important in shaping behaviour, suggests that the relationship between colonial web-building and variance in prey capture is more complicated than originally thought (Uetz, pers. comm.)

The work of Guillemette et al. (1992) supports a risk sensitive interpretation of foraging behaviour of common eiders but has a lot of untested assumptions, such as what food items the eiders were ingesting on each dive. Finally, the work of Barkan (1990) which showed risk averse behaviour by black capped chickadees on a positive energy budget remains unchallenged, which is perhaps unsurprising as the strongest evidence for risk sensitivity in laboratory studies comes from work with passerine birds seeking to avoid energetic shortfall.

Risk sensitive foraging under field conditions thus seems most likely when a limited range of alternative foraging options or foraging - life history tradeoffs are available. Sessile sit and wait foragers might be expected to have a smaller set of foraging choices given that many alternative options involve mobility e.g. changes in patch type (the sit and wait foragers in Gillespie and Caraco 1987 which had a mobile option). Trap - making sit and wait foragers offer many advantages to field workers because foraging investment, as measured by trap dimensions and foraging bout length, and foraging returns from prey capture, are easily quantified.

In this thesis, I investigate risk sensitive foraging in trap design in a sit and wait forager - orb weaving spiders. Traps are generally considered species specific structures. Orb webs, arguably the most well studied trap structure, have only recently been
acknowledged to vary at the level of the individual (Eberhard 1990, Higgins 1990, Higgins and Buskirk 1992, Higgins 1995, Sherman 1994). This individual variation, which results in an inverse relationship between condition (energy accumulation) and web size, has been attributed to foraging - growth or foraging - reproduction tradeoffs.

Consideration of web function suggests that this relationship between condition and web size is a consequence of tradeoffs between interception and retention of prey types according to web design. Web design differences thus result in differences in variance around mean net energy return and risk sensitive foraging. In Chapter 2, I develop a dynamic programming model to examine risk sensitive foraging in orb-weavers. The basic premise of the model is that web design leads to different probabilities of prey capture resulting in web types which differ in variance in energy return. I examine the effect of mean net return, fitness function shape, limits and thresholds on web type selection. I also compare the results of the model to predictions of a foraging - growth tradeoff hypothesis. In Chapter 3, I evaluate the potential role of risk sensitive foraging in a generalist orb weaving spider in the field. I determine relationships between web parameters and condition using *Argiope trifasciata* (Forskal), a sessile orb weaver, as a model organism. The effects of a food supplementation experiment on web building dynamics is investigated. Mean and variance in energy return from field web types are examined to test the basic assumption of the model in Chapter 2. The effect of web design on capture of prey types is also examined. Finally, the effect of age class on the relationship between condition and web parameters is considered.
Chapter 2

Modelling risk sensitive decision-making in orb-weaving spiders

Introduction

Animals are termed risk sensitive foragers if their choice of foraging option depends on the variance as well as the mean net rate of energy gain associated with that option (see reviews by Real and Caraco 1986, Stephens and Krebs 1986, Caraco and Lima 1987). Risk sensitivity should arise in any situation in which the relationship between energy gain and fitness is non-linear (McNamara et al. 1991). When the relationship between energy gain and fitness is an accelerating function, a foraging option with greater variance results in a greater expected fitness gain than a less variable foraging option with the same expected energy gain. The more variable foraging option is referred to as the "risk prone" option. Conversely, if the relationship between fitness and energy state is a decelerating function, a given increase in energy gain results in a smaller increase in fitness compared to the same given decrease in energy gain. In this case, the forager is predicted to take the less variable foraging alternative and is referred to as a "risk averse" forager. If the relationship between fitness and energy state is a linear function, foraging options with greater variance result in the same overall expected fitness gain than a less variable foraging option with the same expected energy gain and the forager is said to be "risk indifferent". In this chapter, I examine the choice of web design options in a risk sensitive context.

Individual variability in orb web design has been largely ignored by foraging theory. Web design differences between individual spiders were first noted by Witt et al. (1968), although many researchers continued to advocate the paradigm that webs varied only at the species level. Causes of individual variation, even under controlled laboratory conditions, have been described as "mysterious" (Eberhard 1986). Recent studies have assigned daily changes in web design to tradeoffs between foraging and

In all these studies, individual spiders experiencing low foraging success and consequently poor condition, built webs with longer web radii given their body size, using more silk and more energy compared to spiders enjoying higher foraging success (good condition). Sherman (1994) stated that larger webs represent the best chance for an orb weaver to capture a large prey item which would replenish its energy stores. Although well-fed spiders have more greater energy reserves with which to produce large webs, they have "less need" to do so, resulting in this inverse relationship between foraging success and web size (Sherman 1994). An alternative explanation is that some variation in web design corresponds to tradeoffs within foraging tactics rather than tradeoffs between life history parameters and foraging. Because female fecundity increases with increased size (foraging success) (Riechert and Tracy 1975, Harrington 1978, Fritz and Morse 1985, Miyashita 1986, McLay and Hayward 1987, Beck and Connor 1992, Higgins 1992, Wise and Wagner 1992) one would expect a direct relationship between past foraging success and web size if larger webs capture larger prey. The observed inverse relationship between condition and web size suggests that large webs have disadvantages in some aspect of prey capture.

Traditionally, orb webs are believed to passively filter insects from the air, and therefore orb web mesh, the intersection of spiral threads and radial threads, should approximate target prey size. Alternatively, insect capture by orb webs may be a function not only of prey interception but also of prey retention (Chacon and Eberhard 1980, Olive 1980, Eberhard 1986). These two functions of webs may be antagonistic. Large web diameter may affect prey capture through increased interception of prey. It may also influence retention of non-flying insects, like orthopterans, which tend to rip down vertically through web threads which increase in number with increased web diameter (Olive 1980). A denser meshed web would also increase retention of strong
prey. However, large webs of diurnal orb weavers may be more visible to visually acute insects, like pollinators, than small webs and lead to decreased capture of these prey types. Mesh density may also affect prey capture of diurnal insects. If insects can see the orb web only at close range and then swerve to avoid individual threads, then denser mesh could improve both interception and retention (Chacon and Eberhard 1980). If the insects are able to detect the web from a greater distance and thus entirely avoid it, then closer spacing could lower interception by increasing web visibility (Chacon and Eberhard 1980).


Web geometry clearly effects the probability of capture of different prey types. Given that prey types differ in their energy value and their abundance, web geometry may result in different levels of variance around mean net energy gained. Spiders are then expected to choose web designs in a risk sensitive framework, according to their condition and the relationship of condition to fitness. Risk sensitive foraging can thus create particular patterns of web design with condition.

In this chapter, I use dynamic programming to investigate the effects of the shape of the fitness function, limits, mean return, and reproductive threshold on web type selection. How limits and thresholds interact with the shapes of fitness functions has just begun to be explicitly explored (Bednekoff and Houston 1994; Bednekoff MS).
I also compare the results of the model to an alternative explanation: a foraging-growth tradeoff (Higgins 1995).

**Model**

**Introduction**

Risk sensitive foraging scenarios have commonly been modelled using dynamic programming (Gillespie and Caraco 1987; McNamara *et al.* 1991; Bednekoff and Houston 1994). Dynamic programming works by calculating backward from a terminal condition to determine the optimal behavioural decision for each preceding time and state combination (Mangel and Clark 1988). The state of an animal may be any characteristic that influences the expected fitness of that animal as defined by the terminal fitness function. Dynamic programming is an apt technique to model orb weaving spider behaviour as: (i) foraging decisions are made by individuals at the same time scale (webs are usually renewed on a daily basis); (ii) most temperate and arctic zone orb-weavers face a strict time horizon (univoltine and are killed by cold temperatures in autumn, (Olive 1981)) and; (iii) the state variable condition has been shown to effect web design decisions (Olive 1982, Higgins 1990, Higgins and Buskirk 1992, Sherman 1994).

The premise of the model is that web design effects prey capture probabilities. Two web designs are available in the model. Both web types give the same mean net return but differ in variance due to their differing capture probabilities for different sized prey. Web 1 is more likely to catch medium-sized prey and less likely to catch large-sized prey than web 2; web 1 is the less variable or the risk averse option. In each time interval, the model calculates for spiders at every condition state the web type that maximizes expected fitness.
Model parameters

The basic model parameters and values are summarized in Table 2.1. The model is run with 56 discrete time periods with each time period corresponding to a day, since webs are usually renewed on a daily basis. This number of time periods represents two months of adult life. The final time step represents the end of the season, at which time fitness (defined as egg number) is realized. Time intervals are denoted by \( t \).

The state of the spider at time \( t \), is denoted \( X(t) = x \). It is a measure of energy accumulated energy or condition (Chapter 3). Energy state varies according to the energy gained from prey capture events, and the expenditure of energy for web-building. The values of these parameters are arbitrary and unitless. The state variable ranges from 1 to 30 and is constrained at upper and lower bounds. The upper limit, \( X_{\text{max}} \), represents the maximum amount of energy reserves a spider can carry. The lower limit, \( X_{\text{min}} \), represents the minimum energy reserve necessary for survival.

The decision in this model is a choice between two web types, which have the same mean net energetic return but differ in variance. This variance arises from the differing probabilities of capture of different sized prey by two web types, \( P_{(i,j)} \). The more variable web type, web type \( i = 2 \), has a greater probability of catching large prey and a lower probability of catching medium prey relative to web type \( i = 1 \). Web type \( i = 2 \) is assumed to be larger with denser mesh relative to web type \( i = 1 \), and thus trades off decreased interception of visually orientated flying prey and increased retention of large, jumping prey. The probabilities of each prey capture event (of which there are four arbitrary possibilities: none arrive \( j = 1 \), medium prey capture \( j = 2 \), large prey capture \( j = 3 \), both prey capture \( j = 4 \) ) are then computed for each web type.

In the basic model, costs of web-building, \( (\alpha_i) \), are small compared to average energy gain from prey since spiders have been observed to build webs for many days without food (Foelix 1982). The rate of energy expenditure while web-building is calculated to be about double that incurred while resting and spiders are known to have
Table 2.1. Model parameters and values for the basic run of the model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter Value</th>
<th>Parameter description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( t )</td>
<td>1.56</td>
<td>time period</td>
</tr>
<tr>
<td>( X(t) )</td>
<td>1.30</td>
<td>Energy state at time ( t )</td>
</tr>
<tr>
<td>( X_{\text{min}} )</td>
<td>1</td>
<td>lower boundary of ( X(t) )</td>
</tr>
<tr>
<td>( X_{\text{thresh}} )</td>
<td>6</td>
<td>reproductive threshold of ( X(T) )</td>
</tr>
<tr>
<td>( X_{\text{max}} )</td>
<td>30</td>
<td>upper boundary of ( X(t) )</td>
</tr>
<tr>
<td>( i )</td>
<td></td>
<td>web types:</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>risk averse (small web)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>risk prone (large web)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>risk indifferent (chosen when fitness differential of (</td>
</tr>
<tr>
<td>( \alpha_i )</td>
<td>0.15</td>
<td>cost of web</td>
</tr>
<tr>
<td>medium prey</td>
<td>2</td>
<td>energy value and behaviour modelled after hymenopterans</td>
</tr>
<tr>
<td>large prey</td>
<td>5</td>
<td>energy value and behaviour modelled after orthopterans</td>
</tr>
<tr>
<td>( j )</td>
<td></td>
<td>prey arrival events:</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>none</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>medium</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>large</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>both</td>
</tr>
<tr>
<td>( \beta_j )</td>
<td></td>
<td>energy from prey arrival events</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>none</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>medium</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>large</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>both</td>
</tr>
<tr>
<td>medium insect arrival</td>
<td>0.40</td>
<td>0.20</td>
</tr>
<tr>
<td>large insect arrival</td>
<td>0.07</td>
<td>0.15</td>
</tr>
<tr>
<td>( P(\hat{w}_{i,j}) )</td>
<td>0.558</td>
<td>0.680</td>
</tr>
<tr>
<td></td>
<td>0.372</td>
<td>0.170</td>
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<td></td>
<td>0.042</td>
<td>0.120</td>
</tr>
<tr>
<td></td>
<td>0.028</td>
<td>0.030</td>
</tr>
<tr>
<td>mean return</td>
<td>1</td>
<td>mean net return</td>
</tr>
<tr>
<td>variance in return</td>
<td>2.41</td>
<td>3.61</td>
</tr>
</tbody>
</table>
low metabolic rates (Peakall and Witt 1976; Prestwich 1977). The model was run with both equivalent and disparate costs for the two web types. In the latter case the more variable option, web type 2, was twice as costly as in the basic model and the probability of large prey capture for web type 2 was increased so that the mean net return remained equivalent for both web types (Table 2.2). Large and medium prey correspond to large, jumping prey such as orthopterans and visually orientated flying prey such as hymenopterans, respectively. Large prey yielded 2.5 times the energy of medium prey. Small prey are ignored in the model as they are thought to add little energy to the forager (Olive 1980, but see dissenting opinion Nentwig 1985).

These parameters were adjusted to examine the effect of mean net energetic return on model output and to perform sensitivity analyses.

Dynamics and functions

The objective of this model is to choose the web design \((i=1,2)\) that maximizes expected reproductive output at end of the season, given current state \(x\). This concept may be formulated mathematically as follows:

\[
F(x,t) = \max_i E(\Phi(X(T)) \mid X(t) = x)
\]

where \(F(x,t)\) is the expected reproductive output of a spider with energy state \(x\) at time \(t\), \(E\) denotes expectation and \(\Phi\) is the function relating condition to fecundity (the terminal fitness function).
Table 2.2. Model parameters and values which differ from the basic model when web costs are disparate.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Parameter Value</th>
<th>Parameter description</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \alpha_i )</td>
<td>i=1</td>
<td>( \alpha_i ) 0.15 0.30 web cost</td>
</tr>
<tr>
<td>medium insect</td>
<td></td>
<td>maintain arrival probability of medium prey from basic model with equal web cost</td>
</tr>
<tr>
<td>arrival</td>
<td></td>
<td>.4 .2</td>
</tr>
<tr>
<td>large insect</td>
<td></td>
<td>increase arrival probability of large insects</td>
</tr>
<tr>
<td>arrival</td>
<td></td>
<td>.07 .18</td>
</tr>
<tr>
<td>( P(i,) )</td>
<td></td>
<td>probability of arrival events.</td>
</tr>
<tr>
<td></td>
<td>i=1</td>
<td>0.558 0.656 none</td>
</tr>
<tr>
<td></td>
<td>i=2</td>
<td>0.372 0.164 medium</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.042 0.144 large</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.028 0.036 both</td>
</tr>
<tr>
<td>mean return</td>
<td></td>
<td>1 mean net return</td>
</tr>
<tr>
<td>variance in return</td>
<td></td>
<td>2.41 3.88 variance around mean net return</td>
</tr>
</tbody>
</table>
Terminal fitness functions

The three forms of \( \Phi \) investigated are:

Linear: \( \Phi_1(x) = x \)

Accelerating: \( \Phi_2(x) = 1.5 e^{0.1x} \)

Decelerating: \( \Phi_3(x) = \frac{60x}{30 + x} \)

All three of these relationships of fecundity to a body size measure have been reported for spiders in the literature (Riechert and Tracy 1975 (decelerating), Harrington 1978 (linear), Fritz and Morse 1985 (linear), Miyashita 1986 (accelerating), McLay and Hayward 1987 (Linear), Beck and Connor 1992 (linear), Higgins 1992 (linear), Wise and Wagner 1992 (linear)). These functions were selected so that the fitness payoff at the maximum value of the state variable was nearly the same (approximately 30) across the three terminal fitness functions.

For each terminal fitness function and parameter set, the fitness value of the state variable was limited between an upper \((X_{\text{max}})\) and lower bound \((X_{\text{min}})\) as follows:

\[
F(x, T) = \begin{cases} 
  \Phi_k(X_{\text{max}}) & \text{for } x = X_{\text{max}} \\
  \Phi_k(x) & \text{for } X_{\text{min}} < x < X_{\text{max}} \\
  \Phi_k(X_{\text{min}}) & \text{for } x = X_{\text{min}}
\end{cases} \quad \text{where } K = \{1, 2, 3\}
\]

The influence of a threshold below which spiders could not reproduce was investigated for each fitness function. This threshold \((X_{\text{thresh}} = 6)\) corresponds to the 20\% threshold size requirement for reproduction, which has been reported for some spiders in the literature (Fritz and Morse 1985; Beck and Connor 1992).
\[ F(x, T) = \begin{cases} 
\Phi_k(x_{\text{max}}) & \text{for } x = x_{\text{max}} \\
\Phi_k(x) & \text{for } x_{\text{thresh}} < x < x_{\text{max}} \\
0 & \text{for } x \leq x_{\text{thresh}} 
\end{cases} \quad \text{where } K = \{1, 2, 3\} \]

**State dynamics**

For \( t < T \), for all fitness functions, the value of the state variable in the next interval \( t + 1 \) (denoted \( x' \)), depends on the energy gained from each prey capture event \( (\beta_j) \), minus the expenditure of energy for web-building \( (\alpha_i) \),

\[ x' = x + \beta_j - \alpha_i \]

The state variable is maintained within bounds using a chop function,

\[
\text{chop } x' = \begin{cases} 
(x_{\text{max}}) & \text{for } x' > x_{\text{max}} \\
x' & \text{for } x_{\text{min}} \leq x' \leq x_{\text{max}} \\
x_{\text{min}} & \text{for } x' < x_{\text{min}} 
\end{cases}
\]

The fitness value assigned to the chopped state variable is defined as:

\[
F(\text{chop } x', t + 1) = \begin{cases} 
F(x_{\text{max}}, t + 1) & \text{for } x' > x_{\text{max}} \\
F(x', t + 1) & \text{for } x_{\text{min}} \leq x' \leq x_{\text{max}} \\
0 & \text{for } x' < x_{\text{min}} 
\end{cases}
\]

The expected fitness value resulting from each prey capture is weighted by the probability of capture for that web type \( (P_{(i,j)}) \). The weighted fitness values for each prey capture event are summed for each web type, and the total fitness expected by each web type compared. The web choice that maximizes fitness is chosen. These steps culminate in the dynamic programming equation:

\[
F(x, t) = \max_i \left[ \sum_{j=1}^{4} P_{(i,j)} F(\text{chop } x', t + 1) \right]
\]
The dynamic programming equation model was applied recursively for the six fitness functions, and each of several parameter sets chosen to give a range of mean net returns. The model was executed using a program written in QUICK BASIC (see Appendix)(Hergert 1994).

Results

The main results from the model are presented in a series of decision matrices. On the vertical axis of the matrices are condition states from 1 to 30. On the horizontal axis are the days of the season from 1 to 56. Each cell in the matrices represents the optimal web type for that condition-time pair given model parameters. I first examine the effect of the form of the terminal fitness function on web building behaviour using the basic model where mean return = 1 and no reproductive threshold exists. Second, I investigate the effect of a reproduction threshold in the basic model. Third, I examine the effect of varying mean return.

Effect of terminal fitness function

Risk indifferent web choices are expected for the linear fitness function, risk prone decisions (web type 2) are expected for the accelerating function and risk averse decisions (web type 1) are expected for the decelerating function (Real and Caraco 1986, Stephens and Krebs 1986, Caraco and Lima 1987). These decisions are observed as expected for some time-condition pairs, however other decision patterns also emerge. For example, risk averse decisions are observed in parts of matrices for all fitness functions (Figure 2.1).

Risk averse decisions are observed for the top condition states for all fitness functions near terminal \( T \). This region arises because both web options put the forager
Figure 2.1. Decision matrix of web type choice by spiders. The case presented here: linear, accelerating, decelerating terminal fitness functions; threshold absent; mean return $= 1$. $\dagger$ = risk averse web, $\ddagger$ = risk prone web. In the region labelled "" the fitness of the two web types differs by 0.0001. In the final time step, $\ast$ = no decision.
above the $X_{\text{max}}$ boundary. As there is a chop function, fitness over that boundary does not carry over (c.f. Stephens and Krebs 1986; see also Bednekoff and Houston 1994). This boundary, combined with the decreasing fitness values for condition states below $X_{\text{max}}$ makes risk averseness profitable because the combination acts like a decelerating curve. For the decelerating fitness function, risk averse decisons are further selected by top condition states near terminal $T$ because of the shape of this terminal fitness function. This risk averse region extends through lower condition states earlier in the season as fitness values increase such that the $X_{\text{max}}$ fitness boundary is accessed at lower condition states.

Risk averse decisions are also seen for low condition states near the end of the season for all fitness functions to avoid falling below $X_{\text{min}}$ condition states just before reproduction. These two risk averse regions come together and extend back around the regions of risk indifference (linear function) or risk proneness (accelerating function). Risk averse decisions extend back until the fitness difference between the two web options is less than 0.0001 at which time the risk indifferent option is again selected. This second region of risk indifference has a positive slope as lower condition states reach fitness values near $\Phi_k(X_{\text{max}})$ later in the season than higher condition states.

**Effect of a reproductive threshold.**

The region of risk aversion for high condition states near terminal $T$ remains (Figure 2.2). The lower region of risk aversion is now shifted up to states around the threshold for all three fitness functions. This area again arises to avoid falling below the minimum reproductive condition states for condition states around the reproductive threshold at the end of season. The exact position and shape of this region depends on the distribution of energy return from which foragers sample. Below this region of risk aversion, is a region of risk proneness for low condition states near terminal $T$ for all
Figure 2.2. Decision matrix of web type choice by spiders. The case presented here: linear, accelerating, decelerating terminal fitness functions; threshold present; mean return = 1. * = risk averse web, o = risk prone web. In the region labelled " " the fitness of the two web types differs by 0.0001. In the final time step, * = no decision.
three terminal fitness functions. This area arises to maximize the possibility of escape from condition states which are already below the minimum.

**Effect of mean return**

Figure 2.1 presented the basic model where mean return = 1. In Figure 2.3, the case where mean return = 0 is presented. A risk prone region now appears for all fitness functions even in the absence of a threshold, as foragers whose possible foraging future extends below the $X_{\text{min}}$ states are risk prone, depending on the distribution of energy return from which they sample. Some regions of risk aversion arise to minimize falling below $X_{\text{min}}$ (Figure 2.3). The introduction of a threshold further increases the size of the risk prone area for the linear and decelerating function, and increases the areas of risk aversion for the accelerating function near the end of the season (Figure 2.4).

When the mean return is further lowered to -1, the shapes in the decision matrices for linear and decelerating fitness function are similar with and without the threshold (Figure 2.5 and 2.6). The risk prone area is large, sloping negatively from terminal $T$ and then asymptoting at a high condition state because of the $X_{\text{max}}$ chop function. The risk averse area increases with appearance of a threshold.

For the accelerating fitness function, foragers are risk prone across the season for most condition states when no threshold is present, except for the top condition states where the effects of the chop function lead to risk averse behaviour. When the reproductive threshold is introduced, risk averse behaviour is observed for foragers whose foraging future projects them around the threshold condition states at the end of season.
Figure 2.3. Decision matrix of web type choice by spiders. The case presented here: linear, accelerating, decelerating terminal fitness functions; threshold absent; mean return = 0. ≤ risk averse web, ≥ risk prone web. In the region labelled "•" the fitness of the two web types differs by 0.0001. In the final time step, ≤ no decision.
Figure 2.4. Decision matrix of web type choice by spiders. The case presented here: linear, accelerating, decelerating terminal fitness functions; threshold present; mean return = 0. = risk averse web, * = risk prone web. In the region labelled "" the fitness of the two web types differs by 0.0001. In the final time step, * = no decision.
Figure 2.5. Decision matrix of web type choice by spiders. The case presented here: linear, accelerating, decelerating terminal fitness functions; threshold absent; mean return = -1, = risk averse web, = risk prone web. In the region labelled " " the fitness of the two web types differs by 0.0001. In the final time step, = no decision.
Figure 2.6. Decision matrix of web type choice by spiders. The case presented here: linear, accelerating, decelerating terminal fitness functions; threshold present; mean return = -1. = risk averse web, . = risk prone web. In the region labelled "." the fitness of the two web types differs by 0.0001. In the final time step, . = no decision.
Sensitivity analyses of model

Sensitivity of the model to parameter values was investigated by adjusting combinations of web costs, insect energy values and capture probabilities to generate the same mean return, as well as by modelling the effects of disparate web costs with increased large prey capture for web 2. These changes did not significantly alter the general patterns observed in the decision matrices. Some small scale differences arise since the foragers are sampling from slightly altered distributions of energy.

Discussion

The model is most sensitive to mean return. If foragers are on average losing condition, results of the model are similar for all terminal fitness functions. Terminal fitness functions have the greatest effect on the patterns of web selection observed when mean return is positive. The effects of reproductive thresholds and limits are most apparent near the end of season. The presence of thresholds and limits act to modify all fitness functions into reward functions which are accelerating at low condition states and decelerating at high condition states. Caraco (1980) and McNamara and Houston (1992) have argued that a forager's fitness function should generally have this shape, however with the inflection point representing a threshold.

Assumptions of the model

Since the model represents foraging behaviour of orb-web spiders, the suitability of the model, its limitations and implications of its assumptions to biological reality must be explored.
1. **Chop functions**

Chop functions act in the dynamic program to maintain the dimensions of the fitness array during computations. The chop function at $X_{max}$ makes intuitive biological sense as portions of any food item that exceed gut limitations cannot be consumed and so the forager cannot further improve its condition beyond $X_{max}$.

The chop function at $X_{min}$ maintains the state variable at $X_{min}$. However, the fitness value assigned to the chop function at $X_{min}$ is zero, so foragers are penalized for decisions which would lower their condition below $X_{min}$, an event comparable to starvation or total reproductive failure.

2. **Costs of web-building, $\alpha_i$, are the same for all condition states**

Since spiders ingest their webs and recycle most of the silk proteins, the cost incurred for web-building includes only the energetic equivalent of walking the distance of the thread length in the web (Peakall and Witt 1976; Prestwich 1977). However, cost of web building also depends on mass of the spider because heavier spiders will have a higher cost per distance moved. I am unaware of any empirically derived functions relating cost of web-building to spider mass in the literature. If cost became prohibitive, large spiders might be precluded from using a risk prone option if it were a more expensive choice, when it would be otherwise optimal. However, risk averse webs were uniformly chosen for all fitness functions and mean returns by good condition spiders in the model.

3. **Web types are discrete.**

In the field, web parameters are continuous, so this is a simplification, but the principles remain the same.
4.  *The energy gained from each prey capture event* ($\beta_j$) *is independent of condition state* (unless *chop function* for $X_{max}$ *is activated*).

Spiders have an extensive intestinal system with many gut diverticula which has been implicated as their means of surviving without food intake for long periods of time (Foelix 1982). Whether this gut degenerates in size or function when spiders are near starvation, as has been observed for birds (Klasseen and Biebach 1994), or grows as necessary following the ingestion of large quantities food as seen in reptiles (Diamond 1994), has not been addressed in the literature. If regeneration were required for poor condition spiders, they might increasingly choose risk prone webs which have a greater probability of returning large prey.

5.  *The energy gained from each prey capture event* ($\beta_j$) *is consumed in one time period*.

There is a seasonal effect in the time required to process prey of the same size due to changes in temperature and spiders may retain prey in webs for more than one day (pers. obs.) I do not know if this additional feeding time results in degradation of prey such that it could not be as fully consumed as it would have been under warmer conditions. If prey is fully consumed in a protracted feeding period then this assumption of the model is not critical.

6.  *Capture probabilities are the same across all condition states*.

The assumption that web design is the critical factor in determining prey arrival and capture and not spider condition seems biologically reasonable.

7.  *Foragers in the model are all the same body size, and differ only in abdomen volume.*
By assuming that all spiders in the model have the same body size, condition is an absolute measure which has a defined relationship with a fitness measurement. Clear predictions regarding the expected risk sensitive responses to condition can be made and compared with the observed decision matrices. Differences in web design and prey capture abilities related to body size are then also avoided. This assumption seems reasonable for an analysis of the effect of capture variability due to web type, but I acknowledge that body size affects web design and prey size selection (Olive 1980, Brown 1981, Murakami 1983, Nentwig 1983, McReynolds and Polis 1987).

8. All fitness is realized in the final time step.

This assumption means that all spiders lay one "clutch" at the end of the season (T). Those spiders who reach $\Phi_k(X_{max})$ cannot "bank" some fitness by laying a clutch of eggs and then re-building their mass and relaying. If this assumption was relaxed, the chop function at $X_{max}$ would have a very reduced effect on dynamics and more risk prone behaviour would be observed to allow multiple clutches.

9. No predation in the model.

In a model in which the forager could have multiple clutches, the effect of background mortality on foraging option selection depended upon the sign of mean net gain (McNamara et al. 1991). When mean net gain was positive, the optimal policy was to be risk averse at low reserves (condition) and risk prone at high reserves. When mean net gain was negative, the risk prone option was always chosen. The results for mean positive gain are opposite to the decision matrices observed from my model but this is due to the opportunity for repeated reproduction. Without the opportunity for multiple clutches, background mortality should have no effects on dynamics in my model.

Differential mortality risk would have effects on web type selection. If foragers in poor condition were more vulnerable to predation, there should be additional incentive
to gain condition and an increase in risk prone behaviour should be observed. If foragers in good condition were more susceptible to predation, an increase in risk averse behaviour should be observed (Bednekoff and Houston 1994). Although differential mortality would shift the selection of foraging options at various states, it should not lead to a general reversal of foraging option selection by condition states.

An alternative explanation for the inverse relationship between condition and web size.

Other studies examining individual variability in orb-web size have also observed that poor condition spiders build larger webs than good condition spiders (Higgins 1990; Higgins and Buskirk 1992; Sherman 1994). These studies suggest that good condition spiders shunt resources into growth or egg production, instead of foraging and hence build smaller webs. The inverse relationship between spider condition and web size arises as a consequence. Why this particular pattern of web size with condition was indicative of a foraging-growth tradeoff is not immediately clear. These authors subscribe to the idea that webs function as filters seiving insects from the air, though Sherman (1994) noted that larger webs also take larger insects. Given a non-linear relationship between web size and prey volume, and the fact that good condition spiders have more resources to allocate than poor condition spiders, one can envisage alternative optimal web size-condition relationships. For example, the same large web would be constructed by all spiders and leftover resources would be shunted into growth. In such a scenario, good condition spiders would still be allocating more energy to growth. I believe that the foraging-growth tradeoff would have to be modelled or more thoroughly set out to show why this inverse pattern of web building with condition would result from such a tradeoff.

Recently, individual variability in juvenile orb-web design was explicitly modelled as a function of foraging-growth tradeoffs (Higgins 1995). Higgins notes that
common resources are used for both growth and foraging, and argues that the objective of the spiders is to minimize the potential for weight loss, as it strongly reduces the fitness of female spiders (Higgins and Rankin 1996). Hence, explicit predictions can be made concerning the allocation of resources under different foraging conditions. In her model, weight gain is a sigmoidal function of food level, whereas web size follows a normal distribution with the largest webs made at an intermediate level of food. In a three food-level experiment with *Nephila clavipes* (Linnaeus) as a model organism, the following predictions were made: under low food conditions, the residuals of the relationship of web size to weight gain (corrected for body size) are expected to be lower than average, under medium food conditions residuals of web size are greater than average and residuals of weight gain are lower than average, and finally under high food conditions, residuals of web size are smaller than average while residuals of weight gain are higher than average. These predictions match the observations for weight gain but not for web size. Web sizes for the low and medium food treatment were not significantly different.

The food levels were generated in the Higgins's 14 day experiment (which is slightly longer than the mean intermoult interval for the instars of spider used in the experiment) by feeding the spiders the mean number of prey captured per day in the rainy and dry season respectively, at different instar (size) stages. There was mortality during the experiment and not all spiders managed to moult. Few poor condition spiders gained weight, although none lost weight (Higgins 1992). I estimate that mean return, or growth rate, in this experiment was positive but small.

In my model, which posits an alternative explanation - risk sensitivity - for the relationship between orb web size and condition, poor condition spiders switched web types near the terminal time period, medium condition spiders switched to risk prone webs and very good condition spiders were risk averse for an accelerating fitness function with mean returns around one and a threshold present (An exponential
relationship between body length and fecundity has been reported in the literature for a *Nephila* species (Miyashita 1986). All individuals in my model were considered "adults", so spiders did not have to reach particular threshold condition states in order to "moult" through successive instars to reach adulthood and gain mass for eggs before the end of season. Given that time limitation creates these patterns with a threshold for reproduction in effect, this pattern should be repeated in a model where moulting is introduced and the attainment of minimum condition states is required to make it to the next instar at each moulting event.

In her experiment, Higgins (1995) compared the mean size of webs of each juvenile individual from all days of the experiment among feeding treatments. Although she states that web sizes changed for individuals over the experiment, she does not state whether these patterns of change appeared to differ among treatments. By inspecting the last 14 days of the decision matrix created with an accelerating fitness function, a mean return of one and a threshold present, for the average web type chosen across the condition states, I get the same results for average web size as Higgins' (1995). Medium and very low condition spiders choose both small and large web types while very good condition spiders choose mostly web type 1 (small web). From inspection of the matrix results, I would predict that very poor condition spiders would have larger webs on average than good condition spiders in Higgins' (1995) experiment and this is what appears to have occurred (Higgins 1995, see Figure 2) although average web sizes of the high and low food treatment were never directly compared. In her model, Higgins (1995) assumes that both very good and very poor condition spiders would make the same sized small webs. My model appears consistent with the data from Higgins (1995). Both mechanisms could be occurring and complementary depending on the formulation of the foraging - growth tradeoff, resulting in these relationships between web size and condition. It remains imperative to determine empirically whether foraging options differ in mean and not variance, the mean net return experienced by spiders and the
fitness functions to which they are responding for these data sets, to further support the hypothesis of risk sensitive foraging in spiders.
Appendix

The program below is a run of the basic model for the linear fitness function where mean return is 1 and there is no threshold present. To run the basic model with a threshold present, $X_{thresh} = 6$ in parameter input, and in the intialization module for $x = 1$ TO $X_{thresh}$, $\Phi(X) = 0$. The program appears as it would in QBASIC except for the formatting of characters.

***Optimal Web Choice Program***

'a run of the basic model for linear fitness function

'** Parameter Input**'

$X_{thresh} = 1$
$X_{min} = 1$
$X_{max} = 30$
$T_{min} = 1$
$T_{max} = 56$

Webt = 2
Inst = 4

DIM Alpha(Webt), Beta(Inst), Event(Webt,Inst)
DIM Exptobe($X_{max}$)
DIM F($X_{max}$, $T_{max}$), Decision($X_{max}$, $T_{max}$)
DIM Phi($X_{max}$)

'*web cost*
DATA .15, .15
FOR I = 1 TO Webt
    READ Alpha(I)
NEXT I

'*insect types: none, medium, large, both*

DATA 0, 2, 5, 7
FOR J = 1 TO Inst
    READ Beta(J)
NEXT J

'*probability of each possible outcome- none, medium, large, both prey captured*

DATA .558, .372, .042, .028
DATA .68, .17, .12, .03

FOR I = 1 TO Webt
    FOR J = 1 TO Inst
        READ Event(I, J)
    NEXT J
NEXT I

' *** Main Program ***
'Initialize F(X, K)

K = T_{max}
FOR x = 1 TO X_{thresh}
    Phi(x) = x
    F(x, K) = Phi(x)
    Decision(x, K) = 0
NEXT x

FOR x = X_{thresh} + 1 TO X_{max}
    Phi(x) = x
    F(x, K) = Phi(x)
    Decision(x, K) = 0
NEXT x

'solve DPE

FOR K = T_{max} - 1 TO 1 STEP -1

FOR x = 1 TO X_{max}
    Bestenergy = 0
    Bestdecision = 0

    FOR I = 1 TO Webt
        Msum(I) = 0 'keeps track of energy accumulated across prey capture events

    FOR J = 1 TO Insect
Flag = 0    'flags state variables that fall below $X_{\text{min}}$

$X_1 = x - \alpha(I) + \beta(J)$

IF $X_1 > X_{\text{max}}$ THEN $X_1 = X_{\text{max}}$
IF $X_1 < X_{\text{min}}$ THEN Flag = 1
IF $X_1 < X_{\text{min}}$ THEN $X_1 = X_{\text{min}}$

'interpolation procedure

Higher = $(X_1 + 1)$
IF Higher > $X_{\text{max}}$ THEN Higher = $X_{\text{max}}$

One = F(FIX(X1), K + 1)
Two = F(FIX(HIGHER), K + 1)
Remainder = $X_1 - \text{FIX}(X_1)$

State = One + (Remainder * (Two - One))

'apply probabilities and assign fitness penalty if state variable fell below Xmin

Exptobe = $(\text{Event}(I, J) * \text{State})$
IF Flag = 1 THEN Exptobe = 0

$M_{\text{sum}}(I) = M_{\text{sum}}(I) + \text{Exptobe}$
NEXT J

'keep fitness within bounds
IF Msum(I) > Phi(X_{max}) THEN Msum(I) = Phi(X_{max})

'make web choice
IF Msum(I) > Bestenergy THEN

Bestenergy = Msum(I)
Bestdecision = I

END IF

IF ABS(Msum(I - 1) - Msum(I)) < .0001 THEN

Bestenergy = Msum(I)
Bestdecision = 3

END IF

NEXT I

F(x, K) = Bestenergy
Decision(x, K) = Bestdecision
NEXT x
NEXT K

' *** File I/O ***

OPEN "d:\output\basicdec.txt" FOR OUTPUT AS #1
PRINT #1, "basicdec.txt"
FOR x = X_{max} TO 1 STEP -1
  PRINT #1, USING "##"; x;
  FOR K = 1 TO T_{max}
    PRINT #1, USING "#"; Decision(x, K);
  NEXT K
PRINT #1,
NEXT x
CLOSE #1

OPEN "d:\output\basicfit.txt" FOR OUTPUT AS #1
PRINT #1, "basicfit.txt"
FOR x = X_{max} TO 1 STEP -1
  PRINT #1, USING "##"; x;
  FOR K = 1 TO T_{max}
    PRINT #1, USING "##.###"; F(x, K);
  NEXT K
PRINT #1,
NEXT x
CLOSE #1
Chapter 3

Risk sensitive web design in a field population of *Argiope trifasciata*?

**Introduction**

Individual variation in web design has been noted for a number of generalist spider species (Higggins 1990, Higgins and Buskirk 1992, Higgins 1995, Sherman 1994). In spider populations, spiders in poor condition make larger webs than spiders in good condition (Higgins 1990, Higgins and Buskirk 1992). Risk sensitive foraging is suggested as the cause of such patterns wherein some web designs offer more variable returns in energy than other web designs and thus individual spiders select different web designs according to their condition (Chapter 2).

I examine this idea of risk sensitive using a generalist spider species. I chose *Argiope trifasciata* (Forskal) as a model organism for a number of reasons. The web parameters of *A. trifasciata* have been observed to change after condition has been experimentally altered (Olive 1982), although the experiment was not designed to test this effect.

The diet of *A. trifasciata* includes flying and jumping prey, although taxa within these categories may differ substantially between habitats (see review by Eberhard 1996). *A. trifasciata* makes stabliamenta, zig-zag swaths of silk in the web which are UV reflecting, suggesting that this species is sensitive to the visual acuity of pollinating insects and may try to attract them to the web (Craig 1994). *A. trifasciata* is proficient at "wrap attack" where its long legs are used to throw silk onto large and dangerous prey like grasshoppers (Robinson 1975, Olive 1980). The diet breadth, attack behaviour and web structures available to *A. trifasciata* suggest that individuals may select web designs which offer different amounts of variance. Differing levels of variance might be
achieved by trade-offs between the web functions of prey interception and prey retention resulting in the capture of particular prey types. Webs designed to capture flying prey are expected to be smaller with widely spaced spirals with decreased retention of jumping prey. Webs designed to capture jumping prey are expected to be larger with dense spirals but with decreased interception of flying prey. Larger webs would be more variable in return than smaller webs (Chapter 2).

I predicted a priori that poor condition spiders would make larger and more densely-meshed webs than good condition spiders as has been observed in other studies. I tested the assumption of the model (Chapter 2) that webs of poor condition spiders would offer more variable return than webs of good condition spiders. I also hypothesized that this variance would result from large webs capturing more jumping prey such as grasshoppers than flying prey such as hymenopterans compared to good condition spiders.

In this chapter, I discuss the effects of natural and manipulated condition on web design of individual Argiope trifasciata females. I examine age class differences in relationships of web parameters to condition. I also investigate the effects of web design on mean and variance in energy return as well as prey type, in relation to risk sensitive foraging decisions.

Methods

Study site

Argiope trifasciata individuals were observed in 2 ha of old field belonging to the Tsawwassen First Nation. This field is located on the landward side of a sea dike just before the causeway that leads to the Tsawwassen ferry terminal near Vancouver, British Columiba. Old driftwood is still located on the field near the dike. Parts of the field are
wet with temporary brackish ponds and channels, while other parts of the field are very dry and grass covered. Vegetation utilized by *A. trifasciata* included grasses, sedges (especially clumps of *Scirpus microcarpus*), wild rose (*Rosa* spp), brambles (*Rubus* spp), dock (*Rumex* spp), field pennycress (*Thlaspi arvense*), vetch (*Vicia* spp), cow parsnip (*Heracleum lanatum*), asters (particularly clumps of yarrow *Achilea millefolium*), thistles (*Cirsium* spp.), american glasswort (*Salicornia virginica*), lamb's quarters (*Chenopodium album*), and european bittersweet (*Solanum dulcamara*). Plants were identified using Pojar and MacKinnon (1994).

**Observational data collection: web parameters, prey capture and condition**

Spiders observations were conducted in sessions of two or three days from mid August to late September. All spiders were naive to observation. Spiders were located by sight and web sites marked with numbered yellow or orange flagging tape the day before observation.

Web parameters were measured in the early morning throughout the hours of 7:30 and 10:00. Measuring webs during this time frame ensured that webs were not too damaged by prey capture so as to interfere with accurate measurement. In addition, webs were more visible in the early morning light. Measurements were taken using clear plastic 30 cm rulers, except for web height which was measured with a wooden 1 m ruler when web height exceed 30 cm. Vertical diameter of the web was measured through the longest vertical straight line of the web from the bottom-most spiral to the uppermost spiral. Horizontal diameter was measured through the widest part of the web at the outermost spiral. The length of the hub was measured vertically across the innermost spiral. It could be distinguished from the catching spiral of the web as its thread was thinner and appeared less sticky. It was often rather messy compared to the organized catching spiral. Mesh size was defined as number of spirals per centimeter and was determined by counting all the spirals in the bottom half of the web, from the lowest
spiral to the hub spiral and dividing by the distance from this bottommost spiral to the hub. Radials were counted by choosing a starting radial and counting around the web.

Stabilimenta, (zig-zag strands of thickened silk), were measured using the ruler and their direction (up, down or angled) was noted. Barrier webs, sheets of silk that could vary in complexity, were scored as single if present on only one side of the web, and double if present on both sides of the web. Barrier webs were structured on one extreme to appear like additional orb webs while on the other extreme they were messy, thin, small clumps of silk. It was only noted if the barrier webs were extensive or older and decayed.

On the first day of observation, prey capture was observed in webs from 10:00 until 14:00. Webs were surveyed every 15 min. Prey types were categorized by size and order. Unidentifiable prey were scored as unknown. The approximate time of prey capture was noted and the condition of the prey (unwrapped or wrapped). Time of initiation of feeding, feeding interruptions and end of feeding was also recorded. Other behavioural actions and natural history events were also recorded.

On the second day of observation, spiders were collected in glass jars after web measurement. We tried to capture spiders without causing autotomy of appendages and without damaging their web as they were later returned to the same web site. Males associated with observed females were captured where possible. Spiders were brought to a laboratory at Simon Fraser University. They were anesthetized with carbon dioxide in the catching jar. Spiders were observed for any missing or regrown body appendages. They were weighed on a Sartorius balance to 0.0001 g. Dial calipers were used to measure cephalothorax width and abdomen length, width and depth to 0.005 cm. Calipers were placed between the second and third pair of legs to measure cephalothorax width. The widest part of the abdomen was usually one of the white colour rings about 2/3 down the length of the abdomen. Depth of abdomen was always measured just in front of the spinnerets.
Experimental manipulation of condition

This experiment was performed over a three day period on September 6-8 and 22-24. Pairs of spiders less than 1.5 m apart were chosen and were assigned to either a "supplemented" or "control" group, such that range of body sizes between the two groups would be equivalent. By pairing spiders, I hoped to avoid bias from natural fluctuations in prey levels according to microhabitat. Spiders in the "supplemented" group were given a live flesh fly with a wet weight of about 0.1 g on the first two consecutive mornings. All spiders were observed to wrap and feed on the prey item. Control spiders were exposed only to natural prey conditions. Webs from both groups were measured before the feeding on the three days as described in the observational section. Spiders were brought into the lab on the third day and their body measurements were taken as described in the previous section.

Statistical analysis

Separation of age classes

Spider observational data were divided into two groups which I characterized as juvenile and adult age classes. These two groups overlap in cephalothorax width. The instar of reproductive maturity can differ among individuals of a population and between populations (Enders 1974; Brown 1981; Benton and Uetz 1986; Higgins 1992). I separated these groups to avoid comparisons between gravid and non-gravid spiders. Body length-weight relationships are quite different for non-gravid and gravid females of Nephila clavata (Koch) (Miyashita 1986) and abdomens of gravid female spiders swell conspicuously (Miyashita 1986; pers. obs.). The perception of gravid and non-gravid spiders of their condition and their response as mediated through web parameters might be different even though these spiders could have equivalent condition as measured in the laboratory.
Age classes of females of the species *Argiope aurantia* (Lucas) have been identified in the field by leg colouration; females switch from a banded leg pattern to all-black when they reach sexual maturity (Howell and Ellender 1984). There was no easily observable morphological character to distinguish adult females from juveniles in *A. trifasciata*. I found no literature values for minimum abdomen volumes of adult *A. trifasciata*. As I suspected that cephalothorax size at maturity might be more variable than timing of maturity, I chose date as the indicator of age class. I considered all spiders to be adults as of the September 8 collection period. The last juvenile collection day was August 29.

**Condition and web parameters**

Condition for the two classes was assessed by regressing the natural log of abdomen volume on cephalothorax width. The residuals from this analysis, hereafter condition, were then regressed as the independent variable against web parameters, the dependent variables. The effects of body size were partialled out as web parameters increase with increasing body size (Olive 1980, Brown 1981, Murakami 1983, Nentwig 1983, McReynolds and Polis 1987) A correlation analysis of web parameters showed they were correlated. Given that MANOVAS examining the effect of body size and condition on web parameters were the appropriate statistical technique to deal with correlated dependent variables, univariate analyses of the effect of body size and condition on singular web parameters were still performed to identify important web parameters. Spiders from the supplementation experiment were included in the adult analysis. Web parameters from the third day of observation, which was the day these spiders were collected, were used in the analysis.

All non-normal continuous variables were log-transformed, except for hub length in juveniles which approximated a normal distribution more closely when untransformed.
Count data, such as radials were normalized by log-transformation. Counts of stablimentia and barrier number were strongly non-normal. They could not be normalized after log, reciprocal and square-root transformations were attempted and so these parameters were dropped from the analysis.

Sometimes spiders did not change their web from day to day. This action might indicate that the spider was preparing to moult and hence would not feed. Since the question I was interested in was, how does spider condition affect foraging decisions, I dropped these spiders from the analysis (n=3). It is possible that not completely renewing a web would be a foraging decision made by a spider in either particularly poor condition or particularly good condition, although it would not be a very common strategy. Of these three spiders, one was in relatively poor condition with a large cephalothorax and low abdomen volume, indicating perhaps low foraging success following a recent moult, one was a large-bodied spider with a large abdomen attended by 4 males suggesting that she would soon moult to adulthood and the third seemed rather average. Eliminating these spiders from the analysis should not introduce any systematic bias.

Characteristic moulting webs, which signaled an imminent moult within the next few days were identified. These webs tended to be irregular in shape, have few spirals (less than 10) because the web was not repaired although stablimentia might be reworked daily. The old silk of these webs was covered with dust and plant debris and was not sticky. All of these webs had extensive barriers. Three of these spiders moulted directly in the catching jar. These webs were also excluded from the analysis (n=13).

All analysis was done using SAS statistical software (SAS Institute. Inc. 1990). The $\alpha$-level is $0.05$, tests were two-tailed and F-statistics are based on partial (type III) sum of squares.
**Experimental manipulation of condition and its effect on web parameters**

A design similar to a paired t-test was employed by subtracting web parameters on the first day from web parameters on the third day for each spider in both classes "supplemented" and "control". These differences were then compared between the two groups using an ANOVA design. Height, radial number and mesh size were all log-transformed to meet the assumptions of equal variances and normality. Some of the webs in the second half of the experiment might not have been completely renewed as webs seemed less sticky than expected, but were not removed from the analysis due to uncertainty of this observation and low sample size.

All analyses were done using SAS statistical software (SAS Institute. Inc. 1990). The $\alpha$ level was 0.05 and the tests were two-tailed.

**Prey capture: mean, variance, prey type and web parameters**

Prey types were grouped into 5 size categories. Energy value of prey types was determined either by averaging direct measurement of insect type mass in the laboratory or by converting insect lengths observed in the field to mass via the equation $W = 0.0305L^{2.62}$ where $W =$ body mass in mg and $L =$ body length in mm (Roger *et al.* 1976) and then by multiplying these masses by an average energy content 23 J mg dry weight (see Riechert 1991)). These calculations gave a rough estimate of energy value of prey types given that I was unable to exactly measure lengths and masses of insects consumed by spiders in the field. Energy value of all prey captured was determined for each web.

Web parameters were entered in a Principal Component Analysis after checking that web parameters were correlated. The first principal component (prin1) was interpreted as indicative of web size. The second principal component was more difficult to interpret, explained little variation and interacted with date in analyses described below and so is not discussed further. Prin1, hereafter web size, was treated as a class
variable and grouped into two categories, large and small. Web size was entered into an ANCOVA with date as a covariate and energy value of all prey capture was the dependent variable. The interaction between date and web size was not significant and so was dropped from further analysis. The analysis tested whether the means of the two groups of web size were significantly different. The residuals from this analysis were used in an ANOVA as the dependent variable and web size as the independent variable. This analysis tested whether residuals were significantly different for the two web size groups, which is analogous to testing whether variances between the two groups were equivalent.

All analyses were done using SAS statistical software; α is 0.05, tests are two tailed and F statistics are based on partial (type III) sum of squares (SAS Institute. Inc. 1990).

Web size was also entered in Poisson regressions as the independent variable with the number of each prey type as the dependent variable, where the effects of date were partialled out. An interaction of web size with date was tested for each analysis and the interaction dropped from further analysis if insignificant. This analysis tested whether web design, controlling for date, effected capture number of prey types at fairly gross levels of taxonomic distinction or mode of locomotion (corresponding to flying or jumping suggestive of visually orientating or not). The most common prey type, dipterans < 0.5 cm, was examined and prey were also grouped into classifications such as hymenopterans, heteropterans, orthopterans, jumping prey, flying prey, and all prey. These categories were necessarily overlapping. As the data were overdispersed, since the variance in prey capture for all webs was greater than the mean for all webs, the deviance was scaled by the degrees of freedom. Over-dispersion is common in behavioural studies where there is inter-subject variability (McCullagh and Nelder 1989).

Both adult and juvenile spiders were included in this analysis. Sample size and individuals in the analysis differs from the adult and juvenile condition tests. This
difference is due to the fact that some spiders measured on the first day of web observation moved web sites. As well, some first observation days were rainy or windy and webs were altered during prey capture observation. These spiders were dropped from the analysis. Two webs observed during alate ant swarms were also eliminated from the data set as their inclusion strongly affected the Poisson distribution of prey captures for their prey class. It seemed clear that these webs had caught so many ants as a result of their fortunate position rather than their web design. Finally, moulting webs or any webs with missing values for any parameters were eliminated from the analysis.

All statistics were done using SAS statistical software; $\alpha = 0.05$, $\chi^2$ statistics are based on type 3 sum of squares, comparable to the type III sum of squares used in traditional general linear models (SAS Institute Inc. 1993).

**Results**

**Separation of age classes**

Adult spiders overlap both in cephalothorax width and abdomen volume with immature spiders (Figure 3.1) but the slope of the relationship is significantly different for the two classes (interaction between class and cephalothorax width, $F_{1,155} = 37.82$, $p = 0.0001$). The range in residuals from the regression line of volume on cephalothorax width is much greater in adults than juveniles. The mean and range of cephalothorax width and volume is much greater for adult spiders (Table 3.1; Figure 3.1). Mean standard error of untransformed web parameters are also presented in Table 1 for both age classes.
Figure 3.1 Relationship of abdomen volume to cephalothorax width for immatures and adults, showing lines of best fit.
Table 3.1. Mean and standard error for web parameters and body measures of adult and juvenile age classes.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean±S.E. juveniles</th>
<th>Mean±S.E. adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>height (cm)</td>
<td>30.3±1.7</td>
<td>33.6±1.5</td>
</tr>
<tr>
<td>vertical diameter (cm)</td>
<td>20.4±0.7</td>
<td>25.7±0.8</td>
</tr>
<tr>
<td>horizontal diameter (cm)</td>
<td>14.9±0.4</td>
<td>20.3±0.7</td>
</tr>
<tr>
<td>hub diameter (cm)</td>
<td>4.3±0.2</td>
<td>6.9±0.3</td>
</tr>
<tr>
<td>radials (number)</td>
<td>38.5±1.0</td>
<td>36.5±1.4</td>
</tr>
<tr>
<td>mesh (number spirals/cm)</td>
<td>5.4±0.2</td>
<td>4.3±0.3</td>
</tr>
<tr>
<td>barrier (number)</td>
<td>0.9±0.1</td>
<td>0.1±0.04</td>
</tr>
<tr>
<td>stabilimenta (number)</td>
<td>0.5±0.1</td>
<td>1 web only</td>
</tr>
<tr>
<td>cephalothorax width (cm)</td>
<td>0.275±0.006</td>
<td>0.361±0.010</td>
</tr>
<tr>
<td>volume (cm³)</td>
<td>0.033±0.002</td>
<td>0.257±0.029</td>
</tr>
</tbody>
</table>
Condition and web parameters

The MANOVA for the effect of condition on web parameters was significant for juveniles ($F_{6,44} = 3.07, p = 0.0134$) and highly significant for adults ($F_{6,44} = 5.71, p = 0.0002$). The MANOVA for the effect of cephalothorax width on web parameters was significant for juveniles ($F_{6,44} = 4.04, p = 0.0026$) and highly significant for adults ($F_{6,44} = 5.71, p = 0.0002$).

In univariate tests, the effects of condition on log vertical diameter and log mesh size were significant for juveniles (Table 3.2). Both of these parameters decreased with increasing condition. The effect of condition on log horizontal diameter was marginally significant and this parameter also decreased with increasing condition. For adults, the effect of condition on vertical diameter, log radial number and height above ground were all significant (Table 3.3). Vertical diameter and log radials decreased with increasing condition whereas log height increased with increasing condition.

The effects of body size (cephalothorax width) also differed among age classes. Body size was highly significant in its effect on log height, vertical diameter, log horizontal diameter and mesh size, and significant for log hub length and log radials in adults (Table 3.3). In all cases it varied steeply and positively with increasing size of web parameter. It was a stronger effect than condition in all parameters except log radials. In juveniles, body size had a significant effect on log height, log vertical diameter, horizontal diameter and hub length (Table 3.2). Again, for all tests, body size increased in a steep positive manner with increasing value of the web parameter. It was a stronger effect than condition for horizontal diameter but less powerful than condition for vertical diameter.
Table 3.2. Slope, F value, significance and R² for the relationship of web parameters to condition and body size of juvenile spiders.

<table>
<thead>
<tr>
<th>Web parameter</th>
<th>Spider Parameter</th>
<th>Estimate</th>
<th>F_{1, 49}</th>
<th>p</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>log height</td>
<td>condition</td>
<td>2.96</td>
<td>ns</td>
<td>0.229</td>
<td></td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>3.29</td>
<td>11.01</td>
<td>0.0017</td>
<td></td>
</tr>
<tr>
<td>log vertical diameter</td>
<td>condition</td>
<td>-0.192</td>
<td>11.49</td>
<td>0.0014</td>
<td>0.277</td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>1.47</td>
<td>6.38</td>
<td>0.0148</td>
<td></td>
</tr>
<tr>
<td>horizontal diameter</td>
<td>condition</td>
<td>-1.8</td>
<td>3.89</td>
<td>0.0541</td>
<td>0.196</td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>25.8</td>
<td>7.46</td>
<td>0.0087</td>
<td></td>
</tr>
<tr>
<td>hub diameter</td>
<td>condition</td>
<td>0.78</td>
<td>ns</td>
<td>0.210</td>
<td></td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>17.15</td>
<td>11.91</td>
<td>0.0012</td>
<td></td>
</tr>
<tr>
<td>mesh size</td>
<td>condition</td>
<td>-8.99</td>
<td>4.55</td>
<td>0.0379</td>
<td>0.120</td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>2.43</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>radials</td>
<td>condition</td>
<td>2.50</td>
<td>ns</td>
<td>0.048</td>
<td></td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>0.01</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.3. Slope, F value, significance and R² for the relationship of web parameters to condition and body size of adult spiders.

<table>
<thead>
<tr>
<th>Web parameter</th>
<th>Spider Parameter</th>
<th>Estimate</th>
<th>F₁₄₉</th>
<th>p</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>log height</td>
<td>condition</td>
<td>0.109</td>
<td>4.33</td>
<td>0.0427</td>
<td>0.274</td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>1.92</td>
<td>13.89</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td>vertical diameter</td>
<td>condition</td>
<td>-2.60</td>
<td>7.80</td>
<td>0.0074</td>
<td>0.412</td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>47.66</td>
<td>27.14</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>log horizontal diameter</td>
<td>condition</td>
<td>1.66</td>
<td>ns</td>
<td>0.359</td>
<td></td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>1.87</td>
<td>26.07</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>log hub diameter</td>
<td>condition</td>
<td>0.78</td>
<td>ns</td>
<td>0.207</td>
<td></td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>17.15</td>
<td>11.91</td>
<td>0.0012</td>
<td></td>
</tr>
<tr>
<td>log mesh size</td>
<td>condition</td>
<td>0.18</td>
<td>ns</td>
<td>0.329</td>
<td></td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>-3.159</td>
<td>23.70</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>log radials</td>
<td>condition</td>
<td>-0.118</td>
<td>7.22</td>
<td>0.0098</td>
<td>0.210</td>
</tr>
<tr>
<td></td>
<td>body size</td>
<td>-0.96</td>
<td>4.95</td>
<td>0.0307</td>
<td></td>
</tr>
</tbody>
</table>
Experimental manipulation of condition and its effect on web parameters

The MANOVA for a class effect of supplemented versus control spiders was significant ($F_{6,18} = 2.85$, $p = 0.0394$). There was a significant class effect on change in vertical diameter, and trends for a class effect on change in horizontal diameter, radial number and mesh size (Table 3.4). The direction of change for supplemented spiders was a decrease in vertical diameter, horizontal diameter, radial number and mesh size (an increase in number of spirals/cm) which was opposite to that of control spiders.

Body size, measured as cephalothorax width, was equivalent between the two feeding classes ($F_{1,24} = 0.05$, $p = 0.8223$) Condition after the experiment was highly significantly different, as assessed by regressing cephalothorax size on abdomen volumes and then testing whether the residuals from the regression were unequally distributed between feeding classes ($F_{1,24} = 18.72$, $p = 0.0002$). Of the fourteen supplemented spiders, eleven of them had positive residuals, and of the twelve control spiders, ten of them had negative residuals. Flies from the previous day were often being fed on the next day in the first run of the experiment.

Prey capture: mean, variance, prey type and web parameters

The first principal component of web parameters explained 37.5% of the variation in web design and corresponds to web size as horizontal and vertical diameter have the highest loadings (Table 3.5). Both of these web parameters load positively. The second principal component of web parameters explained an additional 14.9% of the variation and corresponded to web position and web density, as height, radials and mesh
Table 3.4. Direction of mean change, F value, significance and R² for the relationship of web parameters to feeding class.

<table>
<thead>
<tr>
<th>Web parameter</th>
<th>Feeding class</th>
<th>Direction of mean change</th>
<th>F₁,₂₃</th>
<th>p</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Δlog height</td>
<td>supplemented</td>
<td>-</td>
<td>3.43</td>
<td>0.0768</td>
<td>.130</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δvertical diameter</td>
<td>supplemented</td>
<td>-</td>
<td>9.78</td>
<td>0.0047</td>
<td>.30</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δhorizontal diameter</td>
<td>supplemented</td>
<td>-</td>
<td>3.71</td>
<td>0.0664</td>
<td>.140</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δhub diameter</td>
<td>supplemented</td>
<td></td>
<td>1.78</td>
<td>ns</td>
<td>.07</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δlog mesh size</td>
<td>supplemented</td>
<td>+</td>
<td>4.15</td>
<td>0.0534</td>
<td>.153</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Δlog radials</td>
<td>supplemented</td>
<td>+</td>
<td>4.74</td>
<td>0.0654</td>
<td>.140</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3.5. Principal Component Loadings for web parameters of all individuals (n=84)

<table>
<thead>
<tr>
<th>Web Parameter</th>
<th>Principal Component 1 (Prin1)</th>
<th>Principal Component 2 (Prin2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>vertical diameter</td>
<td>0.449</td>
<td>0.006</td>
</tr>
<tr>
<td>horizontal diameter</td>
<td>0.506</td>
<td>0.037</td>
</tr>
<tr>
<td>height</td>
<td>0.182</td>
<td>0.507</td>
</tr>
<tr>
<td>radial number</td>
<td>0.209</td>
<td>-0.448</td>
</tr>
<tr>
<td>hub diameter</td>
<td>0.368</td>
<td>0.199</td>
</tr>
<tr>
<td>mesh size</td>
<td>-0.329</td>
<td>-0.452</td>
</tr>
<tr>
<td>stablimentia number</td>
<td>-0.355</td>
<td>0.291</td>
</tr>
<tr>
<td>barrier number</td>
<td>-0.305</td>
<td>0.457</td>
</tr>
</tbody>
</table>
size, and barrier have the highest loadings. Height and barrier load positively and mesh size and radials load negatively (Table 3.5).

The ANCOVA for the effect of the class variable web size and the covariate date on energy return of webs showed that web size had an insignificant effect ($F_{1,82} = 0.11$, $p = 0.7431$) but the effect of date was a significant ($F_{1,82} = 8.56$, $p = 0.0044$) The ANOVA testing for a difference in residuals from the ANCOVA between groups of class variable web size showed that residuals were significantly different ($F_{1,83} = 10.97$, $p = 0.0014$).

The Poisson regressions for the effect of web size and date on number of prey types captured were insignificant after Bonferroni adjustment (Table 3.6.).
Table 3.6. Slope and significance of the relationships of prey type on principal components 1 & 2 from Poisson regressions.

<table>
<thead>
<tr>
<th>Prey category</th>
<th>Parameter</th>
<th>Estimate</th>
<th>$\chi^2$</th>
<th>p</th>
<th>Bonferroni adjusted p</th>
</tr>
</thead>
<tbody>
<tr>
<td>all prey</td>
<td>web size*date</td>
<td>6.6189</td>
<td>0.0130</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td>flying prey</td>
<td>web size*date</td>
<td>5.9969</td>
<td>0.0143</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td>dipterans &lt;5 mm</td>
<td>web size</td>
<td>0.4985</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>date</td>
<td>-0.0404</td>
<td>4.2419</td>
<td>0.0394</td>
<td>ns</td>
</tr>
<tr>
<td>hymenopterans</td>
<td>web size*date</td>
<td>6.7528</td>
<td>0.0094</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td>jumping prey</td>
<td>web size</td>
<td>0.4079</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>date</td>
<td>0.1069</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>heteropterans</td>
<td>web size</td>
<td>-0.3793</td>
<td>6.8164</td>
<td>0.0090</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>date</td>
<td>-0.0676</td>
<td>3.7057</td>
<td>0.0542</td>
<td>ns</td>
</tr>
<tr>
<td>orthopterans</td>
<td>web size</td>
<td>0.5140</td>
<td>ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>date</td>
<td>0.2085</td>
<td>10.3311</td>
<td>0.0013</td>
<td>ns</td>
</tr>
</tbody>
</table>
Discussion

Condition, web parameters, and age classes

The relationship between condition and web type might be expected to be more subtle and thus undetectable in juveniles (given the smaller amplitude of variation in condition for juveniles), if the two age classes are following similar risk sensitive strategies. Juveniles might be expected to follow distinct foraging strategies given that juveniles face different life-history decisions than adults. For example, juveniles encounter consecutive moulting time horizons, and thus the scale at which mean net energy was equilibrated between foraging options would be critical. If that scale was greater than the maximum intermoult interval, then juvenile spiders might be constrained to choose low variance options.

Despite this consideration, a significant inverse relationship of condition to vertical diameter was found for adult and juvenile age classes, suggesting both age classes follow similar foraging strategies. The same changes in vertical diameter with condition were reported for Nephila clavipes by Higgins (1990) and Higgins and Buskirk (1992). Differences in relationships of other web parameters to condition between juveniles and adults are best explained by constraints particular to age classes (seasonal changes in vegetation (height and horizontal diameter), seasonal changes in prey type availability (spiral rich design) and body size (horizontal diameter, spiral rich design)), rather than as a result of of lack of sensitivity in the analysis, but these constraints due not preclude risk sensitive foraging.

Horizontal diameter of the webs was significantly effected by condition in juveniles but not in adults. Horizontal diameter could be constrained in adults by web site choice. Argiope species have high web site tenacity in the field, with adults being sedentary unless their web site is destroyed (Enders 1975, pers. obs.) and juveniles moving mostly in the few days following a moult (Enders 1975). Given that both
vertical diameter and horizontal diameter are strongly affected by body size, which increases during the season, that plant growth increases during the season, and that adults are more sedentary by nature than juveniles, they are much more likely to be at the limit of expanding horizontal diameter of their webs in the vegetation gaps available. Rather than move to a new site in order to adjust horizontal diameter, an individual might compensate by further altering other web parameters such as vertical diameter.

Differences in the effect of condition on web density observed for adults and juveniles were likely to related to constraints of body size and/or prey availability. Poor condition juvenile spiders decrease mesh size to create a denser web whereas poor condition adult spiders increase number of radials. A spiral rich web is more sticky; a radial-rich web has greater ability to breath the momentum of heavy and powerful prey. The upper range of adult cephalothorax widths was non-overlapping with juvenile cephalothorax width. Murakami (1983) showed that cephalothorax width was linearly related to distance between the first and third legs (L distance) in Argiope amoena (L. Koch). The upper limit of prey size coincided with the distance between these legs which were used for prey handling and wrapping. Olive (1980) describes the Argiope prey capture technique as "wrapper" in which the long back legs are used to maintain greater distance from and through silk onto dangerous prey like relatively large Orthoptera, Homoptera, Coleoptera, and stinging Hymenoptera. Juvenile spiders were likely excluded from utilizing these larger prey classes. Jumping prey for juvenile spiders consisted of leaf hoppers which are much smaller than large orthopterans, which were only available nearer the end of season. Juveniles may be better served with sticky mesh to hold onto smaller jumping prey tearing down through the web rather than a rich radial design to absorb momentum.

These age classes may modify web types through sampling or as a result of the evolution of a hard-wired response to shift web types with age (time). Given that large temporal variation in prey capture is a feature of spider life history (Gillespie and Caraco
1987) recent experience may not give a good indication of long term prey availability and thus hard-wired responses to condition may be the only viable alternative. There is some experimental evidence that might support this view. Olive (1982) conducted an experiment with *A. trifasciata* to determine if changes in attack time, capture success, or web design were caused by increased experience with prey types. He had two treatment groups, one group he fed with a maintenance diet of grasshoppers for two weeks, and then flies for two weeks, and the reverse for the second group. An equal biomass of flies and grasshoppers was provided. He compared webs at the beginning of the two week trial to webs at the fifth feeding period. Olive found that in both treatment groups, there were decreases in the vertical diameter in the first two weeks regardless of prey type. There were no significant changes in web diameter in the second two weeks. This experiment suggests that *A. trifasciata* may have a hard-wired response to condition.

Another difference in web types between juvenile and adult spiders is the change in height with condition which was observed for adult spiders. At the population level, *Argiope* spiders tend to move higher in the vegetation as the season progresses (Enders 1974, Olive 1980). This move is suggested to be a tactic to take advantage of Hymenoptera abundance as plants come into flower. Good condition spiders were observed to move higher into the vegetation in this study, however few Hymenoptera were observed in this study except for some alate flights of ants (Dave Carmean pers. comm.) which are not pollinators. This move higher into the vegetation is also suggestive of a hard-wired response to shift web parameters with age (time). Juvenile spiders are then not expected to shift height with condition. It is possible that shifts in web height with condition may occur for both age classes for an alternative reason but juveniles may not appear to be changing web heights with condition because the vegetation is much shorter earlier in the season and the range of sturdy vegetation heights may be smaller.
**Experimental manipulation of condition and its effect on web parameters**

Experimentally induced condition effects on vertical diameter and hub diameter are similar to the results of the data set which included adult observational data. There was a trend for condition to effect horizontal diameter. In the first run of the experiment, web sites were located in a yarrow stand which was less dense than some of the other available herbaceous and grass habitat, so perhaps these experimental spiders were more able to adjust horizontal diameter to condition than observational adults. There was a significant effect of condition on mesh size but it was in the opposite predicted direction, i.e. mesh became more dense (more spirals/cm) as condition increased. Olive's (1982) experiment showed that changes in mesh size appear to lag behind changes in web diameter. Mesh size was not significantly different in the first two week periods for either prey regime, but was significantly different for both second trials. If this same trend occurred during my three day experiment, then one might expect mesh diameter not to have changed rather than decreased. However, spirals are farther apart near the edge of a web than at the hub (Eberhard 1986). That is why I measured the whole bottom length of the web and counted the sticky spirals, so as to get an average mesh size. When the supplemented spiders reduced the diameter of the web, mesh size would appear to decrease even if the spider did not shift spiral distance over that diameter during the three day experiment.

One criticism of this experiment is that the condition effect observed in this experiment may be an artifact of the prey type offered. By offering only flies, I might provide information to spiders that they should make small open webs to take advantage of this new food source (Bernie Roitberg, pers. comm.) However, the fact that prey type offered did not effect the condition effect observed in Olive's (1982) experiment suggests that my experiment was not confounded by an informational aspect.
Prey capture: mean, variance, prey type and web parameters

The first principal component prin1 was interpreted as web size as horizontal diameter and vertical diameter have the highest loadings. The first principal component explains less than 40% of the variation observed in web parameters and the highest loadings are less than 0.51. The low explanatory power of prin1 exists because web parameters do not change in concert with another as discussed above, especially as adults and juveniles are combined in this analysis.

Given this consideration, no difference in estimates of mean energy return was observed between large webs whereas difference in estimates of variance around mean energy return was observed with large webs being more variable than small webs. This finding supports the basic premise of the model in Chapter 2 that webs types differ in variance around mean return. In the model, mean net return was considered. No measurements of costs were performed. One way to get at the idea of mean net return would be to measure growth rate of spiders in the field. Spiders would have to be weighed over the season and a daily growth rate obtained, while controlling for a handling effect. Other assumptions critical to model include the shape of the fitness function and presence of reproductive thresholds. I was unsuccessful at developing a protocol to determine reproductive thresholds or reproductive success for A. trifasciata in the field or in the lab, although I suspect that there were adults who failed to reach a minimum size for reproduction.

Another assumption of the model was that differences in variances among web types resulted from differences in capture probabilities of different prey types. However, no trends were found with numbers of prey caught from specific taxonomic groupings and web design. What I hoped to see from this analysis was an effect of visual orientation versus large body size and momentum on web design and to see specifically which insect groups could drive tradeoffs between web interception and web retention functions. The two problems with this analysis are the method of grouping prey types.
and date. The categories I used probably grouped insects which differed greatly in their visual acuity or their strength. For example, hymenopterans included alate flights of ants which are weak flyers and would not have the capacity to avoid webs like other pollinating insects. Diptera likely differed greatly in their visual abilities but were divided into subcategories only by size; heteropterans and orthopterans which are both included in the jumping prey category differ greatly in terms of size and agility (Bernie Roitberg, pers. comm.) Thus, the current categories of flying prey and jumping prey includes prey types that should not be considered in a web interception and web retention tradeoff from those broad categories. Identification of insects at lower taxonomic levels may have led better resolution of their abilities. Insects should have been categorized according to the web function critical to capture i.e. interception or retention.

Concentrated field observations would have allowed comparisons within a sampling date instead of statistically controlling for date. With the present groupings, date appeared more important than web type, because abundance of taxonomic groups changed over the season. Both adults and juvenile webs were included in this analysis and these age classes may differ in prey capture behaviour. Juveniles may be unable to retain large prey even if their webs intercept them, so pooling these groups may have obscured trends. Again, concentrated observations to allow comparisons within a sampling date would have avoided this confound of age class. Then comparisons across sampling dates might give a better understanding of the behavioural differences between adults and juveniles.

An alternative explanation for an inverse relationship between web size and condition in the field - predation risk

I observed wasp predation and autotomy of limbs in my study population and nearby A. trifasciata populations. Predation risk leading to asset protection (Clark 1994)
has thus been suggested an alternative explanation to risk sensitive foraging for the relationship between web size and condition in the field (Larry Dill pers.comm.). Under predation risk scenarios in which predators cull spiders according to spider condition or size, web selection is still risk sensitive foraging as spiders should consider mean and variance in deciding on optimal policy (see also McNamara et al. 1991, Bednekoff and Houston 1994). Predation risk may simply alter the shape of terminal fitness function to which the forager responds.

As discussed in Chapter 1, background levels of mortality risk would not effect web-building behaviour if all reproduction was concentrated in a single effort at the end of the season. If A. trifasciata were capable of laying multiple clutches, then a determination of mean net return and fitness function would be necessary to ascertain whether field patterns match predictions of the effect of predation risk.

Differential mortality risk (under the assumption of single reproductive effort) would also have effects on web type selection. If smaller or poor condition spiders were more at risk (Tanaka 1992; Fincke et al. 1990) then more risk prone behaviour should be observed. If larger or good condition spiders were in greater danger (Endo and Endo 1994), then more risk averse behaviour should be observed to narrowly maintain condition.

The preceding discussion assumes that predators cue directly into some measure of accumulated energy in the forager, not to activities of the forager. If predators are alerted by the foraging effort, the web, than good condition spiders would decrease web size to protect their asset, whereas risk of starvation or reproductive failure would predominate over predation risk for poor condition spiders and increased foraging effort or web size is predicted (Clark 1994). Under these condition where the foraging effort attracts predators, predation risk can effect web size without including an explanation of risk sensitive foraging.
Olfactory predators may cue into foraging effort directly by using scent from webs to locate spiders. In the presence of olfactory predators, good condition spiders should protect their asset and make smaller webs. Visual predators are more likely to cue into condition of araneid spiders like *A. trifasciata* since they are conspicuously large and colourful and thus the relationship of condition to predation risk must be determined.

*A. trifasciata* web building behaviour suggests that adults were less sensitive to predation threat than juveniles. Adults did not create barrier webs, whereas they were quite common in juveniles. Barrier webs, tangled webs of silk adjacent to the foraging web, are associated with increased levels of predation risk and observed to deter both insect and bird predation in *Nephila clavipes* (Higgins 1992b). Given that adults have a greater asset than juveniles, the lack of barrier webs suggests that predators are not using web size, or foraging effort, to locate spiders. Thus smaller webs for good condition spiders do not support asset protection in the absence of risk sensitive aspects. If the presence of barrier webs for juveniles is indicative of differential mortality for smaller size, then larger webs for poor condition individuals may represent risk sensitive foraging where fitness functions are modified by predation risk.
Chapter 4

General Summary

The model in Chapter 2 was most sensitive to the mean net return experienced by foragers. If mean net return was positive, the shape of the terminal fitness function had the greatest effect on dynamics. Thresholds and limits in the model act to modify fitness functions into reward functions which are accelerating at bottom condition states and decelerating at top condition states. This result is particularly interesting as it suggests that risk sensitive behaviour might be more common than expected. Many studies, which report linear functions of some state variable to a surrogate of fitness, either ignore individuals in the population which fail to reproduce or do not include them when reporting fitness functions. For example in the spider literature, linear fitness functions were reported for crab spiders, however, approximately a fifth of female spiders in these population did not reproduce (Beck and Connor 1992, Fritz and Morse 1985). Wise and Wagner (1992) also report a linear fitness function but collected only females with egg sacs. Studies which report non-linear functions also relate that smaller females did not reproduce (Turnbull 1962, Miyshita 1983).

The effects of modification of fitness function by threshold and limits are most apparent near the end of season, demonstrating the importance of time limitation on behaviour. The presence of alternative choices is most likely at the end of season as well as switches in risk sensitive behaviour.

Finally, results of the model are compared to work from an alternative perspective which posits that the relationship between web design and condition is a consequence of foraging -growth tradeoffs. The model appears to in accord with observations attributed to the foraging-growth tradeoff hypothesis. Both mechanisms could be occurring and complementary depending on the formulation of the foraging -
growth tradeoff. It is necessary to determine empirically the mean net return and variance experienced by spiders and the fitness functions to which they are responding in these data sets, to further support the hypothesis of risk sensitive foraging in spiders.

An analysis of *Argiope trifasciata* spider condition and webs in the field showed that variance in energy return was greater for larger webs made by poor condition spiders, compared to smaller webs made by good condition spiders (Chapter 3). Mean return did not differ between these groups. This finding supports the validity of the assumption of the model in Chapter 2 that web types differ in variance in energy return, and suggests risk sensitive foraging in this species. Web types appear not to influence type of prey capture, although this result is attributed to the method by which insects were grouped in analyses. Insects should have been categorized according to the web function critical to capture i.e. interception or retention. A comparison of web type to these categories is needed to support the assumption of the model that web types differ in their ability to capture different prey types.

Web designs of adult and juvenile *A. trifasciata* were compared. A similar significant relationship of condition to vertical diameter was found for adult and juvenile age classes, even though variance in condition is smaller among juveniles and they have different life history decisions than adults. Differences in relationships of other web parameters to condition between age classes seem best explained by constraints related to age class rather than lack of sensitivity of analysis, but these constraints do not preclude risk sensitive foraging.

Knowledge of spider reproductive histories and assessment of costs in the field would allow approximation of the shape of the fitness function, the presence or absence of a reproductive threshold and mean net return. Estimates of these parameters would enable comparison of field results to the model to test whether risk sensitive foraging in spiders leads to predicted relationships between spider condition and web design.
Literature Cited


