LACK OF TASK DIFFERENTIATION DURING PREY CAPTURE IN THE GROUP LIVING SPIDER *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

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ABSTRACT.   *Stegodyphus mimosarum* of the African savanna form communal nests consisting of few to several hundred individuals and co-operate in nest construction and maintenance, brood care and prey capture. We tested large and small individuals for differential responses to different prey risk types. To date, there has been no conclusive evidence of tasking in these or other social spiders. If tasking occurs, small spiders should approach and attempt to subdue less dangerous prey items such as flies more often than the more dangerous prey items such as bees. Hungry individuals were significantly more willing to venture out of the nest refuge and thus accept the costs associated with prey capture than were satiated spiders. Apparent depletion of poison in previous prey captures did not significantly affect an individual's response to a prey item. Spiders treated more dangerous prey (bees) more carefully than less dangerous prey (flies), but there was no difference in the response of large versus small spiders to prey. The two-way interaction between spider size and prey type was never statistically significant, indicating a lack of tasking in this species.

Keywords: Foraging, co-operation, social, communal

Recent approaches to eusociality and co-operative breeding suggest that these two concepts should not be treated as discrete phenomena. Rather they should be viewed as points along a continuum uniting fundamentally similar social systems, whose main differences lie in the distribution of lifetime reproductive success among group members (Keller & Reeve 1994; Sherman et al. 1995). The social spiders may be best placed near the co-operative breeding end of the scale, in which many individuals in the colony may reproduce (Lubin 1995). Unlike social insects, no co-operative breeding spiders studied to date have shown evidence of either ethological or morphological caste systems (Tietjen 1984; Ward & Enders 1985; Lubin 1995; but see Rypstra 1993). Nevertheless, there are several activities within the spider communities which may be subject to division of labor. These include prey capture (the focus of this paper), brood care, web-building and nest maintenance. Task specialization could increase the overall efficiency of performance of these activities, thereby increasing colony success (Oster & Wilson 1978; Lubin 1995).

Stegodyphus mimosarum Pavesi 1883 are social spiders which inhabit dry African savanna. They form communal nests containing few to several hundred individuals which co-operate in nest construction and maintenance, prey capture and brood care (Seibt & Wickler 1988). A great variety of prey is captured in the field ranging from small flies to large grasshoppers (Ward & Enders 1984; pers. obs.). By leaving their refuge (nest) in order to approach a prey item, spiders become vulnerable to predators and parasites and also run the risk of becoming injured by large prey.

Given individual variation in size there may be differential effectiveness at prey capture. Under such circumstances it may be advan-

tageous for tasking among individuals, with each individual allocating its resources to the most effective use. Furthermore, we expect tasking to evolve under either an individual selection or group (kin) selection argument. We tested the hypothesis that prey capture is subject to task differentiation, with tasks determined by spider size in relation to danger (handling difficulty) posed by the prey. We predicted that larger spiders would approach more dangerous prey, while small individuals would avoid large prey in favor of smaller, less dangerous prey items. Note that the range of prey items used in this experiment was well within a size that more than one colony member would share in feeding. Only very small items are eaten by single spiders. Note also that not all individuals feed on every prey item.

The test that we provided may be confounded by two factors: (1) motivation differences due to time since previous feeding; and (2) depletion of poison from previous capture attempts. We tested whether these may be confounding factors by separate experiments using a similar design.

Only juvenile female spiders were used in this study. Eight active *S. mimosarum* nests were removed during March and April 1997 from the Weenen (28°50′S; 29°40′E) and Itala (31°13′E; 27°31′S) Game Reserves in KwaZulu-Natal. They were held in the animal house at the University of Natal (Durban). The nest is usually built around a central branch which functions as a support for the entire structure. These colonies were divided into smaller colonies using individuals from the same original nest, and placed in glass jars together with small *Acacia* branches. The number of spiders in the colony was determined for each experiment. The colonies were then left for about 7 days to provide time to settle into a colony and construct a retreat and capture web. The experiments were performed indoors under daylight conditions, and spiders were housed in rooms with windows allowing natural light cycles. During the task experiment (see below) a desk lamp was placed near the colonies to increase spider responsiveness. The lamp was turned on 0.5 h before observations, and turned off after observations (all experimental groups treated equally). The experiments were carried out from May–September 1997.

The colony sizes that we established were relatively small at 4–6 spiders (see below). Although *S. mimosarum* colonies can range up to several hundred individuals, it is common to find nests of fewer than 10 spiders. This is particularly so at colony foundation. Examining the payoffs of individual strategies in small group size is the essence of the study of the evolution and maintenance of sociality. We believe that although the colony sizes chosen for this study are at the small end of the size distribution, they do reflect natural circumstances, and particularly, reflect critical colony sizes in terms of individual selection of strategies.

Effect of hunger on spider response.— Ten spider colonies, each consisting of six spiders, were established. Spiders were marked on the abdomen using paint-pens, with individuals in a colony receiving the same color. Five colonies were presented with a house fly *Musca domestica* on a daily basis for a period of 3 days. The other five colonies remained without food for 7–14 days prior to commencing the experiment.

Colonies consisting of 8 spiders were used to construct pre-existing webs for the experiment. Once web construction was complete, these spiders were removed. This was done to ensure that both the hungry and the satiated spiders were equally unfamiliar with the web into which the prey item was placed. Spiders which construct their own capture web are expected to be more familiar with the architecture of the web and therefore more capable of directly approaching the prey item (Downes 1994).

Three spiders from each colony were then placed into a glass jar containing a pre-existing web. A house fly was then placed in each capture web. A house fly was used as the prey item so as to exclude the possible influence of danger on the spider's response. The individual which approached the prey first and the amount of time taken before the first spider reached and bit the prey item was recorded.

Mann-Whitney U-tests were used to detect significant differences in the approach time between satiated and hungry spiders. Each colony was an independent sample with the fastest spider to emerge of the 3 hungry spiders and the fastest to emerge of the three sated spiders being used for each colony. G-tests were used to determine significant differences

in the number of responses from hungry and satiated spiders. The counts were tested against a 50:50 expectation.

Effect of prior capture attempt on spider response.—Eight colonies, each with four individually marked spiders, were established in glass jars as described earlier. A house fly was placed in the capture web and the subsequent events were recorded. We noted which spider was the first to bite the prey and the time at which this occurred. The spiders were left to bite, and presumably inject venom and enzymes, until the first spider had been biting for a time period of not less than five min but not exceeding 15 min. Spiders were allowed sufficient time to inject the prey with venom and enzymes but not to feed. This is based on observations of another social species, *S. dumicola* Pocock, 1898, where there was little or no mass gain by spiders during the first 20–30 minutes of ''feeding'' (Whitehouse & Lubin 1999; Amir et al. 2000).

After the designated time period, the prey item was removed. The colony was immediately presented with another prey item and subsequent spider behavior was recorded and timed. This was repeated a third time with a third prey item. Immediate presentation of the second and third prey items was necessary in order to limit the amount of time that the spider had to recover from the previous attack and to replenish its venom supply. The identities of the individuals that bit the first, second, and third prey items were noted to determine whether the spider that approached the second or third prey item was the same individual that approached the first prey item. If venom and enzyme availability affects a spider's readiness to approach and attempt to subdue prey, or if there is physical or sensory fatigue or adaptation, the individuals that had previously attacked the prey would be unlikely to approach subsequent prey.

Spiders' responses were classified into two groups: (1) spiders that approached more than one prey item and were assumed to show no venom depletion or fatigue; and (2) spiders that approached only a single prey item and in which depletion or fatigue may have occurred. These data were analyzed using a G-test (with William's correction) on the counts of these two classes.

Task differentiation in *S. mimosarum*.—Sixteen independent colonies were estab-

lished, with the experiment run as two sets of eight colonies. Each colony consisted of two large and two small individuals, and each spider in each colony was marked using a paintbrush. The first set of replicates was carried out from 6 June–14 July 1997, while the second set of replicates was carried out from 17 June–15 September 1997. Each colony was presented with each prey type three times with the median response to these being used as the measure of the response of that colony to that prey type. This served to increase the internal validity of the results without pseudoreplication affecting the power of the test because each colony was represented once for a response for each spider size to each prey type.

Each colony was randomly presented with two different prey items which represented different degrees of danger. Less dangerous prey was represented by a housefly, and more dangerous prey was represented by a honey bee *Apis mellifera*. Prey items were presented either every 24 h or every 48 h, depending on the amount of capture web present. On several occasions, previous prey captures had resulted in extensive web damage and thus the colonies were not fed until the web was sufficiently repaired. This occurred within 2–7 days after the previous prey capture. Because we combined responses using the median of three replicates prior to analysis, such variation in prey presentation would not bias the data. Each colony was observed from the time of prey presentation until the prey had been subdued to the point at which the prey item could no longer move or escape from the spiders. Spider behavior was assigned to the following categories: (1) spider approached the prey. This behavior included any movement spiders made towards the prey. (2) Spider made contact with and held onto the prey. This behavior was allocated to the spider each time the spider touched or held on to the prey item, but did not actually bite the prey item. (3) Spider made contact with the prey and bit it. (4) Spider retreated. This behavior included any movement of the spider away from the prey item.

In some cases involving honey bees, major web destruction by the bees resulted in them being able to escape. In these cases, bees were immediately placed back into the capture web and timing resumed. If, however, a bee managed to escape more than five times within

half an hour, the experiment was terminated and repeated at a later date. The amount of time the prey item took to escape ranged between 7–90 min depending on the size of the capture web the spiders had constructed. This time period was sufficient to enable us to ascertain which spiders approached more frequently, and which spiders made contact with the prey.

The results of these experiments were analyzed using a two-factor analysis of variance (ANOVA) with an interaction term. This term represents the interaction between spider size and prey type, and is critical in interpreting whether task differentiation occurred. A significant interaction term indicates task differentiation, as it suggests that large and small individuals respond differently to the two prey types. We analyzed seven independent variables using ANOVA: (1) handling time that was the sum of the mean amount of time which a spider spent approaching, holding and biting the prey item. This variable was analyzed first, as it represented the most likely variable to reveal task differentiation in these colonies. (2) The mean number of times small and large spiders approached the prey item. (3) The mean number of times small and large spiders bit the prey item. (4) The mean time large and small spiders spent in contact with the prey item. (5) The mean time spiders spent biting the prey. The final two variables related to the reluctance of the spiders to approach a prey item. These included: (6) the mean number of retreats; and (7) the mean amount of time spent retreating from and not approaching the prey item. The independent factors included in the ANOVA were prey type (bee and fly) and the spider size (large and small), with an interaction term.

Given that we analyzed the same data set seven times, we performed a Bonferroni adjustment to the data (Schork & Remington 2000). In this case we changed the critical p-value for rejection of the Null Hypothesis from 0.05 to 0.007 (0.05/7).

RESULTS

Effect of hunger on spider response.— The degree of satiation did affect a spider's willingness to approach and attempt to subdue a prey item (G-test: $Gadj = 5.44$, $df = 1$, $P < 0.05$). Hungry spiders were significantly more likely to approach a prey item than sa-
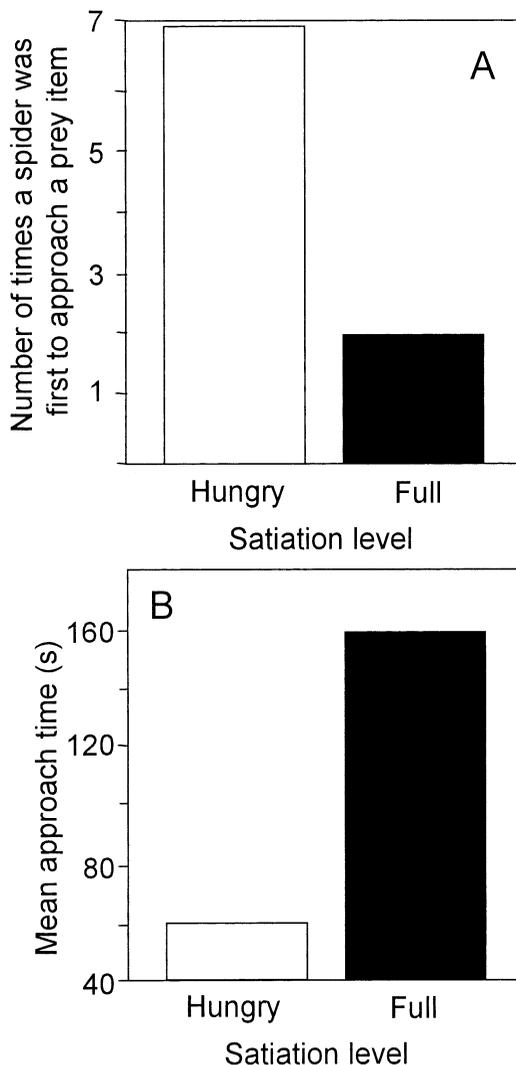

Figure 1.—Effect of satiation level on response of spiders to house flies placed in their webs. (A) First approach to prey item by either category and (B) mean time to approach of unfed (hungry = open bars) and fed (full = closed bars) spiders. $n = 9$ colonies.

tiated spiders and therefore this factor is important in driving the prey capture process (Fig. 1A). Hungry spiders responded faster to the prey item than satiated spiders. The mean approach time for satiated spiders was 159 sec (range: 60–258) while the mean approach time for the hungry spiders was 60 sec (range: 8–88) (Mann Whitney-U test; $Z = -1.84$, $n = 9$, 1-tailed $P = 0.03$) (Fig. 1B).

Effect of prior capture attempt on spider

response.—Given that there were four spiders in each colony, we expected each individual to come out 25% of the time. When comparing the second prey item to the first, in 2/8 (25%) colonies it was the same spider responding to both prey items. When comparing the third prey item to the second prey item, in 3/8 (38%) colonies it was the same spider responding to both prey. Spiders do not appear to alternate in approaching consecutive prey items (Gadj = 2.18, df = 1, $P > 0.05$). This suggests that enzyme or venom depletion did not occur, nor did spiders show fatigue or sensory adaptation.

Task differentiation in social spiders.—Using the more conservative statistical interpretation analysis (for all values above $P = 0.007$, the Null Hypothesis of no difference was accepted), only three dependent variables showed significant main effects. In all cases there was a significant Prey Type effect on handling time (Fig. 2) (a combined variable indicating time approaching, in contact with, and biting the prey item), mean number of contacts (Fig 3A), and mean number of retreats (Fig. 4). Spiders spent significantly more time handling, had significantly more contacts with, and showed significantly more retreats from the dangerous bee than the less dangerous fly. These results were not effected by spider size (main effect spider size $P > 0.007$ in all cases).

However, there was one analysis where spider size was marginally not significant. There was a trend for large spiders to bite more often (regardless of prey type). We have interpreted this as not statistically significant based on a Bonferroni adjusted critical p-value. However, under a conventional analysis with P-critical (alpha) = 0.05, this result would be interpreted as statistically significant.

In all of the above tests, the two-way interaction between spider size and prey type was not statistically significant ($P > 0.007$ in all cases). Thus, spiders did not modify their behavior toward different prey types in accordance with their body size differences.

DISCUSSION

The degree of hunger experienced by the spider determined the spider's willingness to approach prey. Hungry spiders responded significantly more often and approached the prey more quickly than satiated spiders. The degree
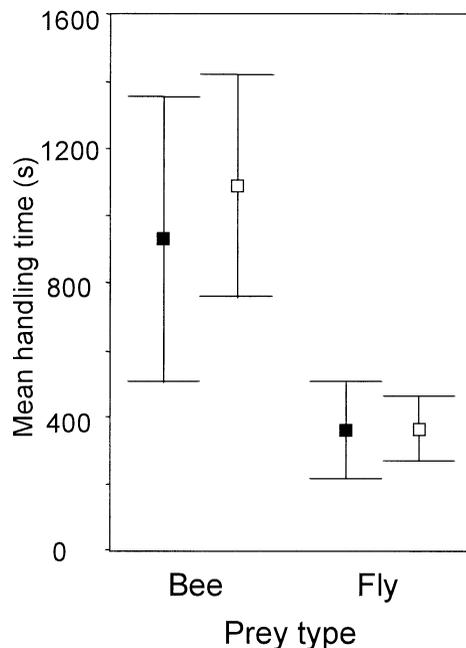

Figure 2.—Effect of prey risk on handling time by small (black box) and large (white box) spiders. Mean ± 95% Confidence limits. Sample size = 16 colonies. Values for each colony are the average of three measurements per spider size per prey type. Bee = dangerous prey; Fly = safe prey. ANOVA results: prey type: F = 21.16, $P = 0.001$; spider size: F = 0.34, ns; interaction term: F = 0.3, ns. Note that critical P-value (alpha) = 0.018 through Bonferoni adjustment. Df = 1, 60 in all cases.

of hunger is one of the basic factors determining the feeding occurrence and the amount of food an organism ingests. In spiders, the food ingested stays in the gut for a long period of time and a wide range of hunger levels can develop (Nakamura 1987). Therefore, spiders may assess their level of hunger and trade off the need to capture prey against the risks associated with prey capture. Hunger stress increases a spider's willingness to accept the risks and energy expenditure associated with prey capture (Lubin & Henschel 1996).

Based on our experimental analyses we concluded that behavioral tasking in prey capture does not occur in *S. mimosarum.* The only hint of tasking was in the greater number of bites by large spiders (interpreted here as a non-significant difference). There may be therefore a hint that larger spiders are dedicating more effort to prey capture than smaller spiders, whereas smaller spiders may allocate
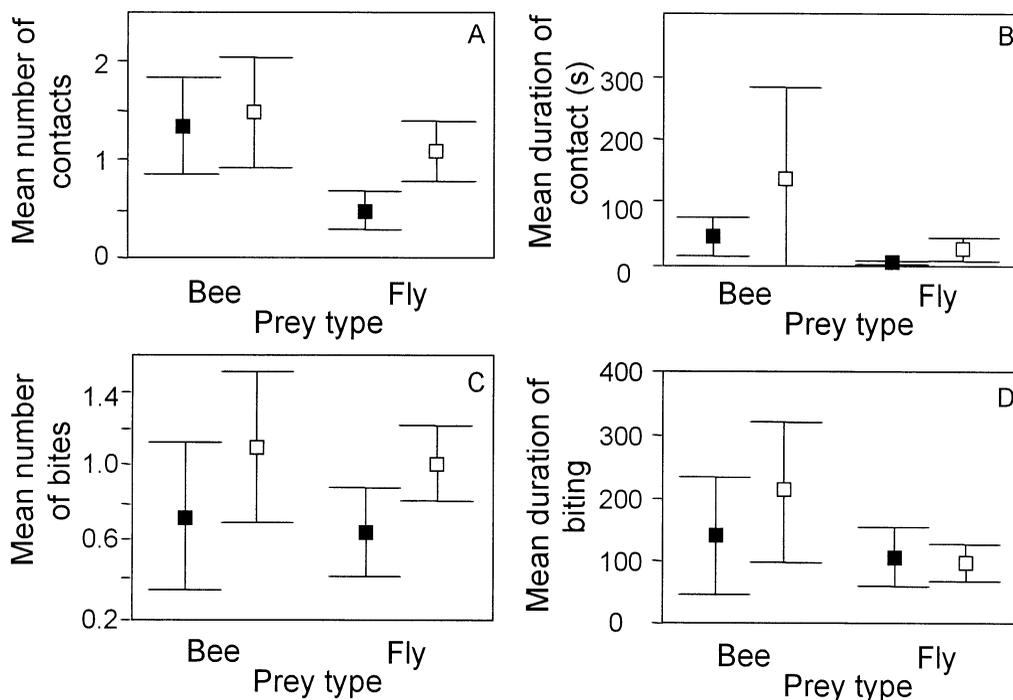
Figure 3.—Effect of prey risk on propensity to attack by small (black box) and large (white box) spiders. Mean ± 95% confidence limits of: (A) number of contacts. ANOVA results: Prey type: F = 10.3, P = 0.002; spider size: F = 3.7, ns; interaction term: F = 1.4, ns. (B) Duration of contacts. ANOVA results: Prey Type: F = 4.67, ns (P = 0.035); spider size: F = 2.49, ns; interaction term: F = 0.99, ns. (C) Number of bites. ANOVA results: Prey type: F = 0.32, ns; spider size: F = 5.95 ns (P = 0.018); interaction term: F = 0, ns. (D) Duration of bites. ANOVA results: Prey type: F = 4.07, ns (P = 0.048), spider size: F = 0.64, ns; interaction term: F = 1.2, ns. Sample size = 16 colonies. Values for each colony are median of three replicates per spider size per prey type. Bee = dangerous prey; Fly = safe prey. Note that critical P-value (alpha) = 0.018 through Bonferoni adjustment. Df = 1, 60 in all cases.

relatively more effort to other activities. This aspect needs to be further investigated by examining, for example, web building. Overall, we found no statistically significant indication of behavioral tasking, either within foraging or among foraging and other behaviors.

Task differentiation or division of labor has been observed in several species of Hymenoptera and Isoptera (Hermann 1979; Seeley 1985; King's College Socio-biology Group 1982; Lin & Michener 1972), as well as lions (Stander 1992), and mole-rats (Jarvis 1981; Jarvis et al. 1994). No evidence of task differentiation was found for *S. mimosarum,* nor has previous work on these spiders identified any form of division of labor in social *Stegodyphus* (Ward & Enders 1985; Cobby 1981 cited in Seibt & Wickler 1988). The social theridiid spider, *Achaearanea wau* Levi, also showed no division of labor with respect to

foraging and other web-related activities (Lubin 1995). Darchen and Delage-Darche (1986) stated that although the presence of castes in social insects is a fundamental characteristic of eusociality, any attempt to find them in social spiders has been unsuccessful.

There is some support for tasking in *Anelosimus eximus* Simon, which may have reproductive division of labor (see Rypstra 1993). In *A. eximus* not all individuals reproduce, and under conditions where there is competition for resources, dominance asymmetries result in larger spiders gaining access to more resources, maturing faster, and reproducing (Rypstra 1993). As a consequence of lack of access to resources, small individuals do not breed. However, there is no suggestion that the small spiders forego reproduction in order to undertake some other task that would benefit them or, in the case of *A. eximus,* the
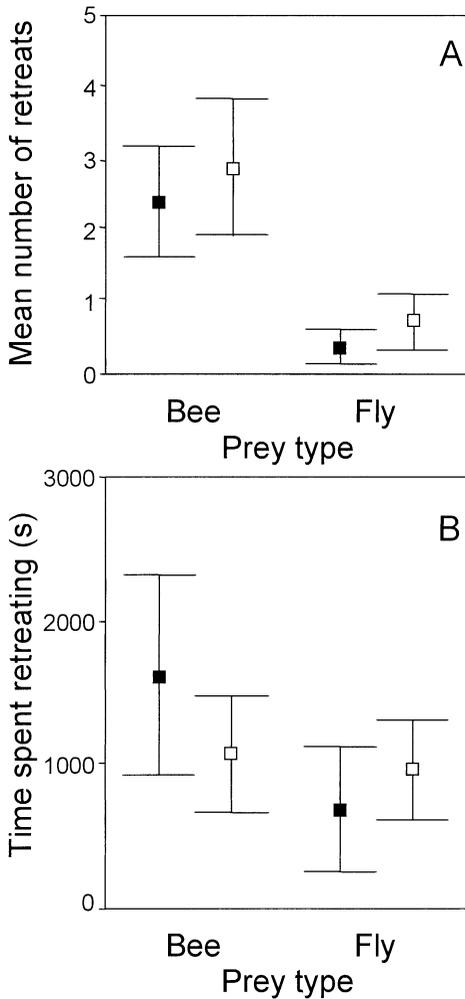
Figure 4.—Effect of prey risk on propensity to retreat by small (black box) and large (white box) spiders. Mean ± 95% Confidence limits of: (A) number of retreats. ANOVA results: Prey type: F = 40.79, $P < 0.001$; spider size: F = 1.66, ns; interaction term: F = 0.04, ns. (B) Time spent retreating. ANOVA results: Prey size: F = 4.79, ns; spider size: F = 0.3, ns; interaction term: F = 2.91, ns. Sample size = 16 colonies. Values for each colony are the average of three measurements per spider size per prey type. Bee = dangerous prey; Fly = safe prey. Note that critical *P*-value (alpha) = 0.018 through Bonferoni adjustment. Df = 1, 60 in all cases.

related colony. We believe that this is not so much an example of selection for behavioral tasking but rather an unselected consequence (effect) of dominance asymmetries (Lubin 1995).

In conclusion, task differentiation with respect to foraging does not appear to exist in these social spider colonies. It should however be noted that, due to the design of the experiment, the behavior of the spiders was observed only until the stage at which the prey was completely subdued. Future work should examine the possibility of role differentiation in other activities such as web construction or brood care.

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