

2000

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Ontogenetic Shifts in the Costs of Living in Groups: Focal Observations of a Pholcid Spider (*Holocnemus pluchei*)

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ABSTRACT.—*Holocnemus pluchei* spiders (Family Pholcidae) facultatively live in groups: sometimes they live alone and sometimes they share webs. In the field groups vary in size and composition and include spiders of all ages and either sex. Group membership is flexible and individuals move frequently among groups. To understand group formation and maintenance it is necessary to understand the costs of group membership. We used focal animal sampling to investigate the cost of group living for spiders of different ages across a range of group sizes. Both spider age and group size affected the costs incurred by group-living spiders. There was no variation among groups of different sizes in the percentage of time focal small or large spiders spent in costly behaviors (moving, web maintenance, bouncing or interactions with conspecifics), but medium-sized spiders spent more time engaged in costly behaviors with increasing group size. Medium and large spiders also had more interactions with greater numbers of different conspecifics when they were in groups larger than three, whereas small spiders interacted rarely with conspecifics regardless of group size. These results suggest that there are significant ontogenetic shifts in the costs of group living in *H. pluchei*.

INTRODUCTION

Living in groups has costs and benefits that may not be distributed evenly over all group members (Lee, 1994). In particular, younger individuals may face different selection pressures resulting from group living than do older individuals. For example, large humpbug damselfish (*Dascyllus aruanus*) feed farther upstream than do smaller fish within the same group. This reduces the food availability for smaller fish and, as a result, the growth rate of small fish in groups with many larger fish is significantly slowed (Forrester, 1991). In the colonial spider *Metepeira incrassata*, trade-offs between predation risk and foraging change as spiders grow, leading to a dynamic colony structure. Both prey availability and predation risk are higher at the periphery of the colony compared to the core. Smaller spiders are more likely to be found at the periphery and larger spiders move to the colony core (Rayor and Uetz, 1993). In general, however, studies of ontogenetic shifts in the ecological demands placed on animals have received relatively little attention, as other authors have pointed out (Sullivan, 1988; Loughry, 1992).

Important species in which to investigate ontogenetic shifts in the costs and benefits of social behavior are those in which group living is facultative and where individuals of all sizes are free to join or leave a group. Studies of such species may provide insight into the evolution of social systems. *Holocnemus pluchei* spiders (Araneae: Pholcidae) are sheet-web weavers that facultatively live in groups. Spiders of all sizes (representing different instars,

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and therefore different ages) are found both in solitary webs and in groups. Groups are generally small (mean = 2.8 ± 1.9 , mode = 2 individuals; Jakob, 1991), although they can range up to a dozen or so individuals. Movement among webs is quite common: in 1995 we marked 89 webs and checked them daily for 4 d, recording the body sizes of individuals in each web. Webs had changes in occupancy (either gaining or losing at least one spider) from one day to the next 60% of the time.

Throughout their lives these spiders face a series of choices. They may seek an available web site and construct their own web or they may join a group. Once in a group, they may stay there or leave to find another group or to search for an appropriate site to build a solitary web. In order to understand group formation and stability we must identify the costs and benefits of each of these choices for individuals of different ages. Some of these have already been examined for *H. pluchei*. For example, spiders that build their own webs must redirect energy from growth and development into the production of energetically costly silk (Jakob, 1991). Spiders that choose to join a group face intense competition for prey. The costs of competition change with age, as generally the largest spider in a web wins a conflict over a prey item (Jakob, 1991; Jakob, 1994). Low rates of prey intake lead to slower development and smaller body size (Jakob and Dingle, 1990), so the loss of prey to competitors is likely to decrease a spider's survival and reproductive success.

In this study we examine several other costs that spiders may face in group webs. First, we examine costs resulting from interactions with conspecifics. *Holocnemus pluchei* spiders frequently interact aggressively in other contexts besides over prey. Interactions between webmates often occur spontaneously in the absence of detectable external stimuli, and we examine these here for the first time. We will examine whether spiders of different sizes (and therefore ages) differ in their propensity to engage in these interactions. Previous work has shown that, in interactions over prey, small *H. pluchei* behave aggressively towards larger spiders even though small spiders rarely win these fights. Game theory suggests that fighting animals should be more likely to take risks when resources are particularly valuable (Parker, 1984), as is the case for *H. pluchei* fighting over prey (Jakob, 1991). However, when prey are not present in the web small spiders should be risk averse and avoid conflict. We test this hypotheses by examining the number of interactions that spiders have and the amount of time they spend in costly activities such as moving and displaying in response to conspecifics.

A second potential cost is the cost of web maintenance. Pholcid webs are not taken down and reingested, as are webs of some other spider families, and webs must be maintained and repaired with the addition of silk. Web maintenance costs may be substantial. For example, in the social orb weaver *Metepira incrassata*, silk expenditure during maintenance of the communal semi-permanent colony framework appears to be important in determining optimal colony size. The cost of web maintenance for solitary *M. incrassata* is so severe that it results in a negative energy budget (Uetz and Hieber, 1997), and thus web maintenance costs favor group living. In this study we examine the web maintenance costs for *H. pluchei* spiders in groups of different sizes. If web maintenance costs favor group living as they do in *M. incrassata*, we expect that costs per spider should be inversely related to group size.

METHODS

Our study site was a large (3 m wide \times 15 m long \times 1 m high) juniper (*Juniperus* sp.) hedge on the campus of the University of California at Davis (see ZFH site in Jakob, 1991). Data were collected in August 1995 and July 1996. *Holocnemus pluchei* populations become extremely dense in the hot, arid Mediterranean climate of the Central Valley, and this site

has well over 600 spiders by late summer. We chose to sample spiders intensively at this site because of its accessibility, freedom from human disturbance and high spider density.

Spider webs were constructed in gaps between the branches of the hedge. Webs were generally within 70 cm of their nearest neighbor. Spiders on the same web sheet were in vibratory contact with one another, and were considered to be members of the same group. (Vision in the family Pholcidae is very poor and vibrations seem to be the most important source of information for these spiders.) Spiders on separate web sheets that were not in vibratory contact with one another were considered to be in separate groups. Because silk is sometimes difficult to see, we verified that spiders were in vibratory contact by touching a ringing tuning fork to the web immediately after the completion of data collection. *Holocnemus pluchei* approach and wrap ringing tuning forks as if they were prey (Jakob, 1991). Only spiders approaching the tuning fork were considered to be members of the same group.

We used the technique of focal animal sampling, in which all behavior patterns of a focal individual are noted for a specified time period (Altmann, 1974). This is generally the most satisfactory method for studying the behavior of individuals in groups (Martin and Bateson, 1986). We observed only one spider per web in order to ensure independence of data points. At the end of an observation, the web was marked and was not resampled during the remainder of the field season. Because individual spiders were not marked, we cannot be sure that we did not resample individuals that moved from web to web between observation periods; however, it is unlikely that entire groups moved together to a new web and were resampled.

All authors conducted observations and we took care to ensure interobserver reliability. Each observer had a minimum of one year's experience in observing *Holocnemus pluchei* in the laboratory (e.g., Blanchong *et al.*, 1995). We simultaneously observed several spiders in order to ensure that we were in agreement on how we recorded behaviors. All observers worked at the same time so that any questions could be resolved with EMJ, the coordinator of the study. The behaviors selected for analysis (*see below*) were unmistakable. We tested for differences among observers with Kruskal-Wallis tests.

We selected 145 focal individuals for study. Spiders were categorized into three size classes of small, medium or large. These three classes correlate with spider age: small roughly corresponds to second and third instar juvenile, medium to fourth instar juvenile and large to fifth-instar penultimates and fifth- or sixth-instar adults (Jakob, 1991). Immature *Holocnemus pluchei* cannot be sexed in the field. We used only adult females; adult males do not build webs, although they forage on webs constructed by juveniles or females. We observed focal spiders in each of the following group sizes: solitary individuals; groups of two (*i.e.*, the focal spider plus one other individual), groups of three; and groups of more than three. We attempted to sample evenly across groups of various compositions, but were constrained by their availability in the field: groups of three or more individuals were particularly rare, and we sampled every one available (Table 1).

Observations were conducted at dusk and during the first few hours of darkness (2000 to 0030 h) because spiders rarely move during the heat of the day (*pers. obs.*). We used flashlights and headlamps covered with red acetate to illuminate the spiders; the reddish light had no apparent effects on behavior. We observed each focal spider for 30 min or until it moved off the web and either was lost from sight or entered a different group.

We identified seven categories of behavior. Of these, we classified four categories as costly. (1) Movement, which includes walking and other relatively slow movements, requires some energetic expenditure. In addition, it is likely to be detectable by webmates, leading to interactions. (2) Web maintenance is likely to be costly. It includes the cost of slow move-

TABLE 1.—Percent time (SE) spent performing four costly behaviors for three size classes of spiders: large (L), medium (M) and small (S). P values are presented from Kruskal-Wallis tests for each behavioral category and represent differences across group sizes for a particular size of focal spider. When sequential Bonferroni corrections are applied, only differences marked with an asterisk are significant at the 0.05 level

	Size	Group size				H_{corr}	P
		Solitary	2	3	>3		
Sample sizes	L	12	17	10	7		
	M	10	29	6	6		
	S	10	21	7	6		
Web maintenance	L	5.03 (2.39)	2.58 (1.83)	0.53 (0.25)	0.63 (0.63)	3.432	NS
	M	0.93 (0.83)	1.84 (1.21)	7.00 (3.28)	2.30 (1.93)	3.998	NS
	S	0.74 (0.43)	0.45 (0.21)	3.87 (2.56)	0	4.490	NS
Move	L	2.10 (0.74)	3.06 (1.34)	3.58 (1.46)	2.94 (1.34)	1.411	NS
	M	0.63 (0.45)	2.16 (0.90)	2.78 (1.12)	7.58 (3.36)	11.000	0.012*
	S	3.75 (1.59)	2.10 (0.66)	2.79 (1.69)	10.51 (5.75)	4.284	NS
Bounce	L	0.76 (0.45)	3.78 (1.61)	4.75 (3.43)	2.70 (0.55)	7.78	0.051
	M	2.84 (1.20)	2.43 (1.38)	7.27 (4.58)	6.12 (2.38)	4.070	NS
	S	1.88 (0.70)	0.09 (0.05)	1.08 (0.89)	0.27 (0.12)	11.533	0.009*
Interactions	L	0.31 (0.31)	1.09 (1.08)	0.34 (0.24)	3.64 (1.42)	17.316	0.001*
	M	0	0.19 (0.13)	0.14 (0.14)	3.15 (1.35)	27.056	0.0001*
	S	0.02 (0.02)	0.13 (0.12)	0.28 (0.28)	0	0.731	NS

ment as well as the cost of silk. The silk of *Holocnemus pluchei* is high in calories, and spiders that are forced to build webs repeatedly grow more slowly than those that are not (Jakob, 1991). (3) Bouncing (dorsal-ventral flexion of the body) and web-plucking (spreading the anterior legs, pulling down sharply on the web and letting it snap back), are vigorous fast movements that require energetic expenditure and are likely to be detectable by webmates, and thus often precede interactions. (4) Interactions between conspecifics may place spiders in physical danger, prevent them from capturing prey or result in spiders being forced out of a web. We followed previous authors (Jakob, 1994; Hodge and Uetz, 1995; Riechert, 1978) in ranking behaviors of interacting spiders according to relative intensity, giving a higher rank to faster and more dangerous movements. We identified two levels of interaction: low-level in which spiders moved towards or away from conspecifics and high-level in which spiders physically contacted, or were contacted by, conspecifics (similar to Level 2 and 3 interactions defined in Jakob, 1994). High-level interactions were assumed to be more likely to result in injury or death than were low-level interactions.

We assumed that the three remaining behavioral categories have little or no energetic cost beyond basal metabolic costs: (5) sit (quiescence, no detectable movement), (6) groom (a spider cleans its tarsi by very slowly drawing them through its chelicerae) and (7) prey capture (any events culminating in the capture or consumption of prey; we define this as a “no-cost” behavior because prey capture results in a net energy gain).

We noted whether focal individuals left the web and the percentage of time focal individuals spent in each of the seven behavioral categories. We addressed the following questions: Does the size of a focal individual or the size of its group affect (1) the likelihood that the focal individual leaves the web, (2) the percentage of time the focal individual spends in costly behaviors and (3) the number of interactions that focal spiders have with conspecifics? In addition, the composition of the group may also be important. Because of

previous work in this species demonstrating that the largest spider in a web is most likely to win competitions over prey (Jakob, 1991), we tested whether the size of the largest spider in the web (same size, larger or smaller than the focal spider) influenced the percentage of time focal individuals spent in costly behaviors.

RESULTS

Interobserver reliability and differences between years.—We checked for interobserver reliability by comparing our results for each of the seven behavioral categories for each of the four group sizes. Of these 28 tests, six showed significant differences among observers (Kruskal-Wallis tests, $P < 0.05$). However, there was no discernible pattern among observers. For example, one observer recorded significantly more bouncing, a very obvious behavior, for solitary spiders than did other observers, but not for spiders in any other group size. We conclude that observer bias was not a problem in this study.

In each of the following analyses we checked for differences between data collected in 1995 and 1996 in nonparametric tests. None were found ($P > 0.3$ in all cases), so data were pooled.

Movement among webs.—Spiders moved frequently among webs, but there was no pattern in either the size of the spider that moved or the size of the groups that spiders entered or left. In 10% of the focal observations (15 of 145) there was a change in the occupancy of the web during the half hour observation period; that is, a spider either left or entered the web. In ten cases an intruder entered the focal spider's web during the observation period. Intruders were of all sizes (five large, two medium and two small intruders and one whose size was unrecorded). Intruders were equally likely to enter solitary or group webs (9% of 32 solitary webs and 7% of 109 group webs were entered; $\chi^2 = 0.327$, $P > 0.5$).

In group webs, focal spiders that interacted with conspecifics were significantly more likely to leave webs than were spiders that did not interact (4 of 29 spiders that interacted left webs and 0 of 84 spiders that did not interact left webs; Fisher's exact test, $P < 0.004$). One of these was a small spider that was knocked out of the web by a conspecific while three large spiders climbed onto the vegetation after their interaction. In addition, one large solitary spider left its web without interacting with a conspecific.

Time spent in costly behaviors.—We found both significant ontogenetic effects and significant effects of group size on the percentage of time spiders engaged in costly behaviors. The percentage data were highly skewed and could not be transformed to meet the assumptions of parametric statistics, and were analyzed with nonparametric tests. Because of the constraints of available nonparametric tests, we could not examine the effects of size class of the focal spider and the effect of group size simultaneously, so we performed separate tests for each of the three size classes of focal spiders. In addition, because of smaller sample sizes of groups of more than three spiders, we tested to see if we could pool groups of four and larger. Kruskal-Wallis tests revealed no differences in any of the variables described below among groups of four spiders or more so we pooled these samples into one category, group size greater than three.

Focal spiders spent an average of 84% (SE = 2 %) of the observation period sitting motionless in their webs. Medium spiders in groups of three or greater than three spent approximately fourfold more time in costly behaviors than did medium spiders that were solitary or in a group of two (Kruskal-Wallis test, $H_{\text{corr}} = 11.790$, $P = 0.008$). No differences across group types were found for large spiders or for small spiders (large: $H_{\text{corr}} = 1.115$, $P > 0.7$; small: $H_{\text{corr}} = 3.527$, $P > 0.3$; Fig. 1). We examined this pattern in more detail by breaking down the percentage of time spent in costly behavior into its four component parts (web maintenance, moving, bounce/web pluck and interactions) and testing each

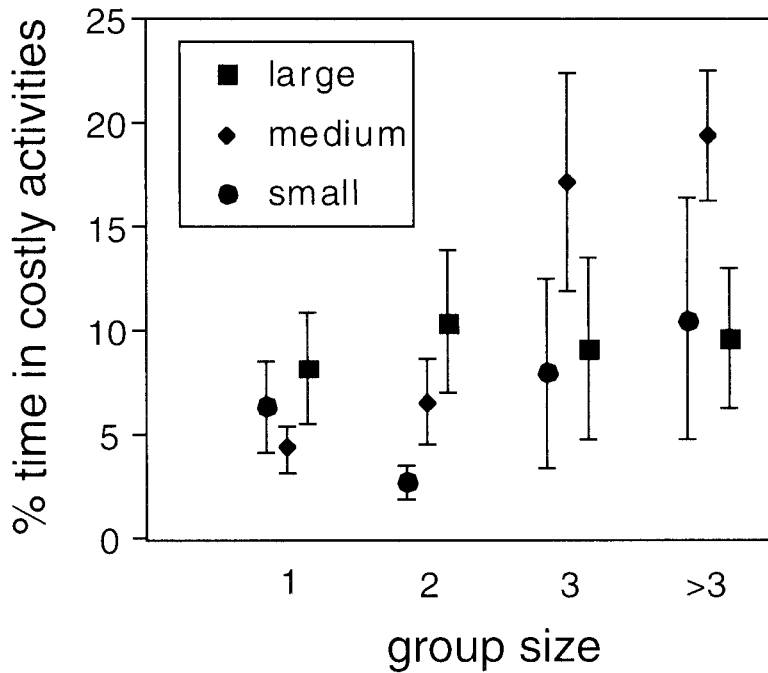


FIG. 1.—Percent of 30-min observation periods that small, medium and large focal spiders spent in costly activities (including web maintenance, moving, bouncing, and interacting) in groups of different sizes. Points are offset so that error bars are distinguishable

separately for each size class (Table 1). Because these data sets were not independent, we adjusted the P values with a sequential Bonferroni correction (Rice, 1989). Medium spiders spent more time in each of the four costly behavioral categories when in groups of three or more, though only the percentages of time spent moving and in interactions were significant.

Interactions between spiders.—We found both significant ontogenetic effects as well as a threshold effect of group size on interaction rates. We observed 27 interactions in 70.5 h of observation. Thirteen percent of focal spiders (19 spiders) had one interaction and 3% (4 spiders) had 3–5 interactions in the half-hour observation period. Only five interactions occurred when prey were in the web; the proximate cause of the remaining interactions could not be determined. The number of interactions increased markedly at a group size of four; the number of interactions was significantly higher in groups of four vs. groups of three (Mann-Whitney U, tied z-value = -2.234 , $P < 0.025$), but did not differ from the number of interactions in groups larger than four (tied z = -0.504 , $P > 0.6$). We therefore combined data from groups larger than three. Both medium and large spiders had significantly more interactions in groups larger than three than in other group sizes (medium: $H_{\text{corr}} = 25.153$, $P < 0.0001$; large: $H_{\text{corr}} = 18.795$, $P < 0.0003$; Fig. 2). Small spiders rarely fought, even in the largest groups, and there was no relationship between group size and number of interactions for them ($H_{\text{corr}} = 0.824$, $P > 0.8$; Fig. 2).

We also examined whether spiders repeatedly interacted with the same individual or whether the number of different opponents also increased with group size. We again saw

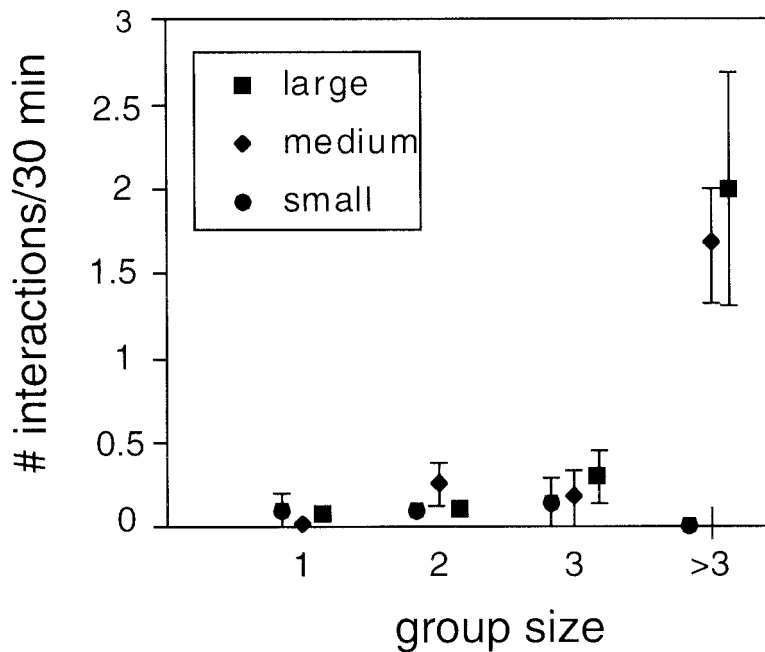


FIG. 2.—Number of agonistic interactions had by small, medium and large focal spiders during 30-min observation periods. Points are offset so that error bars are distinguishable

a threshold effect: both medium and large spiders faced a greater number of opponents in the groups of more than three than in other settings (medium: $H_{\text{corr}} = 12.58$, $P < 0.0001$; large: $H_{\text{corr}} = 18.797$, $P < 0.0003$). There was no difference in the number of opponents for small spiders in groups of different sizes ($H_{\text{corr}} = 0.824$, $P > 0.8$).

The relative size class of the largest conspecific in the web, compared to the focal spider (larger, smaller or same size class) had no effect on the percent of time spiders spent in costly behaviors for any size class (Mann-Whitney U for large and small size classes, Kruskal-Wallis test for medium size class, $P > 0.35$ in all cases). However, larger spiders that shared a web with another large spider had more interactions than did spiders that shared webs only with smaller spiders (sharing with large: 1.00 ± 0.35 , $n = 16$; sharing with smaller: 0.12 ± 0.08 , $n = 17$; Mann-Whitney U, tied $z = -2.615$, $P < 0.01$). No patterns were found for small and medium spiders.

Forty-two percent of interactions reached the higher intensity level. No relationships were found between level of intensity that interactions reached and size of the focal spider, group size or relative size of the largest conspecific in the web (chi square tests, $P > 0.6$ in each case).

DISCUSSION

We found ontogenetic differences in energetically costly or otherwise risky behaviors exhibited by spiders in group webs. Small spiders had very few interactions with conspecifics and spent little time in costly behaviors, regardless of group size. Medium and large spiders had a threshold effect of group size in the number of interactions and the number of opponents: only in the largest groups did interaction rates significantly increase.

What is the cost of interactions in *Holocnemus pluchei*? Riechert (1988) suggests that for the spider *Agelenopsis aperta*, the primary cost of fighting is not the energy expended in the fight, but rather costs associated with injury, potential predation and loss of food that is not captured because of time spent in interactions. Given the amount of time that *H. pluchei* spent in interactions (Table 1), the impact of interactions on lifetime energy budgets is also likely to be negligible in this species. Instead, interactions are likely to have three costs. First, competition over food has biologically meaningful consequences because competition for prey is intense (Jakob, 1991, 1994) and the growth rate of immature *H. pluchei* depends on feeding success (Jakob and Dingle, 1990). However, most interactions observed in this study did not occur in conflict over prey. Although it is possible that interactions between spiders when prey are not in the web allow spiders to establish dominance hierarchies that later determine access to prey, this is unlikely to be very important given the fluid nature of group membership.

Second, interacting spiders face a risk of cannibalism or injury. Although spiders occasionally lose legs during interactions (Jakob, pers. obs.), leg loss does not affect subsequent fighting ability or overall growth rate (Johnson and Jakob, 1991). Cannibalism presents a greater risk. Spiders feeding on conspecifics are frequently observed in the field (Jakob, pers. obs.), but this is difficult to quantify accurately. In a laboratory experiment, 30 of 158 small and medium spiders that joined the web of a single large spider were cannibalized within 20 hours (Jakob, pers. obs.). Although this is likely to be an overestimate of the rate of cannibalism under field conditions, it demonstrates that spiders are quite capable of feeding on conspecifics.

Third, spiders that engaged in interactions were significantly more likely to leave their webs than spiders that did not. Pholcid spiders require a web for prey capture, so spiders forced from a web must either find and enter an occupied web or build one. Merely moving through the environment may present costs. For example, Riechert (1981) found that "floater" spiders (*Agelenopsis aperta*) that did not hold territories lost more body weight than did territory holders. Once an *Holocnemus pluchei* finds an occupied web it may not prove possible to join it, especially for small and medium spiders. Jakob (pers. obs.) mimicked the process of joining a web by introducing "intruder" spiders onto the edge of occupied webs. Over 25% of spiders entering the webs of larger individuals were driven off. As discussed above, the alternative choice of building a web requires substantial energetic expenditure, as an average *H. pluchei* web contains 45 J of silk and spiders forced to rebuild webs repeatedly grow more slowly and are smaller (Jakob, 1991).

As predicted, small spiders engaged in fewer interactions than did larger spiders when prey were not present. They also bounced less in group webs. These results suggest that small spiders may be behaving in a way that is unlikely to attract the attention of larger conspecifics. This contrasts with the behavior of small spiders when prey are present in the web: small spiders are more likely than expected to initiate interactions with large spiders, and most of these interactions occur when large spiders are capturing or holding prey (Jakob, 1994). Taken together, these results indicate that small spiders are willing to engage in risky interactions and challenge large spiders only when the benefits, in the form of prey, are great.

In contrast to *Metepeira incrassata* (Uetz and Hieber, 1997), we did not find a per spider reduction in web maintenance costs with increasing group size. Web maintenance costs do not seem to be nearly as great for *Holocnemus pluchei* as in *M. incrassata*: a maximum of only 7% of a spider's time was spent in web repair (Table 1). The cost in silk production of leaving a web and building a new web (Jakob, 1991) would certainly be greater than maintaining an existing web.

Data such as these are an important step towards the goal of understanding why individuals of different ages may choose to stay or leave a particular group. These data suggest, all else being equal, that: (1) large and medium spiders should avoid large groups and (2) large spiders, which have a significantly high number of interactions when sharing a web with another large spider, should avoid group webs with other large spiders in them. Our study serves to emphasize the importance of measuring costs and benefits of behavioral decisions throughout ontogeny.

Acknowledgments.—C. Heiber, M. Hodge, A. Porter and S. Vessey provided helpful comments on the manuscript. H. Dingle kindly provided laboratory space at UC Davis. This research was supported by NSF IBN 94-07357 and IBN 95-07417 to EMJ, and a Research Experience for Undergraduates supplement in 1995 provided partial funding for the travel of JAB, MAP, KAS and MSS. JAB and MSS were also supported by a Tri Beta Undergraduate Research Award. We thank S. Johnson for assistance in the field in 1996.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**:227–267.
- BLANCHONG, J. A., M. S. SUMMERFIELD, M. A. POPSON AND E. M. JAKOB. 1995. Chivalry in pholcid spiders revisited. *J. Arachnol.*, **23**:165–170.
- FORRESTER, G. E. 1991. Social rank, individual size and group composition as determinants of food consumption by humbug damselfish, *Dascyllus aruanus*. *Anim. Behav.*, **42**:701–711.
- HODGE, M. A. AND G. W. UETZ. 1995. A comparison of agonistic behaviour of colonial web-building spiders from desert and tropical habitats. *Anim. Behav.*, **50**:963–972.
- JAKOB, E. M. 1991. Costs and benefits of group living for pholcid spiders: losing food, saving silk. *Anim. Behav.*, **41**:711–722.
- . 1994. Contests over prey by group-living pholcids. *J. Arachnol.*, **22**:39–45.
- AND H. DINGLE. 1990. Food level and life history characteristics in a pholcid spider. *Psyche*, **97**:95–110.
- JOHNSON, S. A. AND E. M. JAKOB. 1999. Leg autotomy in a spider has minimal costs in competitive ability and development. *Anim. Behav.*, **57**:957–965.
- LEE, P. C. 1994. Social structure and evolution, p. 266–303. *In*: P. J. B. Slater and T. R. Halliday (eds.). *Behaviour and evolution*. Cambridge University Press, Cambridge.
- LOUGHRY, W. J. 1992. Ontogeny of time allocation in black-tailed prairie dogs. *Ethology*, **90**:206–224.
- MARTIN, P. AND P. BATESON. 1986. *Measuring Behavior: an Introductory Guide*. Cambridge: Cambridge University Press. 200 p.
- PARKER, G. A. 1984. Evolutionary stable strategies, p. 30–61. *In*: J. R. Krebs and N. B. Davies (eds.). *Behavioural ecology, an evolutionary approach*, 2nd ed. Sinauer Associates, Sunderland.
- RAYOR, L. S. AND G. W. UETZ. 1993. Ontogenetic shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. *Oecologia*, **95**:1–8.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**:223–225.
- RIECHERT, S. E. 1978. Games spiders play: behavioral variability in territorial disputes. *Behav. Ecol. Sociobiol.*, **3**:135–162.
- . 1981. The consequences of being territorial: spiders, a case study. *Amer. Nat.*, **117**, 871–892.
- RIECHERT, S. E. 1988. The energetic costs of fighting. *Am. Zool.*, **28**:877–884.
- SULLIVAN, K. A. 1988. Ontogeny of time budgets in yellow-eyed juncos: adaptation to ecological constraints. *Ecology*, **69**:118–124.
- UETZ, G. W. AND C. S. HIEBER. 1997. Colonial web-building spiders: balancing the costs and benefits of group-living, p. 458–475. *In*: J. C. Choe and B. J. Crespi (eds.). *Social competition and cooperation in insects and arachnids, Vol. II. Evolution of sociality*. Cambridge University Press, Cambridge.