

GROUP SIZE DOES NOT INFLUENCE GROWTH IN THE THERAPHOSID SPIDER *HYSTEROCRATES GIGAS* (ARANEAE, THERAPHOSIDAE, EUMENOPHORINAE)

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ABSTRACT. Spiderlings of the theraphosid spider *Hysteroocrates gigas* were reared for 12 weeks with a superabundance of prey solitarily and in groups of two and four to examine the influence of rearing group size on growth. This taxon was selected because observations made on captive populations indicate that *Hysteroocrates* spp. tarantulas have an unusually high level of mutual tolerance and captive juveniles have been observed to feed cooperatively on large prey until several months old. Cannibalism was only observed in one instance, in a group of four. There was no significant effect of rearing group size on increase in body mass. There was a tendency for a greater asymmetry in final weight in dyads than in tetrads. No difference was found in the amount of time spent feeding by individuals between the different group sizes. Hence, benefits of group living in *Hysteroocrates gigas* spiderlings were not evident in this study.

Keywords: Tarantula, sociality, Mygalomorphae

Sociality in arachnids is a relatively rare phenomenon. Of approximately 36,000 described spider species, it is thought that only 35 are social; however, sociality has been demonstrated in at least 18 families of Araneae (Curtis & Carrel 1999). There are competing classification schemes for spider sociality (Aviles 1997), and the spectrum of spider sociality ranges from mutual tolerance to active cooperation in prey capture and brood care. One of the most significant thresholds along this continuum is the appearance of cohabitation by ecologically-competent juvenile spiders (i.e., those that could survive solitarily). These types of prolonged sibling aggregations are thought to represent an evolutionary step in the direction of quasisocial behavior in which sexually mature spiders exhibit cooperative behavior (Aviles 1997).

Sociality in spiders has presumably developed because of the benefits that come with direct cooperation and sharing the costs of silk production. Benefits of group living could include an increase in the amount and/or size of prey captured, shared construction costs of the web or increased predator avoidance (Aviles 1997; Uetz & Hieber 1997). Potential costs

include direct competition for prey, increased predation or increased egg sac parasitism (Uetz & Hieber 1997).

Sociality has been widely studied in the araneomorph spiders, but has remained relatively unexamined in the mygalomorphs (Aviles 1997). Jantschke and Nentwig (2001) observed females of the subsocial diplurid spider *Ischnothele caudata* Ausserer 1875 caring for spiderlings by catching and sharing prey. The study by Darchen (1967) on the ischnocoline tarantula *Heterothele darcheni* (Benoit 1966) is the only documented case of sociality in theraphosids of which we are aware. Darchen found that these spiders display no aggression towards others in a group web, though they do not cooperate in hunting (Darchen 1967). Our study involved the theraphosid spider *Hysteroocrates gigas* Pocock 1897. This West African tarantula lives in deep burrows in the rain forests and grasslands of Nigeria, Cameroon and the Congo (Smith 1990; Marshall 1996). *Hysteroocrates gigas* burrows have been found in a wide variety of locations: at the base of trees, beneath rotted logs, in termite mounds, on roadside embankments, on the periphery of village compounds and on flat ground amongst palm groves, heavy grassland brush or dense tropical wet forests (Smith 1990; R. West pers. comm.).

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In this study we observed social interactions of *H. gigas* spiderlings in captivity. In captivity, we have observed this species sharing prey as juveniles up to several months of age. Although there have been no studies of *H. gigas* phenology in the wild, captive individuals may reach maturity in 18–24 months (S. Marshall pers. obs.). Observations in the field in Cameroon show that well-grown young will cohabit in the maternal burrow with the mother (R. West, pers. comm.). In an 11 week study conducted by Reichling & Gutzke (unpub. data), spiderlings of the closely-related *H. crassipes* Pocock 1897 swarmed together on a prey item subdued by the mother, which was then completely devoured. Reichling and Gutzke's observations demonstrate that sociality in *Hysterocrates* siblings can extend well beyond the first instar. In our study, sociality was observed for 12 weeks. We examined how group size (singles, dyads and tetrads) affected weight gain and feeding behavior in juvenile *H. gigas*. Because we had observed extended cohabitation of juveniles in captivity, as well as a unique group feeding behavior (i.e., cluster feeding) we predicted that *H. gigas* spiderlings reared communally would grow faster than those reared in isolation.

METHODS

Test subjects were obtained from two different clutches of spiderlings produced by two wild-caught females collected in Cameroon and purchased from a commercial dealer (vouchers will be deposited at the American Museum of Natural History). The spiderlings remained in their communal sibling groups until we divided them into treatment groups. The treatment group sizes consisted of siblings placed as singletons, dyads or tetrads. The first clutch yielded seven replicates per group size and the second clutch yielded two replicates per group size. To differentiate individuals within groups, each spiderling (singletons included) was paint-marked on the dorsal side of the abdomen using Testors® enamel paint. At the beginning of the study, spiderlings from the two clutches differed in mass (Mean mg \pm 1 SD: Clutch 1; 42.8 \pm 14.2, $n = 49$, Clutch 2; 53.6 \pm 18.7, $n = 14$). Because spiderlings within clutches were randomly assigned to treatment groups, this difference in starting mass was not associated

with treatment group size (ANOVA on spiderling starting mass: Clutch, $F_{1,57} = 8.82$, $P = 0.004$; Treatment Group Size, $F_{2,57} = 1.74$, $P = 0.185$).

Group Size and Weight Gain.—Spiders were housed in translucent plastic 122 ml condiment containers in a 14 L: 10 D cycle. The room was kept at an average temperature of 26.6 °C (range: 23–31 °C) and average humidity of 44.1 % RH (range: 30–63%RH). Substratum was not provided in the rearing container in order to facilitate observation and collection of prey remains. The spiderlings were given approximately 2 ml of distilled water each week in the bottom of the container.

The spiderlings were fed once a week. Prey consisted of pre-killed (by freezing) crickets ranging in weight from 100–450 mg. All treatments received the same size class of cricket at each feeding. This cricket size insured that food would always be in overabundance, eliminating food competition between spiderlings. Pre-killed prey was offered so that very large prey items could be used, items too large for the spiderlings to subdue. In a pilot study it was determined that spiderlings would feed readily on pre-killed prey. Superabundance of prey was verified by the presence of uneaten prey remains, which were collected 24 hours after feeding.

Each spiderling was weighed to the nearest 0.1 mg in a tared plastic vial on an electronic balance before feeding and approximately 24 hours after feeding. The weights of the spiderlings were recorded for a period of 12 consecutive weeks. The average weekly weight gain was calculated within groups as was the coefficient of variation in weight gain for the last 4 weeks. Coefficients of variation are used to standardize variation in order to compare standard deviations of different sample sizes. A repeated measures ANOVA was used to assess the effect of group size on growth rates over the twelve weeks.

Behavioral Mechanisms.—Details of feeding behavior were observed from week 9 until the termination of the study at week 12. Behavioral observations were conducted to investigate any differences in time spent feeding between the spiders of the different sized treatment groups, any agonistic behaviors and occurrences of cluster feeding. Scan sampling was utilized to record the behavior of all spi-

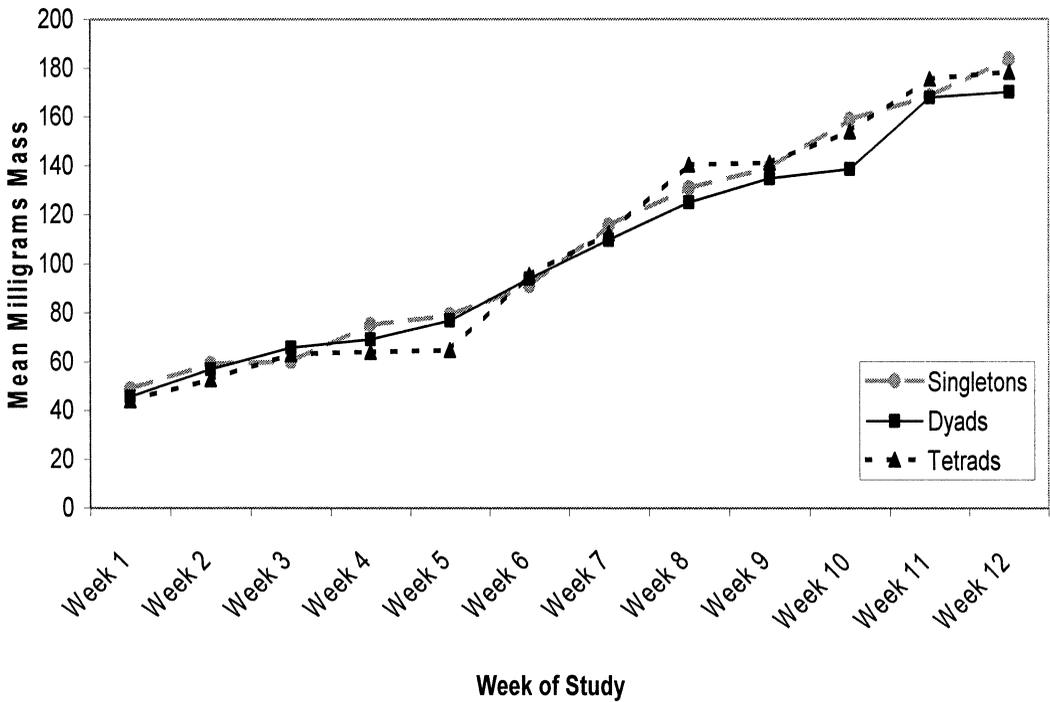


Figure 1.—Average weekly weight of *Hysteroocrates gigas* spiderlings from two different maternal clutches in three treatment group sizes (singletons, dyads and tetrads).

derlings during feeding. The frozen prey was introduced into each rearing container in the afternoon (between 1400–1600 hours). Scan samples were taken once every hour from the introduction of prey until midnight. Spiderlings were observed under red light after dark, unless differentiating the color marks of the spiderlings was difficult, whereupon dim white illumination was used until the scan was complete.

The frequency of feeding behavior was compared across the different group sizes. To compare feeding behavior and weight gain, the proportion of hourly intervals during which feeding was observed was arc sine square root transformed to normalize the data. The transformed proportion of hourly intervals during which feeding was observed correlated with percent weight gain using a one-tailed Pearson's r . A repeated measures ANOVA was used to determine differences in amount of time spent feeding among treatment groups. For all statistics an alpha level of 0.05 was used.

RESULTS

Group Size and Weight Gain.—For 12 weeks all groups of spiders gained weight at

about the same rate. We found no significant effect of rearing group size on mass (repeated-measures ANOVA ; $F_{1,2} = 0.08, P = 0.925$). The average weekly weights showed no distinguishable trend in any one group (Fig. 1). The variability in weight gain as expressed by the coefficient of variation for the last four weeks also showed no discernable trend for any one group (Fig. 2).

Behavioral Mechanisms.—We observed the eight replicates of singletons, eight replicates of dyads and the five replicates of tetrads that remained at the end of the eighth week (unexplained mortality led to the loss of replicates during the course of the study). We recorded these behaviors: Investigating, Feeding, Antagonizing, Grooming and Cluster Feeding. Investigating was defined as the spiderling approaching the prey, contacting the cricket with the spiderling's front legs, but not commencing in consuming the prey item. Feeding was defined as the spiderling contacting the cricket with its mouthparts. Antagonizing was defined as: 1) chase, one spiderling chasing another spiderling around the container, 2) kick, kicking another spiderling

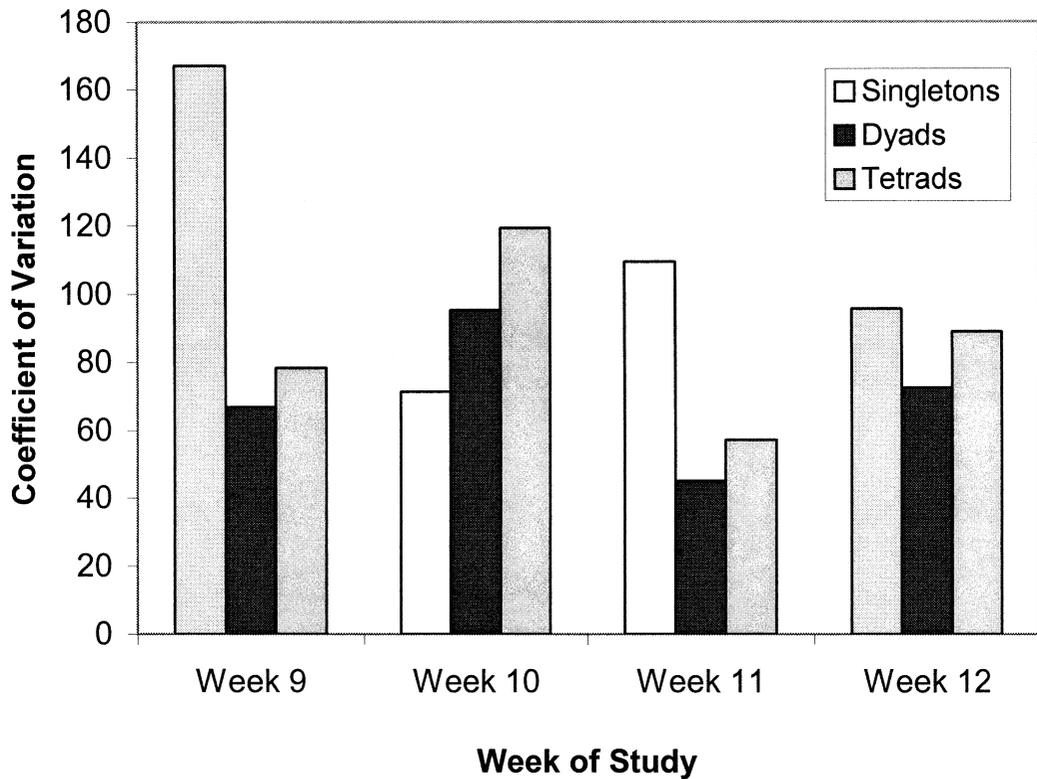


Figure 2.—Variability in weight gain in *Hysterocrates gigas* spiderlings for the final four weeks of the study. No difference in the coefficient of variation of percent weight gain was found between groups.

away from the cricket with its hind legs, or 3) take food, pulling the cricket away from the other spiderlings. Grooming was defined as a spiderling rubbing its legs together, over its abdomen, or over its cephalothorax. Cluster Feeding was defined as multiple spiderlings feeding on the same prey item at the same time, legs intertwined and no movement observed.

The most common feeding behavior we ob-

served among tetrads was spiderlings feeding individually (Table 1). The next most common behavior was two spiders feeding at the same time, but not in contact with each other. Cluster feeding was only observed on 7 occasions (6.9% of observations). All occurrences of cluster feeding were observed in tetrads. Tetrads cluster-fed in groups of two, three or four.

We found a correlation between individual weight gain and the percent of observations

Table 1.—Feeding group sizes for *Hysterocrates gigas* spiderlings in tetrads. Tetrads were observed to feed in different sized groups. Number of occurrences lists number of hourly intervals.

Feeding groups in tetrads	Number of groups in which incident was observed	Number of occurrences	Percentage of occurrences
One spider feeding	5	79	77.5
Two spiders feeding separately	5	15	14.7
Three spiders cluster feeding	3	3	2.9
Four spiders cluster feeding	3	3	2.9
Two spiders cluster feeding	1	1	1.0
Four spiders feeding separately	1	1	1.0

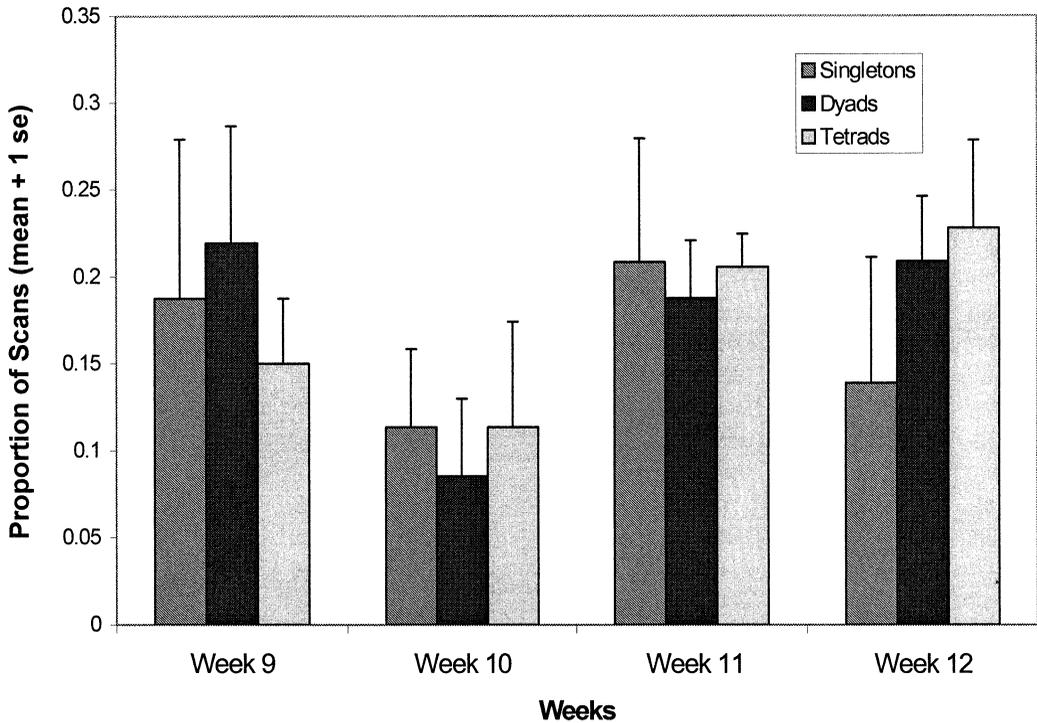


Figure 3.—Proportion of hourly intervals during which *Hysterocrates gigas* spiderlings were observed feeding by group size per week (mean +1 standard error).

during which an individual was observed feeding (Pearson's r : singletons, $n = 32$, $r = 0.488$, $P = 0.002$; dyads, $n = 64$, $r = 0.477$, $P < 0.001$; tetrads, $n = 80$, $r = 0.176$, $P = 0.059$). Using the Bonferroni adjustment for multiple correlations, an alpha level of 0.017 was set. For both the singles and the dyads, proportion of time spent feeding was significantly correlated with percent weight gain. No significant correlation was found in the tetrads.

We found that the proportion of time observed feeding was significantly different over the four weeks for the three treatment groups (repeated-measures ANOVA: $F_{1,3} = 3.077$, $P = 0.035$), showing that individual spiders differed each week in the amount of time they were observed feeding. However, the between-groups comparison indicated that the three treatment groups did not significantly differ from each other in proportion of time observed feeding ($F_{1,6} = 0.754$, $P = 0.609$) (Fig. 3).

A curious difference in mass was noted between individuals in dyads. Coefficients of

variation of the spiderlings' final body weights at 12 weeks of age were used to compare the differences in spider size between dyads and tetrads. However, no significant difference was found between coefficients of variation of body mass of dyads and tetrads at week 12 ($t = 0.781$, $df = 9$, $P = 0.46$). We did find a significant positive correlation of coefficient of variation of final body weights and the number of aggressive incidents observed (Spearman's $\rho = 0.492$, $P = 0.044$, $n = 13$).

DISCUSSION

Over the 12 weeks of the experiment, spiders in each treatment group exhibited similar mass. We had anticipated a positive effect of group rearing based on the putatively adaptive cluster feeding behavior we observed because this feeding configuration appears to facilitate group feeding. So, why didn't we find a growth-related benefit associated with communal rearing conditions? It may be that the superabundance of food provided by design allowed all spiderlings to feed to satiation.

Krafft et al. (1986) demonstrated that conspecific tolerance in juveniles of *Coelotes terrestris* (Wider 1834) could be lengthened when there is an abundant supply of food. Similarly, Rypstra (1986) found that *Achaearanea tepidariorum* (C.L. Koch 1841), a solitary species, remained sociable longer when prey was abundant.

Small and large spiders in the dyads did not differ in the number of hourly scans observed feeding. However it was noted that the larger spider usually fed before its smaller counterpart if a large size discrepancy was present. Perhaps by feeding first the larger spider gained more nutritionally by feeding until satiation. This behavior could be seen as domination, but the smaller spider did feed later and for the same span of time. No difference was seen in the number of hourly intervals observed feeding within the individuals in tetrad groups. The most common feeding display in this treatment group was one spider feeding at a time.

As expected, weight gain correlated positively with hourly intervals observed feeding. Singletons, dyads, and tetrads were all observed feeding during the same number of hourly intervals. If there were some foraging advantage associated with feeding in groups, then individuals in groups of four should gain as much weight, or more, as individuals reared alone and spend less time feeding. Since this was not observed, there may be reasons (other than improved feeding efficiency) for social behavior to exist among young *H. gigas*. These benefits may include a reduced risk of predation, and the advantage of cooperatively seizing live prey.

Tetrads of *H. gigas* spiderlings in this study exhibited cluster feeding only 6.9% of the time. Cluster feeding is a communal feeding behavior that involves the spiders huddling with their legs intertwined. This is an unusual behavior that has been documented in *Aebutina binotata* Simon 1892, a communal cribellate spider (Aviles 1993). Adult *A. binotata* females captured and communally fed on large prey items such as cockroaches and beetles; juveniles fed when the adults left the prey (Aviles 1993). Jantschke and Nentwig (2001) observed spiderlings of the mygalomorph spider, *Ischnothele caudata* feeding together on a prey item provided by the mother, but there was no mention of the

specific cluster feeding behavior such as we observed in *H. gigas*. *Ischnothele caudata* juveniles will also cooperate in catching larger prey for up to 18 weeks. Reichling and Gutzke (unpubl.) found *H. crassipes* spiderlings clustering around food items caught by the mother.

In our study there was only one instance of cannibalism in 18 groups: a spiderling in a tetrad killed its three siblings. Given the time span of the experiment and the number of group-reared *H. gigas* involved, we can tentatively conclude that cannibalism is rare in sibling groups of this species. The occurrences of agonistic behaviors in general may have been undercounted due to the use of scan sampling, because probabilities of recording temporally short displays of hostility or facilitation are low. Although agonistic behavior was observed, more lengthy focal observations might have better documented these interactions. Agonistic displays were similar in incidence in tetrads and dyads but did not occur in higher frequency as expected in tetrads, where more spiders were forced to interact. Aggression was not more readily observed between similarly-sized spiders, contrary to the group-living pholcid spider *Holconemus pluchei* (Scopoli 1763) where fights over prey were most intense between spiders of comparable size (Jakob 1994). Instead, aggression was positively correlated with the coefficient of variation of final weights, showing that replicates containing spiders with large size discrepancies either engaged in more aggressive displays or aggression led to large size discrepancies. This concurs with findings on the social spider *Anelosimus eximius* in which larger females commandeer prey captured by smaller females (Ebert 1998).

Hysteroocrates gigas spiderlings exhibited an unusual level of mutual tolerance, but this sociality did not apparently result in facilitation of feeding behavior, despite the distinctive cluster feeding posture we observed. Tarantulas, like all spiders, are generally cannibalistic beyond a short period of mutual toleration when young. *Hysteroocrates* may be among the most sociable of theraphosid spiders. We have observed that *H. gigas* spiderlings in captivity will cohabit until several months of age. However, in a pilot study we conducted, *H. gigas* spiderlings that had been

first separated and then placed in social groups engaged in high levels of cannibalism, indicating that the suppression of cannibalism may depend on keeping the spiderlings in social groups after hatching. Cohabitation of sibling groups has been observed in at least three other mygalomorph spider taxa: *Nemesia cementaria* (Buchli 1969), *Heterothele darcheni* (Darchen 1967) and *Pamphobeteus* sp. Pocock 1901 (Cocroft & Hambler 1989). It remains to be seen how widespread this behavior is.

For social behavior to evolve organisms must have something to share, in the case of spiders this is a web or retreat, as well as an abundance of prey (Shear 1970; Rypstra 1993; Leborgne et al. 1998; Jantschke & Nentwig 2001). Contrary to Jantschke and Nentwig's (2001) claim that all social spiders must have a shared web for information transfer, very few mygalomorphs build webs. They construct burrows and in some cases the young will stay in the maternal burrow for extended periods of time (Buchli 1969). The burrow may promote sociality in the same way as a prey capture web. The increased level of sociality observed in this tarantula may result from the selective advantages accrued from sharing the deep maternal burrow and receiving protection from predators and harsh environmental conditions. *Hysteroocrates* exhibits a high level of mutual tolerance and even unique feeding behaviors associated with prey sharing, making it an unexpectedly social tarantula. However, we have shown that group size does not influence the rate of growth.

ACKNOWLEDGMENTS

We thank M. Harless and R. Blatchford for assistance in collecting data. We thank S. Reichling, M. Hodge, R. West, M. Ashton and two anonymous readers for their comments on an earlier draft of this manuscript. And finally, we thank Dr. Bruce and Mrs. Janet Johnson for their donation to the J. H. Barrow Field Station Research Fund, which made this research possible.

LITERATURE CITED

- Aviles, L. 1993. Newly discovered sociality in the neotropical spider *Aebutina binotata* Simon (Dictynidae?). *Journal of Arachnology* 21:184–193.
- Aviles, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498. *In* The Evolution of Social Behavior in Insects and Arachnids. (J. C. Choe & B. J. Crespi, eds.). Cambridge University Press, Cambridge, England.
- Buchli, H.R. 1969. Hunting behavior in the Ctenizidae. *American Zoologist* 9:175–193.
- Cocroft, R.B. & K. Hambler. 1989. Observations on a commensal relationship of the microhylid frog *Chiasmocleis ventrimaculata* and the burrowing theraphosid spider *Xenesthis immanis* in southeastern Peru. *Biotropica* 21:2–8.
- Curtis, J.T. & J.E. Carrel. 1999. Social behavior by captive juvenile *Kukulcania hibernalis* (Araneae: Filistatidae). *Bulletin of the British Arachnological Society* 11(6):241–246.
- Darchen, R. 1967. Biologie d'une mygale gabonaise nouvelle: *Macrothele darcheni* Benoit (Araneida, Dipluridae). *Biologia Gabonica* 4:253–257.
- Ebert, D. 1998. Behavioral asymmetry in relation to body weight and hunger in the tropical social spider *Anelosimus eximius* (Araneae, Theridiidae). *Journal of Arachnology* 26:70–80.
- Jantschke, B. & W. Nentwig. 2001. Sub-social behaviour in the diplurid *Ischnothele caudata* (Araneae, Dipluridae). *Bulletin of the British Arachnological Society* 12:12–16.
- Jakob, E.M. 1994. Contests over prey by group-living pholcids (*Holocnemus pluchei*). *Journal of Arachnology* 22:39–45.
- Krafft, B., A. Horel, & J.-M. Julita. 1986. Influence of food supply on the duration of the gregarious phase of a maternal-social spider, *Coelotes terrestris* (Araneae, Agelenidae). *Journal of Arachnology* 14:219–226.
- Leborgne, R., T. Cantarella, & A. Pasquet. 1998. Colonial life versus solitary life in *Cyrtophora citricola* (Araneae, Araneidae). *Insectes Sociaux* 45:125–134.
- Marshall, S.D. 1996. Tarantulas and Other Arachnids. Barron's Educational Series Inc., Hauppauge, NY.
- Reichling, S.B. & W.H.N. Gutzke. Unpublished Manuscript. Maternal food-sharing by the African baboon spider *Hysteroocrates crassipes* affects juvenile growth.
- Rypstra, A.L. 1986. High prey abundance and a reduction in cannibalism: the first step to sociality in spiders (Arachnida). *Journal of Arachnology* 14:193–200.
- Rypstra, A.L. 1993. Prey size, social competition, and the development of reproductive division of labor in social spider groups. *The American Naturalist* 142(5):868–880.
- Shear, W.A. 1970. The evolution of social phenomena in spiders. *Bulletin of the British Arachnological Society* 1(5):65–76.

Smith, A.M. 1990. Baboon Spiders: Tarantulas of Africa and The Middle East. Fitzgerald Publishing, London.

Uetz, G.W. & C. Hieber. 1997. Colonial web-building spiders: Balancing the costs and benefits of group-living. Pp. 458–475. *In* The Evolution of

Social Behavior in Insects and Arachnids. (J. C. Choe & B. J. Crespi, eds.). Cambridge University Press, Cambridge, England.

Manuscript received 31 July 2002, revised 22 August 2003.