1995. The Journal of Arachnology 23:165–170

CHIVALRY IN PHOLCID SPIDERS REVISITED

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ABSTRACT. Cohabiting pairs of adult spiders are likely to interact over prey, and the outcome of these interactions is likely to affect the reproductive success of both individuals. In two species of pholcid spiders, previous workers reported the occurrence of "chivalrous" behavior, in which males cede prey to females. We looked for the occurrence of chivalrous behavior in another pholcid spider, *Holocnemus pluchei*. Pairs of spiders were placed on a web and left overnight without prey. A housefly was then introduced onto the web equidistant from the spiders, and subsequent interactions were noted on audiotape. We found no evidence of chivalry in pairs of unknown mating status or in pairs that had recently mated: males and females were equally likely to win the prey, and intensity of interactions over prey was not influenced by the gender of the winner. The differences in our results compared to previously published work may be attributable to the fact that *Holocnemus* lives in unusually dense populations in nature. This, in combination with a pattern of last-male sperm priority, means that females may be difficult for males to monopolize, and a male will not substantially increase his own reproductive success by ceding prey to a female with which he has mated if others are also likely to mate with her.

Web-building spider species vary tremendously in the duration of male and female cohabitation. Spiders may interact only during courtship and copulation (Robinson 1982), live permanently in the same colony (see reviews by Buskirk 1982; D'Andrea 1987), or exhibit behavior between these extremes (Suter & Walberer 1989). While sharing a web, males and females can interact over incoming prey. These interactions also vary greatly, ranging from cooperative prey capture in some social species (Buskirk 1982), to forceful battles over prey (Suter 1985). Interactions over prey by cohabiting pairs are potentially of evolutionary importance because an increase in a female's prey intake is likely to increase her fecundity (e. g., Turnbull 1962) and cohabitation can be relatively prolonged. The extent to which a cohabiting male benefits from consuming prey himself or allowing a female to consume prey may be influenced by whether he has mated with the female, the number of other mates she has had, the pattern of sperm priority, the female's defendability, and the number of other mating opportunities in the population.

A particularly striking example of interactions over prey is the "chivalrous" behavior reported by Eberhard & Briceño (1983), in which male pholcids ceded prey to females. *Blechroscelis* sp. males, after attacking prey, would sometimes step aside and allow a female to take it. Occasionally, a female would vibrate her abdomen (a display also seen in male courtship, and interpreted by Eberhard & Briceño as "begging"); this behavior was often followed by the male ceding the prey to her. In two *Modisimus* species, males initiated most attacks on prey and then usually ceded the prey to females. In one species, the female would approach the male as he wrapped the prey, then he would step aside and allow the female to take the prey. In the other species, males usually completely wrapped the prey, then plucked the web, and left the prey in the web for the female or carried it towards her. Eberhard & Briceño (1983) termed these behaviors "chivalrous" because males sometimes endured partial starvation while allowing females to feed, and we follow their terminology here.

We looked for the occurrence of chivalrous behavior in another pholcid spider, *Holocnemus pluchei*. Several factors make *Holocnemus* a good species in which to study this behavior. First, it serves as a comparison to the pholcids studied by Eberhard & Briceño (1983). *Holocnemus* often live in dense populations with interconnecting webs and a single sheet of silk may be shared by many spiders of all ages, in contrast to *Blechroscelis* and *Modisimus*, in which only adult pairs cohabit (Eberhard & Briceño 1985). Sec-

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ond, interactions between *Holocnemus* spiders over prey are relatively well known (Jakob 1991, 1994), allowing us to interpret clearly their behaviors. Finally, we have some information about the sperm priority pattern in *Holocnemus*. In *Holocnemus*, the second of a pair of males to mate with a female fertilizes 65–82% (95% confidence interval) of her eggs (Kaster 1995). With this information, the implications of chivalrous behavior for a male's reproductive success are more easily interpreted.

In our laboratory study, we introduced prey onto webs shared by male and female pairs of adult spiders and noted subsequent interactions, watching especially for behavior patterns described by Eberhard & Briceño (1983). We define chivalrous behavior by male spiders to include the following: (1) upon the approach of a female, the male leaves the prey and stands aside as she takes possession, (2) the male wraps and then carries the prey to or in the direction of the female and cedes it to her, or (3) both spiders simultaneously wrap the prey, and the male subsequently moves away, with little or no aggression by the female. If males are chivalrous, they might allow females to attack prey first, and females may be more likely to win interactions over prey. Chivalrous males might cede prey without escalating interactions, so we also examined the relationship between interaction intensity and the gender of the winner. We also analyzed relative frequency of other aggressive behaviors for males and females to look for any gender-specific differences. We studied two groups of spiders: pairs that may or may not have mated (with other spiders or with each other) prior to the test (mating status unknown, or MSU), and previously virgin pairs that were observed to mate with one another prior to the test.

METHODS

Adult and juvenile *Holocnemus pluchei* were collected in Davis, California in the summer of 1994 and shipped to our laboratory in Ohio. Rearing procedures follow Jakob & Dingle (1990) with the following exceptions. Juveniles were reared to maturity with three feedings per week of fruit flies (*Drosophila* sp.) and flour beetle larvae (*Tribolium confusum*). Adults were fed houseflies (*Musca domesticus*) and *Tribolium* larvae twice weekly. Spiders were maintained in a room with 16:8 L:D cycle at a temperature of approximately 27 °C.

The experimental arenas were four 52 × 37 × 22 cm plastic cages. Because *Holocnemus* are slow to build large webs in the laboratory, we introduced spiders onto webs built by conspecifics. In the field, *Holocnemus* routinely use webs that other individuals have built (Jakob 1991), so this is a realistic approximation of field conditions.

We performed two sets of trials. In the first set of 31 trials (mating status unknown, or MSU), field-caught spiders were randomly paired as adults, introduced into a web and left overnight. Because we did not monitor the spiders after pairing and prior to the test, we did not know whether these pairs mated in the laboratory. In the second set of 14 trials (mated pairs), mature virgin spiders were randomly paired and introduced into a test web, where we observed copulation. Testing occurred approximately 24 hours after copulation. Within one-half hour before the start of all trials, we briefly removed spiders from the test arena without damaging the web, and weighed them on a Mettler balance. After their return to the web, spiders were given a few minutes to acclimate before testing began.

At the start of each trial, a housefly was anesthetized with CO_2 and placed in the web with soft forceps approximately equidistant from each member of the pair, which were typically within 25 cm of each other. We made continuous voice recordings of observations with a microcassette recorder, beginning when the fly first moved. We noted whether both spiders oriented to the prey (turned to face the prey), which spider was first to attack the prey, if one spider relinquished the prey without fighting, and which spider ultimately won the prey. We also noted if the prey changed possession during the course of the interaction: that is, if it was first held by one spider in its chelicerae and later by the other. Trials ended when one spider was feeding on the prey and both spiders had been quiescent for at least 10 min. Previous observations suggest that spiders rarely steal prey after feeding begins (Jakob 1991).

We classified interactions over prey into three levels after Jakob (1994). Interactions at lower levels are assumed to have lower risk of injury than interactions at higher levels. *Level I*: Orientation to conspecific (spider turns its body to face conspecific), pushups (slow leg flexion) and abdomen twitching (fast dorsal/ventral twitching of the abdomen). *Level II:* Bouncing (sharply contracting its legs so body moves toward the

Table 1.—Number of trials in which males and females won the prey item. χ^2 goodness-of-fit tests are against expected values of 50:50. Calculations of the power of the test follow Cohen (1977).

	Male won	Female won	χ^2	P	Power
Mating status unknown	10	16	1.397	0.391	0.507
Mated pairs	9	5	1.143	0.428	0.513
All trials	19	21	0.100	0.752	0.764

web), approach conspecific, and web plucking (spider spreads its anterior pair of legs, pulls sharply downward on the web, and releases it so the silk snaps back). *Level III:* Chasing a conspecific, probing and contacting the conspecific with extended front legs, and grappling (locking chelicerae, intertwining legs and appearing to roll about the underside of the web sheet). From tape transcriptions, we calculated interaction time, excluding pauses between activities, for behaviors of all levels combined and for behaviors of Levels II and III only.

For results reported here, we omitted trials in which one of the spiders failed to respond to the prey at any time because we did not know if spiders had detected the vibrations of the prey. In MSU pairs, three males failed to respond to the prey at any time throughout the trial and two females failed to respond. In trials with mated pairs, the male did not respond in one trial and the female did not respond in another. Inclusion of these trials did not change the outcome of the analyses.

We compared the frequencies that males and females attacked and captured prey against expected frequencies of 50% with χ^2 goodness-of-fit tests. We used contingency tests to examine differences in the levels of escalation of interactions when males and females won. Contingency tables were analyzed with G-tests when cell sample sizes permitted and with χ^2 contingency analyses for other cases (Sokal & Rohlf 1981). We used nonparametric tests to examine whether interactions won by males were of the same duration as those won by females.

Table 2.—Number of males and females that won the prey item for three relative weight classes.

	Larger males	Male within 10% of female	Smaller males
Male	5	4	10
Female	2	1	18

RESULTS

General descriptions of interactions.—Males and females were equally likely to attack the prey: in all trials combined, 20 females were first to attack the prey and 20 males were first to attack. MSU and mated trials did not differ significantly: in MSU pairs, 11 males and 15 females were first to attack, and in mated pairs, 9 males and 5 females were first (contingency table, $G^2 = 1.777$, $P > 0.15$). There were competitive interactions over prey in every trial, and every trial ended with one spider feeding on the prey.

Winner of the interaction.—If males were chivalrous, females would be expected to win interactions over prey more often than males. However, males and females were equally likely to win the prey (Table 1). Mated and MSU pairs did not differ significantly (contingency table, $G^2 = 2.456$, $df = 1$, $P > 0.12$).

We were interested in the combined effects of relative mass and prey on the outcome of interactions: chivalry might be occurring if males lost prey to females of smaller mass. This effect might be hidden in the data because, as a group, *Holocnemus* males were significantly lighter than females with which they were paired (Wilcoxon signed-rank test, $Z = -3.737$, $P = 0.0002$). We categorized males as being within 10% of the mass of their partner (hereafter classified as same size), less than 10% of the female's mass (smaller males), or greater than 10% of the female's mass (larger males) (Table 2). Smaller males lost more interactions than expected, but this difference was not significant (contingency table, $G^2 = 5.474$, $df = 2$, $0.06 < P < 0.07$). When we pooled same size and larger males, we found that they were significantly more likely to win fights over prey than were smaller (contingency table, $G^2 = 5.357$, $df = 1$, $P < 0.03$). Thus, contrary to predictions from chivalry, males tended to lose in-

Table 3.—Level of interactions reached by pairs of spiders. Higher interaction levels are considered to be of higher energetic cost and higher risk.

	Level I	Level II	Level III
Mating status unknown			
Male wins	1	4	5
Female wins	0	5	11
Mated pairs			
Male wins	2	1	6
Female wins	0	0	5

teractions only when they were smaller than their partners.

Interaction intensity.—Chivalry might occur in a more subtle way: perhaps males gave up prey without escalating interactions to their highest level. For all trials combined, three interactions did not pass beyond Level I, 10 did not pass beyond Level II, and 27 reached Level III, the highest intensity level. There was no relationship between the level of intensity that interactions reached and the gender of the winner for MSU pairs ($\chi^2 = 2.088$, $df = 2$, $P > 0.35$), mated pairs ($\chi^2 = 2.121$, $df = 2$, $P > 0.3$), or all trials combined ($\chi^2 = 3.836$, $df = 2$, $P > 0.14$) (Table 3). MSU and mated pairs did not differ significantly in the level of interaction that was reached. No relationship was found between relative masses of a pair (male within 10% of its partner's mass, less than 10%, or greater than 10%) and interaction intensity ($\chi^2 = 1.744$, $df = 2$, $P > 0.78$).

Change of possession of the prey.—If chivalry occurs in this species, we would predict that prey would more often change from the possession of the male to the possession of the female. In five MSU pairs, the prey changed possession during the course of the interaction. In three trials, the prey was taken away from the male by the female, and in two trials, the prey was taken away from the female by the male. In mated pairs, the prey changed possession from the male to the female once, and on one occasion, the prey changed from the female, to the male, then back to the female, who consumed it.

Behavior.—No spider ever stood aside as another took the prey, wrapped the prey and then ceded it without aggression, or simultaneously wrapped the prey with another spider and then moved away.

We also looked for more subtle evidence of chivalry by investigating whether females and males differed in their performance of specific agonistic behaviors. We counted the number of trials in which each behavior was performed at least once by the male or female. We found no significant differences in pushups, bouncing, approach, chasing, web plucking or probing. However, the numbers of trials in which the male abdomen twitched was significantly higher than the number of trials in which the female abdomen twitched (contingency table analysis, male: 32 of 40 (60%); female: 14 of 40 (35%); $G^2 = 17.269$, $df = 1$, $P < 0.0001$).

Interaction duration.—If chivalrous males give up prey to females, interactions that are won by females may be shorter in duration. However, we found no significant relationship between gender of the winner and duration of all interactions (excluding pauses) or for duration of all behaviors of level II or III (Mann-Whitney U-tests) (Table 4). When MSU and mated pairs were analyzed separately, no significant difference in any measure of duration was found.

DISCUSSION

Holocnemus pluchei were not chivalrous. Males and females were equally likely to attack and win prey. However, the power of our test comparing the frequency of winning for each gender (Table 1) indicates that we have a 24% probability of a Type II error, or accepting the null hypothesis when it is false; thus, this result alone does not

Table 4.—Mean (±SE) interaction durations (s) in trials that females won compared to trials that males won. P values are derived from Mann-Whitney U-tests.

	Duration of all interaction levels			Duration of II & III		
	Female won	Male won	P	Female won	Male won	P
Mating status unknown	543 ± 134	492 ± 126	NS	193 ± 76	110 ± 36	NS
Mated	932 ± 312	257 ± 76	0.10	389 ± 186	79 ± 27	0.10
All trials	636 ± 128	381 ± 78	NS	171 ± 41	239 ± 73	NS

firmly establish that these spiders are not chivalrous. However, we saw none of the chivalrous behaviors described by Eberhard & Briceño (1983). Fights over prey often escalated. Prey changed hands from male to female approximately as often as it changed from female to male. Males that were within 10% of the body mass of females or larger than females were likely to win prey, suggesting that when males lose prey, it is not because of chivalry but because of a lack of competitive ability. Few differences were found in male and female behavior patterns. Males were more likely to abdomen twitch; the meaning of this behavior is unclear, but we interpret it as a low-risk, low energy behavior. In sum, we found no evidence that males were allowing females an advantage in prey capture.

Eberhard & Briceño (1983) suggest that, for *Blechroscelis* and *Modisimus*, it is to a male's advantage to be chivalrous if it results in an increase in the number of eggs laid by the female that are sired by the male. Although mating was not directly observed in Eberhard & Briceño's (1983) study, it is likely that their spiders had mated; only adult pairs cohabit, and paired males will fight with males that are introduced onto the web (Eberhard & Briceño 1985), which is consistent with the idea that females are a valuable resource worthy of defense (e. g., Parker 1984). The last pholcid male to mate with a female may father many of her eggs: Austad (1984) predicts that, based on the cul-de-sac shape of the spermatheca, haplogyne spiders such as pholcids should show last male sperm priority or sperm mixing. Eberhard et al. (1993) found that in another pholcid, *Physocyclus globosus*, sperm priority pattern for twelve females that were each mated with two males did not differ from that expected for random sperm mixing. If Austad's prediction proves true for *Blechroscelis* and *Modisimus*, it should benefit a male to cede prey to a female with which he has just mated.

Why, then, are *Holocnemus* males not chivalrous? Kaster (1995) found, using the technique of sterilization by irradiation, that the sperm priority pattern in *Holocnemus* is highly variable: the second male of a pair of males fertilized between 2.6 and 100% of a female's eggs. High variability in sperm precedence is common in insects and is as yet unexplained (Lewis & Austad 1990). However, in most of Kaster's pairs of males, the second male fathered most of the eggs ($\bar{x}$ = 73.7%, 95% confidence interval 65.8–81.6%). It seems clear that the first male to mate with a virgin female is not guaranteed to fertilize the bulk of her eggs if the female has subsequent mates. A male that cedes prey to a female may not gain much benefit in reproductive success if another male mates after he does.

Holocnemus differs from the species that Eberhard & Briceño studied in that *Holocnemus* females may not be a defendable resource. *Holocnemus* populations are extremely dense: for example, there may be over 600 spiders on a 3 m × 15 m juniper bush (Jakob unpubl. data). Both males and females move frequently from one web to another (Jakob 1991), so the intrusion rate of potential competitors for a female's attentions and the rate of female encounters with new males are both likely to be high. In the laboratory, females readily remate: Kaster (1995) removed males when they finished copulating with a virgin female and immediately introduced a new male, and found that copulation began again in an average of 437 sec (*SE* = 101.91, *n* = 20). The populations of *Blechroscelis* and *Modisimus* are less dense than those of *Holocnemus*, and webs of individuals or pairs are discrete (W. G. Eberhard pers. comm.). Male *Blechroscelis* and *Modisimus* are more likely to be able to successfully defend females from competitors. An additional effect of the high population density of *Holocnemus* is that males are likely to have other mating opportunities, which would devalue any one mating and make it profitable for a male to increase its energetic intake to allow further searching for mates. Other variables that would affect a male's probability of finding more than one mate include predation risk while searching and the male's expected lifespan. Neither of these, to our knowledge, has been measured for any pholcid in the field. However, *Holocnemus* males can live for over a year in the laboratory (unpubl. data), which suggests they may indeed have ample opportunity to remate in the field.

ACKNOWLEDGMENTS

This work was supported by BGSU Undergraduate Research Scholarships to JAB and MSS, and a Faculty Research Challenge award and NSF grant IBN 94-07357 to EMJ. We thank A. Porter for statistical advice, S. Vessey, A. Porter, A. Rypstra, and W. G. Eberhard for comments on the manuscript, and B. Randall for her tolerance of spiders in the Animal Facility.

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Manuscript received 16 March 1995, revised 6 June 1995.