

## CONTESTS OVER PREY BY GROUP-LIVING PHOLCIDS (*Holocnemus pluchei*)

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**ABSTRACT.** Game theory predicts that resource value and fighting ability should affect the cost of fighting. I tested these predictions in the field with the pholcid spider *Holocnemus pluchei*, a facultatively group-living spider. Three species of prey were tested: fruit flies, house flies, and damselflies. Larger prey species required more time to subdue, but still represented resources of greater value because of their high caloric content. Fights were increasingly more common with increasing size of prey species. However, prey species did not significantly affect the intensity of fights, in contrast to predictions from game theory. Fights were most intense between individuals of the same size, as predicted by game theory. *Holocnemus* spiders do not appear to benefit from interactions with conspecifics in group webs.

Fewer than 0.1% of spider species regularly share webs (Krafft 1982). Of these, some are highly social and cooperate to catch prey or construct webs. Benefits of sociality for these species are clear: individuals in groups may have increased success in prey capture, a reduction in the variance of prey capture success, a reduction in silk output for web construction, and an enhanced "early warning system" for predator detection (reviewed in Uetz 1992). In less social species that share webs but do not cooperate, benefits of group living are often not so obvious. *Holocnemus pluchei* (Scopoli) (Araneae: Pholcidae) is facultatively group living. These spiders may live alone or share a sheet web with as many as 15 conspecifics of all sizes, and group membership appears to be temporally fluid (Jakob 1991). In a previous study of costs and benefits of group living for *Holocnemus* spiderlings, I found that spiderlings in group webs captured less food than solitary spiderlings: spiderlings lost prey to larger spiders (Jakob 1991). However, spiderlings in groups produced less silk, which is energetically costly, than did solitary spiderlings that built their own webs (Jakob 1991). Here I expand this study of the costs and benefits of group living by examining interactions over food among spiders that share a web. If aggressive interactions among spiders are frequent, energetically expensive or dangerous, the costs of group living may outweigh the benefits. Conversely, if the cost of prey capture is decreased

for individuals because more than one spider wraps the prey, spiders may benefit from the presence of conspecifics in groups.

Game theory predicts that several factors should influence the cost of fights. First, fights over valuable resources often reach higher levels of intensity or last longer than fights over less valuable resources (e. g., Wells 1988; Verrell 1986). Second, the cost of fights should be influenced by resource-holding potential or fighting ability (Parker 1974). Fights are more likely to escalate to higher levels of intensity if individuals are closely matched in fighting ability (Parker 1974).

Here I examine the effects of resource value and fighting ability on the intensity of *Holocnemus* fights. In this field experiment, the contested resource was food. *Holocnemus* spiders prey upon a variety of species that are likely to differ in caloric content and handling time (time needed to subdue the prey). If, as game theory predicts, resource value affects fight intensity, spiders may face different costs of fighting depending on the relative abundance of different prey species. Fighting ability in many spider species increases with body size (e. g., Riechert 1978; Wells 1988; Uetz & Hodge 1990; Jackson & Cooper 1991), as is also true for *Holocnemus* (Jakob 1991). If, as game theory predicts, interactions between spiders of similar fighting ability tend to escalate, spiders sharing webs with same-sized conspecifics will incur higher costs of fighting

Table 1.—Mean, standard deviation, and range of lengths of first and second tibiae and cephalothorax width (CW) of field-collected spiders. (Measurements in mm;  $n = 14$  small, 12 medium, and 33 large spiders.)

Size class	Tibia 1	Tibia 2	CW
Small			
Mean (SD)	4.89 (0.88)	3.12 (0.55)	1.00 (0.15)
Range	3.75–5.83	2.25–3.75	0.8–1.2
Medium			
Mean (SD)	7.79 (0.88)	5.21 (1.05)	1.47 (0.16)
Range	6.08–9.17	3.58–7.75	1.16–1.18
Large			
Mean (SD)	12.96 (1.49)	8.54 (0.98)	2.31 (0.25)
Range	9.17–16.17	5.67–10.83	1.72–2.80

than will spiders who share webs with conspecifics of different sizes. Here I document differences in handling time across three prey species and examine the relationship between spider size, prey species, and the frequency and intensity of interactions.

#### METHODS

I studied *Holocnemus plucheii* on the main campus and near the Zoology Field House of the University of California at Davis (UCD). *Holocnemus* webs were plentiful around buildings, such as under eaves, in the openings of cinder blocks, and in bushes (primarily *Juniperus* spp.). All the webs used were outdoors and had not been manipulated prior to the experiment. Data were collected between July and September 1988, between 0700 h and 1430 h. Temperature ranged from 21–24 °C. A full description of the methods is in Jakob (1991); methods are summarized here.

I selected webs with one spider present (“solitary webs”) and with more than one spider (“group webs”). Each web was used only once. I classified spiders as small, medium, or large, which roughly corresponds to second or third instar juvenile, fourth instar juvenile, and adult. In a sample of measured spiders, average tibia lengths and cephalothorax widths differed by a factor of approximately 1.5 between size classes (Table 1).

I used three prey species: fruit flies (*Drosophila melanogaster*; length approximately 2.5 mm), houseflies (*Musca domestica*; length approximately 6 mm) and damselflies (*Ischnura* sp.; length approximately 28 mm). These are among the natural prey of *Holocnemus* in California. Fruit flies were reared by the UCD Genetics De-

partment, houseflies were purchased as pupae from Carolina Biological Supply, and damselflies were captured at a local pond. The insects were sealed in inflated resealable food storage (“Ziploc”) plastic bags for transport to the study area. They were chilled briefly in an ice chest in order to facilitate handling, then a single prey item was haphazardly selected and tossed into a web. Prey recovered and began moving within a few seconds. If prey fell or flew out of the web before any spider detected it, the trial was discarded and a new prey item was introduced.

When prey were introduced, I began continuous recording of observations into a microcassette recorder. The tape was left running so that a time record could be taken during playback. I initially observed approximately 10 group webs until the prey were eaten and discarded. In no case did spiders interact after prey were subdued and feeding had begun. For all subsequent observations, recording was stopped a few minutes after feeding was initiated and all spiders were quiescent. Even though spiders were not marked, in nearly all cases I could keep track of particular individuals from prey introduction until all spiders were quiescent. In cases where I was not sure of the identity of a particular individual, no data from that web were included in the analyses.

**General statistical procedures.**—Parametric tests were used when the data met the appropriate assumptions or could be transformed to meet the assumptions. Nonparametric tests were used when transformations were ineffective. Where appropriate, a sequential Bonferroni correction was applied to adjust significance levels. Details of particular statistical tests are given below.

## RESULTS

A total of 52 solitary webs and 93 group webs was included in the analyses.

**Description of prey handling.**—The following behaviors occurred in the order given in response to prey introduction. *Detection*: a spider moved in response to the prey, either by orienting (moving its body to face the prey), approaching, or bouncing in place. When prey were not present in the web, spiders were generally motionless. *Contact*: a spider touched the prey with one or more legs. *Wrap*: a spider wrapped silk around the prey by pulling silk from the spinnerets with its posterior legs in a smooth and stereotyped motion. After wrapping, the prey was generally completely encased in silk. *Attaching silk lines*: spiders sometimes attached their prey to the web or, more frequently, to nearby branches with silk lines. *Bite*: a spider bit the prey, then released it, generally within 5 s. Typically spiders bit prey several times in the course of subduing it. *Feeding*: a spider held the prey in its chelicerae and was quiescent. “Feeding” was distinguished from “bite” by its longer duration. Once a spider began feeding it rarely moved until the prey was consumed and dropped.

**Prey species and handling time: relative value of food.**—I performed a two-way analysis of variance to determine the effects of prey species and number of spiders responding to prey on handling time. Because of sample size, for this analysis only two categories were used to describe the number of spiders responding to prey: one spider and more than one spider. Six aspects of handling time were analyzed: the time between prey introduction and detection, detection and first contact of prey, first contact and initiation of wrapping, initiation of wrapping and first bite, first bite and feeding, and wrapping duration (the total amount of time a particular prey item was wrapped). I performed a  $\log(x + 1)$  transformation of the data and tested for homogeneity of variances with an *F*-max test (Sokal & Rohlf 1981). All variances were homogeneous except for the time between detection and first contact; variances were heterogeneous at the 0.05 level but not at the 0.01 level of significance, and these results should be treated cautiously. All other transformed data had homogeneous variances. Six separate ANOVAs were performed and *P* values were adjusted with a Bonferroni correction for multiple tests (Rice 1989).

Prey type significantly influenced handling time

in each analysis except for time between first contact and the initiation of wrapping ( $P < 0.01$  in each case; Table 2). In every case where differences were significant, mean handling time was smallest for fruit flies, larger for house flies and largest for damselflies. The effect of the number of spiders responding (one spider vs. more than one spider) and interaction effects were not significant in any case.

Wrapping duration was examined in more detail in order to test whether individuals in a group in which more than one spider wrapped a prey spent less time wrapping than did solitary spiders. In 23 of 25 (92%) cases where more than one spider wrapped a single prey item, the spider that ultimately fed on the prey (the “winner”) did more of the wrapping than did other spiders. For fruit flies and houseflies, there was no significant difference between the time “winners” spent wrapping and the time spent by spiders that were the only individuals to wrap the prey. For damselflies, “winners” spent significantly less time wrapping than did spiders who wrapped alone (mean in  $s \pm SE$ : alone  $784.8 \pm 465.7$ , “winners”  $344.2 \pm 231.8$ ,  $n = 5, 12$ ; Mann-Whitney *U*,  $P < 0.02$ ).

**Description of interaction levels.**—I use the term interaction to describe behaviors given in response to or directed towards conspecifics. Interactions were classified into three levels of intensity. Interactions at lower levels are assumed to have lower levels of energy expenditure (movements are generally slower and shorter in duration) and risk of injury than interactions at higher levels. Interactions were pairwise: though many spiders in a web often interacted over a particular prey, interactions occurred between only two spiders at once.

*Level I*: This level includes gentle movements that did not always attract the attention of a conspecific. Included here are orientation, where a spider turned its body to face a conspecific; push-ups, or slow flexing of the legs that resulted in the spider’s body moving towards, then away from the web; and abdomen twitching, where a spider’s abdomen moved quickly up and down dorsoventrally. These three behaviors often occurred together and were rarely seen in solitary spiders.

*Level II*: A spider moved enough so that it was likely to be detected by conspecifics. This level includes bouncing, where a spider sharply contracted its legs so its body moved towards the

Table 2.—Mean (in seconds), standard error, and sample size for duration of handling time components for three species of prey. *P* values are derived from two-way ANOVA's of log-transformed data, with Bonferroni corrections applied. No interaction terms were significant.

		Fruit fly	House fly	Damselfly	Effect of prey type	Effect of number of responders
Introduction/detection	$\bar{x}$	3.4	5.9	48.8	<i>P</i> < 0.01	NS
	SE	(1.11)	(1.65)	(13.29)		
	<i>n</i>	67	48	19		
Detection/first contact	$\bar{x}$	3.3	23.8	27.4	<i>P</i> < 0.01	NS
	SE	(0.90)	(5.95)	(9.03)		
	<i>n</i>	67	47	19		
First contact/first wrapping	$\bar{x}$	16.5	7.9	32.6	NS	NS
	SE	(7.35)	(2.32)	(10.78)		
	<i>n</i>	67	47	18		
First wrapping/first bite	$\bar{x}$	59.4	141.0	488.8	<i>P</i> < 0.01	NS
	SE	(6.24)	(38.73)	(108.57)		
	<i>n</i>	64	40	18		
First bite/feeding	$\bar{x}$	8.5	57.6	558.9	<i>P</i> < 0.01	NS
	SE	(2.45)	(11.7)	(176.8)		
	<i>n</i>	64	37	17		
Wrapping duration	$\bar{x}$	39.0	106.2	516.3	<i>P</i> < 0.01	NS
	SE	(2.91)	(30.8)	(81.4)		
	<i>n</i>	67	47	18		

web; approach, where a spider moved towards a conspecific; and web plucking, where the spider spread its anterior pair of legs and pulled sharply downward on the web, then released it so it snapped back.

**Level III:** Two spiders interacted aggressively and physical contact generally occurred. Included here is chasing, probing at a conspecific with extended front legs, and grappling with legs and sometimes biting or grappling with chelicerae. Grappling spiders appeared to roll about on the underside of the sheet web. Interactions were brief, lasting from a few seconds to about 15 s. In this experiment, interactions never resulted in biting or death although that has been seen on other occasions (pers. obs.).

**Group size and frequency of interactions.**—As more spiders responded to the prey I introduced into the web, the mean number of interactions per spider increased significantly (simple regression:  $y = 0.352 + 0.149x$ ,  $r^2 = 0.384$ ;  $P < 0.0001$ ).

**Prey type and frequency of interactions.**—More spiders were attracted to larger prey species (mean  $\pm$  SE: fruit flies  $2.59 \pm 0.228$ , house flies  $3.74 \pm 0.412$ , damselflies  $4.25 \pm 0.617$ ;  $n = 17, 27, 12$ ; Kruskal-Wallis test,  $df = 2$ ,  $H_{\text{corr}} = 7.829$ ,  $P < 0.02$ ) but this finding must be regarded cautiously. Strands of silk connecting webs are often

hard to see, so that what appeared to be a small group was often connected to a larger group. Thus, I could not consistently preselect group size and there is a possibility of a bias in the webs I tested with different prey species. However, once spiders were attracted to prey, the number of interactions per spider increased with increasing prey size (mean  $\pm$  SE: fruit flies  $0.59 \pm 0.036$ , house flies  $0.93 \pm 0.068$ , damselflies  $1.15 \pm 0.213$ ;  $n = 17, 27, 12$ ; Kruskal-Wallis test,  $df = 2$ ,  $H_{\text{corr}} = 12.372$ ,  $P < 0.01$ ).

**Prey type and level of interactions.**—I recorded the highest level of interaction that each individual directed at another and found no significant difference across prey species ( $\chi^2 = 5.98$ ,  $df = 4$ ,  $n = 175$ ,  $P = 0.2$ ). The highest interaction level was reached more frequently in interactions over houseflies (55% of trials) than in interactions over either fruit flies (35%) or damselflies (40%); however, when I pooled fruit flies and damselflies, interaction levels did not differ significantly from house flies ( $\chi^2 = 5.32$ ,  $df = 2$ ,  $P = 0.07$ ).

**Spider size and frequency of interactions.**—I compared the frequency of interactions between different size classes to determine if some size classes were more or less likely to interact than others. Spiders can only interact if they share a

Table 3.—Observed frequency of interactions between size classes of spiders compared to expected values. The first animal listed can be either the aggressor or the receiver. (In both tests,  $df = 5$ .)

Size classes	Levels I, II and III		Levels II and II	
	Observed	Expected	Observed	Expected
Small × small	5	5.7	4	4.8
Small × medium	2	7.5	2	6.3
Small × large	20	13.9	17	11.7
Medium × medium	7	17.5	5	41.8
Medium × large	48	49.6	39	41.8
Large × large	45	32.8	40	27.7
	$\chi^2 = 17.619$ $P < 0.005$		$\chi^2 = 17.574$ $P < 0.005$	

web, so I generated expected values by following Altmann & Altmann (1977). For example, in a web with three medium and two large spiders, there are three potential interactions between medium spiders, one between large spiders, and six between large and medium spiders. I summed the potential interactions for all webs to generate expected values for the entire sample population. These expected values represent the frequency of interaction for each size class if all size classes were equally likely to interact. To calculate observed values, I noted for every possible pair of spiders whether or not they interacted, and if they did, the maximum intensity that the interaction reached. In cases where two spiders had more than one fight with each other, I recorded the maximum intensity of all fights. These values were summed for every combination of size classes and compared with expected values.

Significant differences in interaction frequency across size classes were found for total interactions of all intensity levels, as well as when I considered only interactions that reached the higher levels of II or III ( $\chi^2$  goodness-of-fit test,  $P < 0.005$ ; Table 3). In both cases, large spiders interacted with each other more frequently than expected by chance, and medium spiders interacted with each other less than expected by chance. When large/large and medium/medium interactions were omitted from the analysis, the frequency of interactions did not differ from expected.

Spiders were more likely to direct aggressive behaviors toward larger individuals than toward

Table 4.—Highest level of aggression that spiders directed at spiders of equal, larger, or smaller size. Level III is the highest level. Expected values are in parentheses. ( $\chi^2 = 33.805$ ,  $df = 4$ ,  $P < 0.0001$ ).

Aggression directed toward spider of	Level		
	Level I	Level II	Level III
Same size	9 (11.3)	21 (36.0)	60 (42.7)
Larger size	10 (7.4)	38 (23.6)	11 (27.9)
Smaller size	3 (3.3)	11 (10.4)	12 (12.3)

smaller individuals. Of 85 interactions between individuals of different sizes, 59 (69%) were directed at the larger individual by the smaller ( $\chi^2$  goodness-of-fit test with expected values of 1:1,  $\chi^2 = 12.82$ ,  $df = 1$ ,  $P < 0.001$ ). Most behaviors were directed at the spider that possessed the prey; that is, the spider that was handling the prey or holding it in its chelicerae. Of 175 interactions observed, 139 (79%) were directed at the spider that possessed the prey. Only 20 (11%) of the behaviors were performed by the spider that possessed the prey; in most of these, the spider with the prey was responding to an aggressive move by the other individual. Fourteen aggressive acts (8%) were between pairs of spiders that were not in contact with the prey. Three acts (2%) were between spiders that had simultaneously been wrapping the same prey.

**Spider size and intensity of interactions.**—The level of intensity of interaction also depended on the size class of the participants (contingency table test,  $\chi^2 = 33.81$ ,  $df = 4$ ,  $P < 0.0001$ , Table 4). Expected values were too small to allow comparison of each possible pair of size classes separately, so I pooled data to compare the level of interactions between same-sized individuals, behaviors directed at larger spiders, and behaviors directed at smaller spiders. Interactions between same-sized spiders were most likely to reach the highest level. Behaviors of smaller spiders directed at larger spiders were most likely to reach level II, while behavior of larger toward smaller individuals did not differ from expected.

## DISCUSSION

The three prey species tested represent resources of different value for *Holocnemus*. Larger prey were more costly to subdue in terms of time invested and, because spiders spent more time

wrapping large prey, in terms of silk used in wrapping. However, spiders can leave a prey item that has been partially wrapped in order to capture new prey that enter the web (pers. obs.), so increased handling time is unlikely to significantly decrease total prey intake. Larger prey also offered a substantial increase in caloric return: *Drosophila melanogaster* represent about 1.2 calories each (Jakob 1991), houseflies about 12 calories (estimated from dry weight, G. Uetz, pers. comm.), and damselflies approximately 50 calories (caloric estimates for "mixed insects" from Cummins & Wuycheck 1971). Level of prey intake translates into increased growth and decreased development time for *Holocnemus* (Jakob & Dingle 1990). Larger prey in this study thus appear to be more valuable than smaller prey.

According to predictions from game theory, the more valuable the resource, the greater is the probability that the animal will take risks to defend it (Parker 1984). The number of fights per spider did increase with size of the prey species, but there was no relationship between prey species and the level of intensity that fights reached. Two explanations are likely. First, spiders may not be able to assess relative value of these prey species. *Holocnemus* responds primarily to vibrational rather than visual stimuli (pers. obs.). Of the three prey species tested, houseflies generally struggled most and appeared to produce the strongest vibrations. High frequency vibrations are most likely to release prey capture behavior in spiders (Masters et al. 1986). Although fight frequency did increase with prey size, larger prey also attracted more spiders and that in itself might have led to more fights. The fact that the level of intensity of interactions did not vary with resource value also supports the notion that spiders could not assess relative value. Alternatively, all prey may be of high value to these spiders. Prey availability in my study area was low (Jakob 1991) and 47% of interactions reached the highest level (Table 4). It would be informative to increase prey availability and determine if fight intensity decreases for less valuable prey. Similar results have been found in other species: for example, Rypstra (1986) documented a decline in aggressive behavior as prey availability increased for an aggregating species. An orb weaver in a tropical environment with high prey abundance was likely to settle contests with lower levels of aggression than did a closely-related desert spe-

cies with low prey abundance (M. Hodge pers. comm.).

Game theory also predicts a relationship between fighting ability and levels of interactions. Large spiders fought with each other more frequently than expected by chance, perhaps because they most often had the prey and 79% of interactions involved spiders that held the prey. As predicted by game theory (Parker 1974), spiders of the same size class reached the highest level of interaction significantly more often than did pairs of spiders of different sizes. Smaller spiders were surprisingly likely to be aggressive towards larger spiders: 32% of all interactions at Level II and III were directed at a larger spider by a smaller (Table 4), but in the course of this and other studies I have rarely seen (< 6 times) smaller spiders successfully steal prey from larger spiders. It is possible that spiders are testing themselves to see how they measure up to conspecifics, most likely through vibrational cues. Many fights are preceded by a head to head display, where spiders stretch their first legs out horizontally while web-plucking as if to measure one another.

How do interactions with conspecifics shift the balance of the cost and benefits of group living for *Holocnemus*? Larger spiders win the most prey, so sharing a web with a larger individual is clearly disadvantageous because of the loss of food (Jakob 1991). In addition, interactions themselves may have some energetic cost. However, Riechert (1988) argues that energetic losses due to display behaviors are often negligible and that correlated costs of fighting are evolutionarily more important in determining fight intensity. In *Holocnemus*, a likely correlated cost to high intensity fights is risk of injury: although I saw no injuries in fights during this study, I have on at least seven occasions seen high-level interactions result in death. Spiders should thus benefit if they reduce the number of interactions with conspecifics by joining smaller groups or avoid joining groups with spiders of the same size. Given the fluid nature of *Holocnemus* groups, the potential for assessment and choice of groups exists, but whether spiders can and do assess groups in this manner is as yet unknown. Finally, spiders can potentially benefit from interactions with conspecifics if wrapping time is reduced when more than one spider wraps a prey. Group-living winners spent less time wrapping damselflies than did solitary spiders; other group mem-

bers also wrapped the prey before being driven off. However, this effect was not seen for the other prey species tested (possibly because the shape of the damselfly decreased the probability that spiders would detect one another while they wrapped opposite ends) and is probably rarely an important benefit. In sum, unlike more highly social spiders that cooperate in prey capture, *Holocnemus* individuals are unlikely to benefit directly from interactions with conspecifics; indirect benefits may exist in the form of a reduction in the cost of web construction, but these have been documented only for spiderlings (Jakob 1991).

#### ACKNOWLEDGMENTS

During the course of this work, I was supported by a Josephine de Karman Fellowship and a UCD Reserve System Mini-grant. M. McPeck, A. Porter, and M. Gromko provided statistical advice. M. McPeck provided dry weights for damselflies. I thank A. Porter, J. Kaster, K. Fletcher, K. Marshall, S. Vessey, A. Rypstra, and M. Hodge for valuable comments on the manuscript.

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*Manuscript received 12 May 1993, revised 25 March 1994.*