Summer 8-1997

Tests for superfluous killing in five species of web-building spiders

Jennifer Lyn Maupin
University of Tennessee - Knoxville

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Appendix D - UNIVERSITY HONORS PROGRAM
SENIOR PROJECT - APPROVAL

Name: Jennifer Maupin

College: Arts + Sciences
Department: Ecology + Evolutionary Biology

Faculty Mentor: Dr. Susan Riechert

PROJECT TITLE: Tests for superfluous killing in five species of web-building spiders

I have reviewed this completed senior honors thesis with this student and certify that it is a project commensurate with honors level undergraduate research in this field.

Signed: Susan E. Riechert, Faculty Mentor
Date: Oct. 14, 97

Comments (Optional): Great job!
Appendix C - UNIVERSITY HONORS PROGRAM
SENIOR PROJECT - PROSPECTUS

Name: Jennifer Maupin

College: Arts + Sciences
Department: Ecology and Evolutionary Biology

Faculty Mentor: Dr. Susan Riechert

PROJECT TITLE: Tests for superfluous killing in five web-building spiders

PROJECT DESCRIPTION (Attach not more than one additional page, if necessary):
I will observe members of 5 species of web-building spiders in the field and in the lab to see how many milligrams of prey they will capture if they are presented with an unlimited number of prey. I will then compare this weight with the weight of prey actually consumed by spiders tested in the lab. The purpose of this study is to determine if spiders will kill more than they are able to eat (superfluous killing) if prey densities are high. Superfluous killing could have implications for the use of spiders as a natural means of pest control.

Projected completion date: October 1997

Signed: [Signature]

I have discussed this research proposal with this student and agree to serve in an advisory role, as faculty mentor, and to certify the acceptability of the completed project.

Signed: [Signature], Faculty Mentor

Date: Spring 97

Return this completed form to The University Honors Program, F101 Melrose Hall, 974-7875, not later than the end of your 3rd year in residence.
ABSTRACT

Several studies on spiders report that when faced with high levels of prey encounter, individuals appear to kill more than they are able to consume. This behavior, variously referred to as wasteful killing, overkill, or superfluous killing, may have important implications for biological pest control and the development of predator-prey models of population growth. The existence of superfluous killing has been challenged on the grounds that the hypothesis has not been subjected to quantitative study and that it predicts a behavior that is maladaptive. This study tested for superfluous killing by five species of web-building spiders having divergent web types. In lab and field tests, 25 spiders of each species were presented with sequential prey items until they ceased to capture prey. A measure of the mass of prey captured was then compared with the average mass of prey consumed by spiders fed to satiation in the lab (optimal consumption). Lab tests were more useful than those conducted in the field because of the inability to obtain accurate weights of both the spiders tested and prey encountered in field trials. For each species investigated, mean mass captured was significantly greater than the mean optimal consumption level for that species. In four of the five species, some proportion of the individuals tested actively captured far more prey than they were able to consume. The results indicate that superfluous killing is likely to occur when flushes in prey numbers are encountered. Also tested was one possible adaptive explanation for superfluous killing: that spiders can more easily extract nutrients from many partially consumed prey items than from one fully consumed item. This explanation was found to be plausible in only one of the species tested.
# Table of Contents

## Section | Page
--- | ---
Introduction | 1
Density-Dependent Predation | 2
Superfluous Killing | 5
Possible Explanations for Superfluous Killing | 7
Partial Consumption of Prey | 9
Goals of the Present Study | 10

### Methods

- Study Organisms | 11
- Natural Observations of Prey Encounter | 11
- Supplemented Field Observations | 11
- Laboratory Supplements | 12
- Full-time Feeds on Single Prey | 13
- Half-time Feeds on Single Prey | 13

### Results

- Natural Observations | 14
- Superfluous Killing | 14
- Supplemented Field Observations | 16
- Laboratory Supplements | 16
- Single Prey Tests for Feed Rate Over Time | 21

### Discussion

- Natural Observations | 21
- Supplemented Field Observations | 22
- Laboratory Supplements | 23
- Single Prey Tests for Feed Rate Over Time | 24

### Literature Cited

<table>
<thead>
<tr>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
</tr>
</tbody>
</table>
List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. F statistics results for hypotheses tested.</td>
<td>17</td>
</tr>
</tbody>
</table>

List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Holling's (1959) functional response curves</td>
<td>4</td>
</tr>
<tr>
<td>2. Mean number of prey items encountered during natural observations.</td>
<td>15</td>
</tr>
<tr>
<td>3. Ratio of mean mass captured to mean mass consumed by each species in lab trials.</td>
<td>18</td>
</tr>
<tr>
<td>4. Percentage of observations in which prey mass captured exceeds that eaten by spiders fed to satiation.</td>
<td>19</td>
</tr>
<tr>
<td>5. Ratio of average feeding rate during partial consumption to that during full consumption of single prey.</td>
<td>20</td>
</tr>
</tbody>
</table>
INTRODUCTION

The importance of spiders as biological control agents has been long studied and pondered. A classic study conducted by Clarke and Grant (1968) revealed that spiders can play an important predatory role in natural systems. In this study, all spiders were removed from an enclosed area of a maple forest litter community. Clarke and Grant observed a considerable increase in the centipede and collembola densities in the removal plot compared with plots from which no spiders were removed. Because spiders are known to be predators of centipedes and collembola, the authors concluded that predation by spiders was an impediment to growth in centipede and collembola populations. The lack of replication of this experiment is unfortunate, as the results seem to clearly indicate spiders as important predators of centipedes and collembola.

Nyffeler and Benz (1987) reviewed studies conducted on spiders from all areas of the world and several different habitats in order to deduce the role of spiders in natural control of insect populations. They estimated that spiders can reach densities of up to 1000 individuals per square meter. They also cited Turnbull’s (1973) calculation that the mean density of spiders in a sampling of various environments was 130.8 individuals per square meter (in Nyffeler and Benz 1987). When coupled with the fact that spiders are for the most part generalist predators that feed primarily on insects, these overwhelming estimates indicate that spiders are a valuable force in insect control. Nyffeler and Benz (1987), however, concluded that “the significance of [spiders] as natural control agents is still largely unknown”.
Spiders have less of a predatory impact in agricultural systems because in these systems spider numbers and diversity tend to be low (Foelix 1996). While spiders may be important biological control agents of most insect populations, insect pests are more likely to escape the predatory impact of spiders. Insect pests are insects that inhabit agricultural areas and are known to damage crop plants. These insect pests are of great concern because a rapid exponential increase in insect numbers is more likely to occur in an agroecosystem than in stable natural communities (Riechert and Lockley 1984). It is such exponential increases that make the insect pest an economic threat to the agricultural systems it invades.

A number of possible explanations exist for a noted scarcity of spiders in crop ecosystems. These include the absence of year-round vegetation in agricultural lots and the use of pesticides in these areas (Riechert and Lockley 1984). However, Riechert and Lockley (1984) concluded that, taken as an assemblage of various species, a community of spiders in an agricultural system could adequately control insect pest populations, and that “the application of spiders to the pest control effort should be actively pursued in at least some agroecosystems.” Such control would limit the potential of insect pest populations to that seen in natural ecosystems, in which spider assemblages maintain insect numbers at levels low enough to prevent the threat of population explosions. As a basis for these conclusions, Riechert and Lockley point to aspects of the functional and numerical responses of spiders to fluctuating prey populations.

**Density-Dependent Predation**

The functional response and the numerical response represent the two basic components of density-dependent predation (Holling 1966). The
functional response is the behavioral response (change in consumption rate) exhibited by a predator in response to an increase in either prey density or encounter rate with prey. The numerical response is the change in predator densities, caused by aggregation or reproduction, that corresponds to changes in prey densities (Solomon 1949). Because reproductive output is often a function of levels of food intake and nutrition, the functional response is of primary importance and greatly affects the numerical response (Holling 1966).

The functional responses demonstrated by predators can be characterized by one of three response curves, as described by Holling (1959). The Type I functional response curve (Fig. 1a) is characterized by a linear increase in prey attack rates until a point of satiation is reached and the line levels off. This curve is demonstrated by a predator whose search pattern is random and whose search rate remains constant with prey density increases (Holling 1959). Filter feeders are an example of Type I predators. The Type II functional response curve (Fig. 1b) is one in which capture rates decrease with increasing prey encounter rates (Riechert and Harp 1987). The Type II response curve is the pattern described for invertebrate predators (i.e., spiders, wasps, etc.). The Type III response curve, most often demonstrated by vertebrate predators, is one in which an initial lag due to learning how to handle the prey type is followed by an exponential increase in capture rates (Fig. 1c) (Riechert and Lockley 1984). A Type III response curve leads to a maximum attack rate at a time when prey are experiencing exponential increases. Such an increase in attack rates following an increase in prey numbers leads to a stable predator-prey interaction and effective prey population control. As
Figure 1. Holling's (1959) functional response curves. (a) The type I functional response, which signifies a linear increase in attack rates until satiation is achieved. (b) The type II curve, in which rate of capture decreases with increasing prey densities. (c) The type III response, in which, after an initial lag due to learning, capture rates increase exponentially until handling constraints limit capture.
high prey encounter rates persist, the attack rate will be limited by the predator's ability to handle large numbers of prey.

Although spiders are invertebrate predators and are therefore expected to conform to the Type II functional response, several studies conducted on spiders indicate that the species studied do not fit well within this curve, especially at the onset of an increase in prey densities (Riechert and Lockley 1984). When spiders experience an increase in prey densities, the functional response initially resembles that of the Type III curve described. Spiders continue to kill prey at an exponential rate, which often results in a high plateau that exceeds the amount of prey the spider is able to consume. However, as increased prey densities persist, the functional response of spiders takes on the shape of a Type II curve, which levels off at a considerably lower plateau, one that is dictated by the constraints on the spider's ability to handle prey (Riechert and Lockley 1984).

Superfluous Killing

The behavior exhibited by spiders that results in the capture of more prey than can possibly be consumed has been referred to as "wasteful killing", "overkill", and superfluous killing (Johnson et al. 1975, Riechert and Lockley 1984, Conover 1966). The term superfluous killing, attributed to Conover (1966), has been used in the marine invertebrate literature for some thirty years and takes precedence over the other synonymous terms. In Spiders in Ecological Webs, Wise (1993) discusses the idea of superfluous killing as described by Riechert and Lockley (1984). Wise's criticism of the superfluous killing hypothesis lies largely in the use of the term "wasteful". In his own words: "Riechert and Lockley seem to equate failure to extract all the energy from a prey item with wasteful killing,
though this behavior is not necessarily wasteful, as the spiders are collecting usable calories from the captured prey” (1993). Riechert and Lockley refer to superfluous killing as the tendency for spiders faced with high prey encounter rates to kill more than they are able to eat before the prey desiccates. This definition of superfluous killing includes both partial consumption of multiple prey items and total abandonment of captured prey.

The idea of superfluous killing is difficult to explain within an evolutionary context. Because predators are expending energy to capture and kill prey from which they will be unable to gain energy in return, this behavior would seem to be maladaptive, and therefore selected against. In addition, spiders which kill in excess of their need are removing a potential source of future nourishment from their environment. For spiders, which are thought to live a food-limited existence (Wise 1993), it would seem to be to their advantage to preserve the numbers of available prey. The absence of experimentation in which superfluous killing by spiders has been quantitatively analyzed adds to the controversy over the behavior's existence. Several studies involving invertebrate predators have reported incidences of “wasteful killing” or “the overkill phenomenon” (Johnson et al. 1975, Samu and Biro 1993, Coyle and Ketner 1990), but none have actually measured wasteful killing by spiders.

Johnson et al. (1975) refer to wasteful killing in damselfly naiads as the failure to return to and feed upon previously captured and killed prey items. Their experiments involving damselfly predation on Daphnia magna revealed that the damselfly naiads exhibit a large degree of wasteful killing when presented with Daphnia densities of 50 to 500 Daphnia per liter of water. An additional increase in killing was observed at densities
greater than 500 *Daphnia* per liter, indicating that wastefulness increased after this point.

Samu and Biro (1993) studied the feeding behavior of the wolf spider *Pardosa hortensis* at varying prey densities in the laboratory. They observed wasteful killing, as defined by Johnson et al. (1975), and the partial consumption of prey at high densities. Samu and Biro (1993) considered a partially consumed prey item to be wastefully killed if less than 1/3 of the prey's original mass was consumed. The degree of superfluous killing in this study was positively related to prey density.

Coyle and Ketner (1990) conducted a study in which they investigated the predatory behavior of funnel web spiders in the genus *Ischnothele*. Although their experimental design did not involve a means of testing density-dependent changes in consumption rates, they did observe that "when provided with a superabundance of prey, *Ischnothele* exhibit an unlimited functional response (the overkill phenomenon)."

**Possible Explanations for Superfluous Killing**

A few possible explanations for the occurrence of superfluous killing exist. It could be an aggressive behavior under strict genetic control or a physiological response to hunger (Riechert 1974). If the latter is true, one would expect to detect differences in the level of wasteful killing at varying hunger levels. Holling's (1966) analysis of the response of invertebrate predators to varying prey densities defined hunger as "an internal motivational state" that "can be defined operationally in terms of its effect on behaviour". Hunger is also described as the emptiness of the gut. Holling (1966) defines three hunger-related attack thresholds for the mantid: the pursuit threshold (HTP) above which prey are actively
pursued, the capture threshold (HTC) above which prey are captured, and
the eat threshold (HTE) above which prey are consumed.

The relationships among these hunger thresholds vary among species
(Holling 1966, Johnson et al. 1975). Within this context, superfluous killing
would be represented as occurring at a hunger level that surpasses the
HTC but has not yet reached the HTE. Therefore, the individual predator
would be hungry enough to actively capture prey, but would not eat the
prey item once it has been killed. In damselfly naiads, Johnson et al.
(1975) discovered that failure to eat captured prey resulted from a
condition in which the "midgut is not yet full but the foregut is too full to
allow further consumption".

Because spiders digest their prey externally, they may experience a
lag between the time when a prey item is killed and the subsequent filling
of the gut due to feeding. If additional prey items are encountered before
the spider has had the opportunity to digest and consume its current prey,
an aggressive response due to hunger may cause the spider to continue to
attack prey. Spiders may attack prey when hunger levels exceed both the
HTC and the HTE, but as feeding persists and food level in the gut
increases, the hunger level may drop below the HTE. At this point, the
spider would cease to feed, leaving remaining prey items uneaten.
Superfluous killing as a physiological response to hunger would not likely
represent an adaptive behavior, but rather some form of phylogenetic
feeding constraint.

Holling (1966) also described the cat as a predator whose HTP and
HTC thresholds are zero; thus, they are independent of hunger level.
Riechert (1974) proposed that this may also be the case in spider species
such as *Agelenopsis aperta* that appear to capture prey even at very low
hunger levels. Thus, if hunger is not the motivational force in prey capture, superfluous killing may be due simply to a genetic aggressive response or a naturally high level of aggression toward encountered prey. For example, spiders living in areas where prey encounter rates are usually very low might out of necessity develop an aggressive response to prey that they would exhibit even during rare periods of high prey encounter.

Riechert (1974) also suggests that, given the feast and famine existence of spiders, superfluous killing may be an adaptation that enables them to ensure maximal consumption of prey during periods of high prey densities. Additionally, larger or more nutritional prey items may be encountered after the capture of several items of lesser value. If spiders are not guaranteed a consistent prey supply, "A behavior which allows for capture of a large number of prey will be favored, even if it results in overkill under certain conditions" (Riechert 1974).

Partial Consumption of Prey at High Densities

There is one possible explanation of superfluous killing that provides an adaptive incentive for the behavior. If spiders are able to partially consume multiple prey items more efficiently than they can fully consume a single prey item, it may be energetically beneficial to kill and partially consume multiple prey. Several studies have examined the effect of prey density on handling time and partial consumption of single prey (Johnson et al. 1975, Cloarec 1991, Samu and Biro 1993). Handling time is the time the predator spends manipulating and feeding upon a prey item. Partial consumption of prey is a substantial component of superfluous killing and is density-dependent in certain species of damselfly naiads (Johnson et al. 1975) and in the wolf spider species Pardosa hortensis (Samu and Biro
With regards to *Pardosa hortensis*, Samu (1993) suggests that optimal foraging theory predicts such a response because it is energetically efficient for this species to consume only the most valuable and easily obtained parts of individual prey items. Superfluous killing exhibited by other spider species may also be explained by increased efficiency of partial consumption if nutrients are more easily extracted from single prey items at the onset of feeding. Therefore, if other prey items are available, it would be profitable for a spider to discontinue feeding of a single prey item when nutritional returns from that item begin to diminish.

**Goals of the Present Study**

The purpose of the current study was to measure the extent of wasteful killing in several web building spider species. Also tested was a possible adaptive explanation for wasteful killing, which is that partial consumption of multiple prey is more efficient that total consumption of a single prey item. The following specific objectives were completed:

1. When presented with an abundance of prey, will spiders consistently kill more than they are able to consume?

2. Do consumption rates by spiders feeding on single prey items decrease over time?

3. What is the normal prey encounter rate for each species in its natural habitat?

4. How do the predatory habits with respect to density-dependent responses vary among the spider species tested?
METHODS

Study Organisms

Spider species were chosen for this study based on local abundance and web type. We chose the following five species to represent five common web types: Orb web (Argiope trifasciata), sheet-line web (Florinda coccinia), funnel web (Agelenopsis aperta), scaffold web (Acheareania trepidarium), and hackled-band web (Dyctina volucripes). The funnel web species was studied at the Southwestern Research Station in Portal, AZ in July and August, 1996. All other species were studied in Knox Co, TN from May to December, 1996.

Natural Observations of Prey Encounter Rates

We observed webs at random regardless of the sex and age of the occupant. Webs were observed only if the occupant spider was exposed and in a foraging position (at funnel mouth for funnel web species, visible on web for all others). We recorded all activities within a fifteen minute time interval, with particular reference to prey encounter, description of prey items, and spider response to prey. Upon testing, we flagged webs with an identification number to prevent repeated observation of an individual. We observed 25 spiders from each species in these fifteen minute watches.

Supplemented Field Observations

We conducted supplemented field experiments to determine how spiders reacted to high prey encounter rates in a natural setting. We collected data from randomly chosen webs, which were marked in the manner described above. Single prey items were introduced onto the web every three-four minutes until the spider ceased to capture prey. We
ended an observation when the spider ignored a moving prey item for a period of at least five minutes, or when three prey items had escaped from the web. These observations ranged in time from fifteen minutes to an hour, depending on the response of the individual spider. We tested 25 spiders from each species.

**Laboratory Supplements**

We captured immature or adult female spiders from each species at random and brought them into the lab. We kept spiders in the lab for a minimum of three days before testing and fed them crickets, moths, mealworms, termites, or fruit flies, two times a week while in the lab. We tested spiders when they had established a web, and within no fewer than two days of the last feeding.

We selected prey items to be used in tests for each species according to their sizes. Two-week-old European house crickets, *Gryllus domesticus*, served as prey for the funnel web species. Mealworms were fed to the orb web and scaffold web species. The sheet-line web and hackled-band web species were fed termites. Before each test, we weighed the spider and each prey item individually. Termites were weighed five at a time and the average of a series of these weights was used to estimate individual prey weight. We weighed mealworms and crickets individually.

At the time of testing, we removed the lid from the container housing the spider and allowed the spider a five minute acclimation period. We then introduced prey items, one at a time, every three-four minutes until the spider ceased to attack the prey. Time intervals between introductions were adjusted to allow the spider to subdue the current prey item before the next introduction was made. We recorded the entire sequence of events during the test interval, including times at which
events occurred and the specific prey item that was involved. We introduced a minimum of five prey items to each spider to allow for web capture in those species that rely upon the stickiness of their silk to capture prey. Spiders failing to attack any prey item of those offered were not included in the sample and additional samples were taken to achieve a sample size of 25. We ended a particular observation when an offered prey item was not attacked within five minutes of its encounter with the web, or when three prey items had escaped from the web.

Twenty-four hours after each test was completed, we recorded the position of the prey items in the web, removed all prey items, and weighed them. We also noted the condition of each prey item (i.e. living, killed but uneaten, partially consumed, and fully consumed). If a spider was still eating after twenty-four hours, we allowed the spider to continue feeding until satiation and then recorded the information described above.

**Full-time Feeds on Single Prey**

In order to measure the amount of energy obtained from an individual prey item as a function of feeding time, we first determined the average time each species spent feeding a single prey item. This test was conducted on spiders that had previously undergone supplemented lab testing. We introduced a previously-weighed prey item onto the spider’s web and recorded the time of first feeding. We allowed the spider to complete consumption of the prey item, recorded total handling time, and weighed the remains. We tested ten spiders from each species, and the average handling time for a single prey item for each species was calculated. We calculated feeding rate during full feeding bouts (mg consumed/min) for each species.

**Half-time Feeds on Single Prey**
Using the data obtained from the single prey handling time tests, we conducted experiments to measure prey consumption rates during the first half of a feeding bout. These tests were conducted on spiders that were housed in the lab and involved introduction of one previously weighed prey item onto the spider's web. Prey items corresponded to those used in the supplemented lab experiment for each species. The time of initial attack was recorded. Prey items were removed from the spiders at the time that was calculated as half of the average total handling time for that species. At this time weights of the partially consumed prey items were recorded. Twenty-five spiders from each species were tested.

RESULTS

Natural Observations

Spiders observed did not encounter large amounts of prey naturally. For each of the five species observed, prey encounter rates averaged at or below one prey item per fifteen minute observation period (Fig. 2). Prey encountered were typically around 1 cm in length.

Superfluous Killing

Superfluous killing in the supplemented field and lab tests was defined as the difference between the mass captured (and subsequently killed) and the average mass consumed by spiders fed to satiation (optimal consumption) for each species. Because optimal consumption level was determined during lab tests, the results of the field supplements are not as useful as those of the lab tests. We were unable to obtain accurate weights of spiders tested and of prey encounters in field trials.
Fig. 2. Mean number of prey items encountered by each spider species during natural observations.
Supplemented Field Observations

Of the five species tested, only the orb web and sheet-line web species demonstrated significant levels of wasteful killing in the field trials (F statistic p-values = .001 for each species, Table 1). For each species tested, the mean total mass of captured prey exceeded that species' optimal consumption level (as determined by lab tests of spiders fed to satiation). Mean total capture was significantly higher than mean active capture (capture by direct spider contact) in all species except the funnel web species. Because funnel webs did not serve as traps for prey, total capture was equivalent to active capture for the funnel web species.

Laboratory Supplements

All species except the orb web species exhibited significant levels of superfluous killing in the lab trials (Table 1). However, mean total mass captured in the orb web species was considerably higher than mean optimal mass consumed (F statistic p-value = .06). The ratios of mean total mass captured to mean mass consumed under optimal conditions are shown for each species in Figure 3. For all species except the hackled-band weaver, some proportion of the tested spiders actively captured more prey than they were able to consume. Figure 4 shows the number of observations in which the total captured mass exceeded the optimal consumption level for each species. Figure 4 also indicates the number of trials in which actively captured prey mass exceeded the optimal consumption level. The difference between mean mass actively captured and mean optimal mass consumed was significant in the funnel web and scaffold web species (Table 1).
Table 1. F statistics results (P values) for various hypotheses tested. Minus signs before P values indicate relationships that are opposite to those hypothesized. All significant relationships are underlined.

<table>
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<th>Lab Trials</th>
<th></th>
</tr>
</thead>
<tbody>
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<td></td>
<td>Active capture &gt; optimal feed</td>
<td>Total capture &gt; optimal feed</td>
<td>Active capture &gt; optimal feed</td>
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<td>.001</td>
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<td>.079</td>
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<tr>
<td>Hackled-band</td>
<td>-.00001</td>
<td>.1897</td>
<td>-.00001</td>
</tr>
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Fig. 3. Ratio of mean mass captured to mean mass consumed by each species in lab trials. For each species, mean mass consumed is set to 1 below.
Fig. 4. Percentage of observations in which prey mass captured exceeds that eaten (> st err of mean mg consumed) by spiders fed to satiation. (Results of trials completed in laboratory.)
Fig. 5. Ratio of average feeding rate (mg/min) of spiders permitted only partial consumption of single prey to that of spiders completing consumption of a single prey item (set to 1 below).
Single Prey Tests for Feed Rate Over Time

Feeding rates in the funnel web species correlate highly with body size; therefore, all rates indicated for this species have been adjusted. The ratio of the consumption rate during half-time trials to that during full feeding bouts is displayed for each species in Figure 5. Shown in Table 1 are the F statistic p-values indicating the relationship between partial consumption (half-time) feed rate and full consumption feed rate. Only the scaffold web species fed at a significantly higher average feeding rate during partial consumption trials. The funnel web and hackled-band web species generally fed at higher rates when only partially consuming prey, but the orb web and sheet-line web species showed an increase in feeding rate as feeding time increased.

DISCUSSION

Natural Observations

In the natural observations, prey encounter rates observed were not high enough to merit superfluous killing. However, the observations were made in a limited area and within the course of seven months, and were therefore inadequate to detect temporal and spatial variation in prey encounter rates. One would expect sudden increases in prey numbers to be a rare event, particularly if the presence of spiders serves as a stabilizing force that helps to keep insect populations in balance (Riechert and Lockley 1984). However, under special circumstances such as species emergence events and introductions of non-native insect species, insect numbers may greatly exceed normal levels. In these situations, it is likely that spider prey encounter rates will increase also, and superfluous killing
will occur. The opportunity for superfluous killing within the framework of natural occurrences is an idea that should be further explored.

Supplemented Field Observations

Because accurate prey and spider weights were not available for the field supplement trials, correct measurements of the level of superfluous killing exhibited by the spiders tested in their natural webs were difficult to obtain. In the case of the funnel web species, lab tests revealed that captured prey mass correlated positively with spider weight. Assuming this correlation was present in the field also, mass captured in field trials would have to be corrected for weight in order to be effectively compared with the optimal consumption levels measured during lab tests.

Additionally, lab tests were often conducted after many field tests had been completed. Because spiders grow continually throughout their lives, spiders tested in the lab may have been larger on average than those tested in the field. Spiders housed in the lab were fed regularly, and may have been able to grow larger as a result of a consistent prey supply. Because the optimal consumption levels were calculated during the lab trials, this weight difference could account for the lower levels of wasteful killing calculated for the field trials (Table 1). Therefore, it is possible that the optimal consumption mass for those spiders tested in the field would actually be lower than that in the lab.

Despite these inevitable drawbacks in the field trials, conclusions can be drawn from the field data. Spiders tested in the field exhibited a high level of prey capture comparable to that seen in the lab. The orb web species and the sheet-line web species showed significant levels of superfluous killing in the field trials, despite the possible weight bias in optimal consumption levels.
Perhaps the most striking pattern shown by the field data is the difference in prey capture strategies among species. In the sheet-line, scaffold, and hackled-band web species, F statistic p-values for wasteful killing by active capture (Table 1) indicate that without the tangle function of their webs, these spiders would not capture even enough food to completely satiate themselves. The funnel web species, on the other hand, uses its web only for detection of prey (Riechert and Luczac 1982), and must actively capture prey items before they escape from the web surface.

Laboratory Supplements

Results from the lab trials indicate that web-building spiders are likely to exhibit superfluous killing if prey are abundant and are encountered at a high frequency. Although the methods of capture varied among species, the total amount killed at the end of the observations consistently exceeded the amount eaten when the spiders fed until satiation. Because mass of prey lost as a result of desiccation was not corrected for, the estimate of superfluous killing levels shown in Table 1 is conservative. The total weight loss measured during the twenty-four hour period was attributed to consumption by the spider when, in fact, a large amount of this loss may have been due to drying as a result of death. Recall that, in the analyses, this weight loss was defined as the optimal consumption level. The optimal consumption levels indicated for each species, then, are probably skewed higher than the actual mass each species was able to consume. Therefore, if the results indicate that superfluous killing has occurred even when using the high estimate of optimal consumption, one would expect an even greater level of measurable superfluous killing when weight loss due to death is accounted for.
Single Prey Tests for Feed Rate Over Time

The difference between feeding rates in full-time and half-time feeding trials was highly variable among species. While the scaffold, funnel, and hackled-band web species generally fed at higher rates during the partial feeding trials, the orb and sheet-line web species fed at lower rates during the first half of a feeding bout. These differences may be due to varying digestive strategies and prey types. Because spiders digest their prey externally (Foelix 1996), they are unable to consume prey immediately after its capture. Spiders must first secrete digestive enzymes into the body of the prey. These enzymes then turn the digestible parts of the prey into a nutrient fluid, which is taken back up into the spider's body. The species which demonstrated lower feeding rates at the onset of feeding may have actually been waiting for the enzymes to digest the prey item before consumption took place. The effectiveness of digestive enzymes may vary among species and prey items consumed.

Regardless of the physiological explanation for lower feed rate during partial feeding, the implications remain constant: partial consumption of many prey items is not a beneficial feeding strategy for most of the spiders examined in this study. Although some species (i.e., scaffold web species herein) may find it more efficient to partially consume multiple prey items, partial consumption is not a viable explanation for the superfluous killing exhibited by the majority of spiders tested in this study.

These results lead us to consider some of the alternative explanations for superfluous killing. Future studies can be useful in determining whether superfluous killing is caused by a physiological response to
hunger, is an innate genetic aggressive behavior, or is an artifact of a behavioral strategy that was selected for at some point. The behavior may in fact be caused by a combination of these or by some unknown factor.


