

## THE INFLUENCE OF STARVATION ON DISPERSAL IN THE SOCIAL SPIDER, *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

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**ABSTRACT.** Colonies of the social spider, *Stegodyphus mimosarum*, are philopatric and inbred, with limited dispersal capabilities. Colony founding events by mature males and females have been observed periodically. We set out to test the influence of food on the spiders' readiness to leave a colony. Thirty colonies (40 spiders in each) were established under laboratory conditions and confined within netting. For 31 days, 15 colonies were fed daily *ad libitum*, so that the mean amount of food available was greater than the mean requirements of the colony. The other fifteen colonies were starved. The netting was then removed, permitting emigration and movement from colonies was noted for two weeks. Following risk sensitivity theory, we expected more spiders to leave the unfed colonies due to starvation. However, a significantly higher absolute number of spiders left colonies where food was abundant. While fewer spiders left unfed colonies, more of these spiders died, such that the relative number of spiders remaining at the end of the trial was not significantly different between treatments. Even when they were starved, the decision to leave a colony was not based on a lack of food. Low food availability increased mortality, yet it did not alter the remaining spiders' decision to move. Therefore the decision to move is based on factors beyond prey availability, which may include the state of maturity of the spiders, the motivational state, the high cost of migration and reserves.

**Keywords:** Colony founding, food availability, risk sensitivity

*Stegodyphus mimosarum* Pavesi 1883 and *S. dumicola* Pocock 1898 are social spiders that inhabit dry thornbush country in southern Africa (Kraus & Kraus 1988). The life cycle, growth rate and seasonal development of *S. mimosarum* are discussed elsewhere (Crouch & Lubin 2000; Seibt & Wickler 1988a & b).

The low genetic diversity of social spider colonies, (Johannsen & Lubin 1999; Smith & Engel 1994) together with their characteristically patchy distribution, is an indicator of poor dispersal capabilities (Henschel et al. 1995). Further, the high cost associated with dispersal greatly reduces the chances of successful emigration (Crouch et al. 1998; Seibt & Wickler 1988a). Most dispersal has been observed over relatively short distances, i.e., from 1–26 m (Henschel et al. 1995 in *S. dumicola*). However, distances between patches of nests of *S. mimosarum* (and *S. dumicola*) are beyond the spiders' walking range (Seibt & Wickler 1988a), which suggests that additional methods of dispersal exist. Periodic dispersal events have been observed (Crouch et

al. 1998; Seibt & Wickler 1988a) and raised new questions about emigration. Dispersal events seem to be infrequent; dependent on the state of maturity of the spiders (Crouch et al. 1998), the season (Crouch & Lubin 2001), and on specific environmental conditions, e.g., strong, gusty winds (Crouch et al. 1998).

However, even for poor dispersers, when resources in a particular area become depleted, the animals face extinction if they do not leave and find another location before the resources are completely exhausted. Ultimately, most animals disperse to obtain more food or space, such as soon after juveniles are born / hatch out (founder hypothesis), or to escape predation, starvation or high parasite loads (escape hypothesis) (Decae 1987). For spiders, the proximate reasons driving the decision to disperse include access to resources (Ward 1986), the season (wind, temperature) (Crouch & Lubin 2001), and the size of the animal (Miller & Miller 1991). In addition, the developmental stage of the animal (most spiders disperse as juveniles) (Foelix 1996),



its internal state of readiness (e.g., mature males and females) (Seibt & Wickler 1988a) are contributing factors.

Access to resources may be influenced by the mean long-term rate of food available and by variation in intake (Milinski & Parker 1991). Variability in access to resources may be influenced by time, season, position and intra-group competition, so that some spiders obtain a higher quantity of food than others. Consequently, there would be a range of spider sizes within the retreat (Ulbrich et al. 1997; Ward 1986). The influence of variability in access to resources on dispersal was examined in a previous experiment. We found no significant increase in the number of spiders leaving with increasing group size (Bodasing et al. 2001). The mean amount of food obtained by each colony is influenced by nest location (Biere & Uetz 1981), prey availability (Miyashita 1991; Schneider 1996) and season (Crouch & Lubin 2001). Indeed, the mean amount of food obtained per spider determines spider size and hunger levels (Miyashita 1991). In social spiders, the mean quantity of food obtained per spider decreases with increasing group size, so that spiders are ultimately smaller in larger nests (Reichert et al. 1986; Ward 1986). This should have an impact on adult spider size and the time of maturity, so that spiders in nests where the mean amount of food available is less than their mean caloric requirements would reach a smaller adult size, or would mature later. Low levels of resources would ultimately affect reproductive capacity (Schneider 1995). The short-term consequence of reduced spider size may be dispersal (Miyashita 1992). Dispersal would be expected to spread the risk of starvation in related groups, since dispersing spiders may obtain more food (Kuno 1981), while remaining could lead to starvation.

Food resources have been proposed as a proximate stimulation for dispersal in spiders. We test this mechanism in this paper, focusing primarily on a risk sensitive foraging approach. Dispersal decisions have been explained by using risk-sensitivity (Caraco & Gillespie 1986; Uetz 1988). If an individual is meeting its current and long term requirements, remaining at the present site reduces the risk of starvation by reducing the variance in food intake (i.e. foraging in a risk-averse manner). However, when current resources are

fewer than the individual's requirements (i.e. the mean food intake is lower than the long-term requirements) there is a negative energy budget. It is then preferable to move to improve the chance of obtaining resources (i.e. foraging in a risk-prone manner) (Caraco & Gillespie 1986; Uetz 1988).

We tested whether differences in mean feeding rates influenced the decision of *S. mimosarum* to disperse. Colonies of the same size were subjected to one of two treatments: an abundance of food or an absence of food. This created two types of colonies: some where individuals were meeting their long term requirements (risk-averse foragers) and others, where individuals were not meeting their long term or short term energy requirements (risk-prone foragers). If food resources are a stimulus to disperse, and if risk sensitivity is a mechanism, then risk prone spiders in the starved colonies should adopt a strategy of dispersal, as this should increase their chances of obtaining food and eventually reaching maturity, whereas staying could result in delayed maturation, starvation and possibly death. Specifically, we predicted that more spiders would disperse from starved colonies.

## METHODS

Nests of *Stegodyphus mimosarum* were collected from Ashburton, KwaZulu-Natal, South Africa (24° 40' S, 30° 27'E) in March, October and December 1999, and maintained at the School of Life and Environmental Sciences, University of Natal, Durban, South Africa. This provided three complete replicates of the experiment. For two weeks, the spiders were allowed to acclimate. During this time, they were kept under controlled conditions, at 28 °C, and on a 12/12 light-dark cycle to remove the influence of day length. The spiders were fed a diet of adult mealworms, *Tenebrio molitor*, and mist-sprayed with water once a week. Spiders were housed on *Acacia robusta* plants in cages of plastic mesh on a metal frame (1000 mm diameter and 500 mm or 1000 mm high). Each cage had a removable wooden base supported by a metal stand. The stand was immersed in water to prevent predation by ants. A tie-up opening at the top of each cage allowed access for feeding.

In *S. mimosarum*, the size of spiders was smaller in larger nests (Ward 1986) and it is



expected that optimum spider size would be reached in nests of less than 40 spiders (Siebt & Wickler 1988a). We therefore used colonies of 40 spiders for the experiment. During each trial, spiders were removed from their field nests and allocated to ten colonies of 40 spiders each. All spiders used in these trials were juveniles. Each colony contained six large, 26 medium and eight small spiders. However, the size categories were altered in accordance with the sizes of spiders available for each trial. In any single trial, the size distribution between treatment groups (fed and unfed) and among individual colonies was equitable.

Colonies were weighed on a Mettler AE 240 balance and their masses were compared. Each colony mass was adjusted by including spiders of different sizes so that all ten colonies were similar in mass (within 0.1 g), and the colonies were re-weighed. The starting mass of each colony was therefore constant within each trial (10 colonies). The mean spider mass was calculated from the mass of the colony (colony mass divided by 40). A subsample of spiders (15–17 individuals) from each colony was measured (total body length and prosoma width) and mean body length and mean prosoma width were calculated for each colony. Individuals within each colony were color-coded with a combination of two colors (unique to each colony) of water-based poster paints, applied to the dorsal surface of the abdomen, so that the colony origin of moving spiders could be recorded.

Forty-nine *A. robusta* plants (600 mm to 700 mm high) were potted in plastic pots (base diameter = 180 mm, top diameter = 240 mm and height = 205 mm). Each plant was trimmed of all but two or three branches, none of which overhung the pot rim. The plants were arranged in the experimental room, in a grid of seven rows, each row with seven plants. The pot centers were 560 mm apart in each row and approximately 820 mm apart diagonally.

The windowless experimental room was artificially lit with 14 “daylight” incandescent bulbs of 100 watts each. These were mounted on a metal frame suspended from the ceiling. A timer controlled the 12 hour light/dark cycle, which removed the effect of changing day length during different trials. Nests were randomly allocated to plants. However, no nests were placed on the plants nearest the walls to

prevent any edge effect from the proximity of the walls. Each colony was enclosed within a bag made of fine netting, and was tied onto the branch with string. There was sufficient space inside the netting for the spiders to construct a retreat and capture web. The top of each bag had an opening, tied with string, through which the spiders were fed and the prey remains removed. The colonies were left for four days to start building a retreat and capture web (Day 1–Day 4).

Five colonies were randomly allocated to each treatment; either fed for a total of 31 days, or unfed. The feeding treatment consisted of four adult mealworms daily. The bags with the unfed colonies were opened and retied daily to create the same amount of disturbance as that experienced by the fed group. All colonies were mist sprayed with water once weekly. After 20 days (Day 5–Day 24) of this treatment, the spiders were removed from the bags and dead spiders were discarded. Those spiders that had molted were re-painted. The mass of each colony was again measured, and compared with the initial colony mass in each trial. Any missing spiders were replaced from a separate additional source of fed and unfed spiders, which had been housed under the same conditions as the ten colonies. Colonies were weighed again, and the mean spider mass was calculated.

We could not bring the colony back to the original number (40) in all trials, due to the constraints of the number of spiders required for each trial (400 plus extras). Under these circumstances, when we replaced spiders, priority was given to missing individuals first and then secondly to dead ones. The final number was as close to 40 as possible (Mean  $\pm$  S.E =  $34.2 \pm 3.717$ ). The colonies were returned to the netting bags on trees for four days (Day 24–Day 28) to repair their nests and capture webs. This was followed by another four days (Day 28–Day 31) of the fed/unfed regime within the bags. The bags were then carefully removed with as little damage to the capture web as possible. On Day 31, we could not count, measure or reweigh the colonies before the commencement of the observations, as this required taking apart the nest again and further disturbance of the nest and spiders. We therefore used the mean spider mass from Day 24 as the starting point of



the observations, although the treatment continued for another week after this (Day 31).

Daily observations were made on all movements of spiders for the next fourteen days (Day 32–Day 45). No further feeding occurred during this period, but the nests were mist-sprayed once weekly. Each tree or colony was examined for spiders and/or silk. Any spiders within a retreat were left undisturbed, although occasionally the retreat was thin enough to estimate of the number of spiders present. Information was recorded on the source of the spiders based on color, the number of spiders emigrating and where they were finally found. We recorded the total number of spiders moving from each colony, the number left behind and the number missing and/or dead. We calculated the number leaving divided by the total number in the colony on Day 24. These proportions were not normally distributed and all relative numbers were  $\sqrt{\text{arcsine } x}$  transformed. Data were analyzed by ANOVA (assumptions verified), Wilcoxon Signed Ranks Tests and Mann-Whitney U-tests as appropriate, using SPSS version 9.0 for Windows. Voucher specimens were deposited at the Durban Natural Science Museum.

Each experiment (five fed and five unfed colonies) was repeated three times: February–April 1999 (late summer/autumn), October–December 1999 (spring/summer) and January–February 2000 (mid/late summer). The total sample was therefore fifteen fed and fifteen unfed colonies. The trials presented reflect activity during the summer months when spiders are juveniles, subadults and adults. Although adult spiders were observed emigrating, in our experiments the spiders used were all either juvenile or subadult. This was done to remove the confounding effect of maturity, so that only the availability of food differed between treatments.

RESULTS

At the start of each trial, we ascertained that there were no significant differences in mean body length (Fig. 1a), mean prosoma width (Fig. 1b) or mean mass (Fig. 1c) between spiders in the two types of treatment (ANOVA:  $F_{1,9} < 3.470$ ,  $P > 0.100$  in all cases). Spiders were significantly smaller during Trial 2 (October 1999) compared with the other trials (Figs. 1a, b & c).

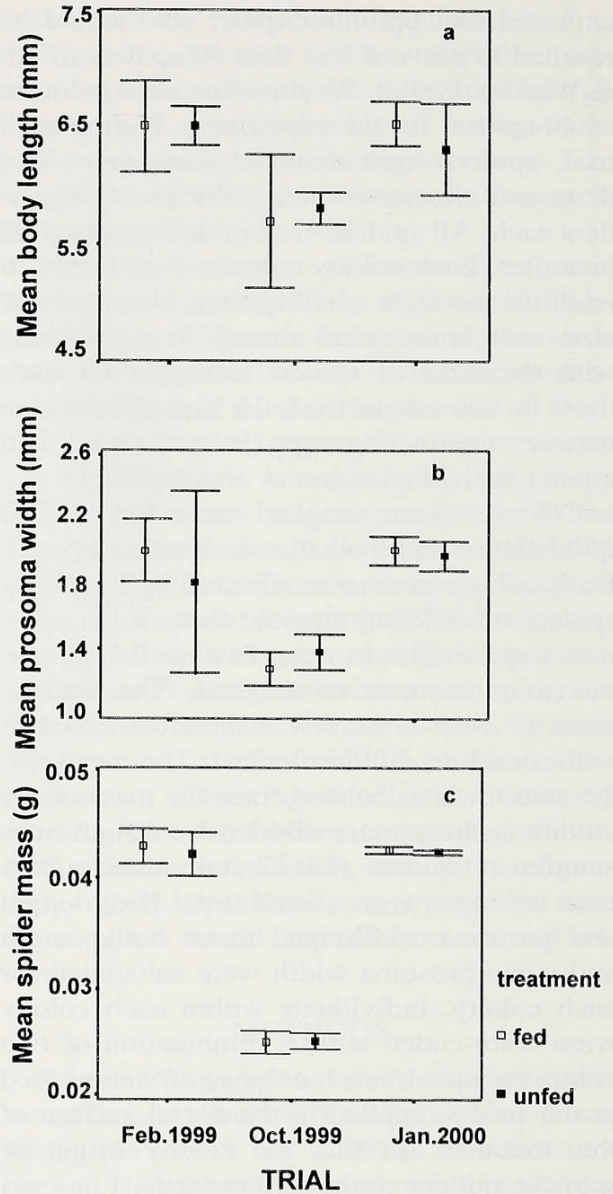


Figure 1.—Comparison of spider size in the fed and unfed groups at the start of each trial. We present the mean body length (a), mean prosoma width (b) and mean mass (c) of spiders  $\pm$  95% confidence limits. There was no significant difference in spider size (body length, prosoma width and mean mass) between treatments (ANOVA  $F_{1,9} < 3.470$ ,  $P > 0.1$  in all cases).  $n = 5$  colonies of 40 spiders in each category. Note that spiders were smaller during the October 1999 trial.

On Day 24, fed colonies were significantly larger than the unfed colonies, (Mann Whitney U-test on colony mass: Trial 1:  $Z = -2.611$ ,  $P = 0.009$ , Trial 2:  $Z = -2.402$ ,  $P = 0.016$ , Trial 3:  $Z = -2.611$ ,  $P = 0.009$ ). Moreover, in the fed colonies, tunnels opening onto the lower surface were visible in the retreats and capture web showed signs of recent maintenance with fresh silk extending onto



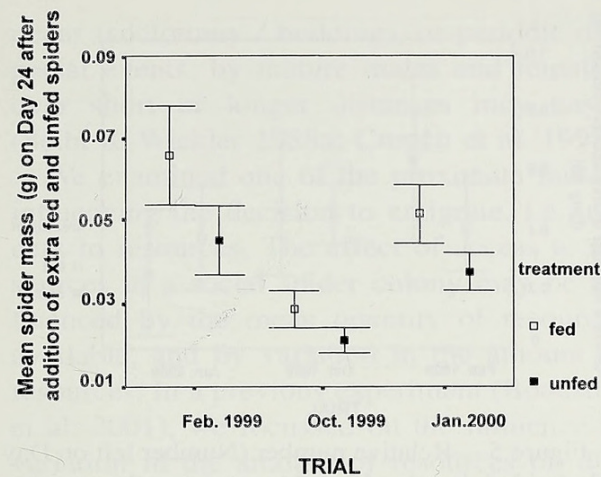


Figure 2.—Spider size (Mean  $\pm$  95% confidence limits) after differential feeding and before dispersal. Comparison of the mean mass of spiders in the fed and unfed groups on Day 24 of each trial. Spiders were significantly larger in the fed groups (except in Trial 2; see text for statistical analysis).  $n = 5$  colonies for each mean.

the netting. Spiders were significantly heavier (higher mean spider mass) in fed colonies than in unfed colonies (Mann Whitney U-test: Trial 1:  $Z = -2.611$ ,  $P = 0.009$ , Trial 2:  $Z = -1.984$ ,  $P = 0.047$ , Trial 3:  $Z = -2.611$ ,  $P = 0.009$ ) (Fig. 2). The unfed spiders were already experiencing the consequences of a lack of resources after 24 days. They were smaller in size (mean spider mass) and were not able to repair their retreats adequately after nests were taken apart on Day 24. A little fresh silk held the retreat together, and only a few tunnels were observed. There was generally very little capture web. Furthermore, the unfed colonies experienced a higher mortality than fed spiders. This is incompatible with reports that *S. mimosarum* kept for three to six months without food and water survived (Steyn 1959).

After adding in the extras, the “new” mean mass on Day 24 was significantly different from the start (Day 0) mass (Mann Whitney U-test: Trial 1:  $Z = -2.611$ ,  $P = 0.009$ , Trial 2:  $Z = -2.611$ ,  $P = 0.009$ , Trial 3:  $Z = -2.522$ ,  $P = 0.012$ ). Adding in the extra fed and unfed spiders on Day 24 maintained the overall effects of the two treatments, so that fed spiders were still significantly larger than unfed ones.

We compared the absolute number of spiders moving from all colonies (Fig. 3a), and significantly more spiders left the fed groups

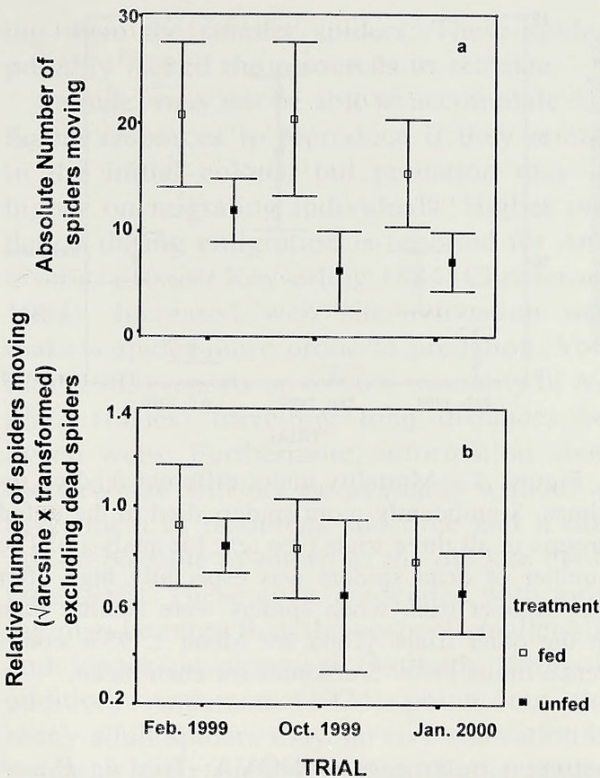


Figure 3.—Dispersal of spiders under different feeding regimes. (a). The absolute number (Mean  $\pm$  95% confidence limits.) of spiders that emigrated from the fed and unfed groups in all three trials. Significantly more spiders left the fed groups than the unfed groups (see text for analysis). (b). Relative dispersal ( $\sqrt{\text{arcsine } x \text{ transformed}}$ ) after accounting for dead spiders. There was no significant difference in the relative number of spiders leaving under the fed and unfed treatments in all three trials.  $n = 5$  colonies for each mean.

(ANOVA: Trial 1:  $F_{1,9} = 11.605$ ,  $P = 0.009$ , Trial 2:  $F_{1,9} = 23.558$ ,  $P = 0.001$ , Trial 3:  $F_{1,9} = 16.40$ ,  $P = 0.004$ ). We also tested the relative number of spiders moving (number moving divided by Day 24 final number of spiders) ( $\sqrt{\text{arcsine } x \text{ transformed}}$ ) in each trial. When the relative number of spiders moving was based on the Day 24 total number of spiders per colony, significantly more spiders left the fed colonies (ANOVA: Trial 1:  $F_{1,9} = 9.982$ ,  $P = 0.013$ ; Trial 2:  $F_{1,9} = 23.823$ ,  $P = 0.001$ ; Trial 3:  $F_{1,9} = 9.711$ ,  $P = 0.014$ ). Fed spiders showed a greater propensity to emigrate than the unfed spiders.

However, when the number of dead spiders on Day 45 was excluded from the Day 24 total, the relative number moving ( $\sqrt{\text{arcsine [number moving divided by (Day 24 total minus number of dead spiders on Day 45)]}}$ , transformed) was not significantly different



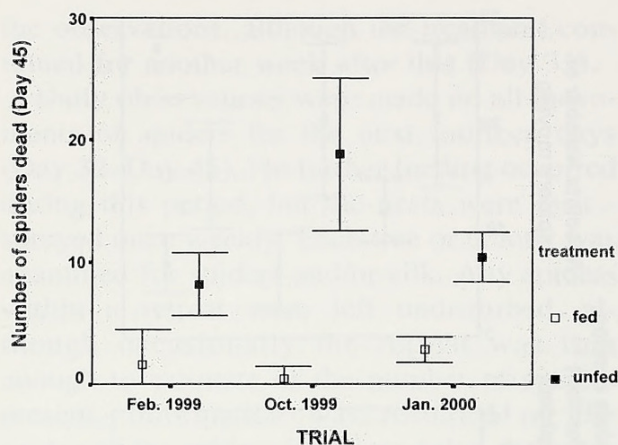


Figure 4.—Mortality under different feeding regimes. Significantly more spiders died in the unfed groups in all three trials (see text for analysis). The number of dead spiders was especially high after the October trial, when spiders were smaller than in the other trials. (Data are Mean  $\pm$  95% confidence limits.)  $n = 5$  colonies for each mean.

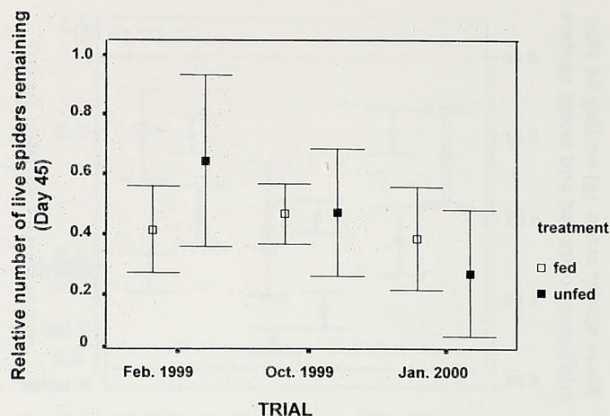


Figure 5.—Relative number (Number left on Day 45 divided by the Day 24 number—the number dead on Day 45) remaining at the end of each trial. There was no significant difference between treatments in the number of spiders remaining at the end of 45 days (see text for analysis). Data are Mean  $\pm$  95% confidence limits.  $n = 5$  colonies for each mean.

between treatments (ANOVA: Trial 1:  $F_{1,9} = 0.704$ ,  $P = 0.426$ ; Trial 2:  $F_{1,9} = 2.086$ ,  $P = 0.187$ ; Trial 3:  $F_{1,9} = 1.842$ ,  $P = 0.212$ ; Fig. 3b). This analysis assumes that those spiders were not available to move, i.e., they were effectively dead on Day 24. Under this analysis, the number of spiders leaving the fed colonies was no different from the number leaving the unfed colonies.

The mean mass of the spiders remaining in the nest at the end of each experiment (Day 45) was not significantly different from the mean mass at the start (Day 0), (Mann Whitney U-test: Trial 1:  $Z = -1.467$ ,  $P = 0.142$ , Trial 2:  $Z = -0.940$ ,  $P = 0.347$ , Trial 3:  $Z = -1.984$ ,  $P = 0.047$ ). In the fed groups, the spiders that remained were possibly the smaller ones at the start of the trial, or spiders that did not gain mass during the experiment (mass  $\leq$  mean mass at the start). In the unfed groups, those remaining could be the spiders that were initially the larger ones (mass of spiders  $>$  mean mass) that lost mass during the experiment, but which managed to survive.

By Day 45, significantly more spiders died in the unfed groups than in the fed groups, in all trials (ANOVA: Trial 1:  $F_{1,9} = 22.926$ ,  $P < 0.001$ ; Trial 2:  $F_{1,9} = 63.879$ ,  $P < 0.001$ ; Trial 3:  $F_{1,9} = 82.514$ ,  $P < 0.001$ ) (Fig. 4). Indeed, by Day 24, significantly more spiders died in the unfed groups (ANOVA: Trial 1:  $F_{1,9} = 33.923$ ,  $P < 0.001$ , Trial 2:  $F_{1,9} = 7.149$ ,  $P = 0.028$ , Trial 3:  $F_{1,9} = 16.794$ ,  $P =$

0.003). This is especially noticeable in the October 1999 trial, when spiders were much smaller than in the other two trials.

The absolute number of spiders left at the end of the experiment was significantly different between treatments in trial 2 (ANOVA: Trial 1:  $F_{1,9} = 0.312$ ,  $P = 0.592$ , Trial 2:  $F_{1,9} = 10.127$ ,  $P = 0.013$ , Trial 3:  $F_{1,9} = 4.128$ ,  $P = 0.077$ ). There was no significant difference in the relative numbers of spiders that remained in the colony at the end of the trial (45 days) (ANOVA: Trial 1:  $F_{1,9} = 3.959$ ,  $P = 0.082$ , Trial 2:  $F_{1,9} = 0.003$ ,  $P = 0.957$ , Trial 3:  $F_{1,9} = 1.399$ ,  $P = 0.271$ ) (Fig. 5). The number of spiders remaining was therefore not associated with the different treatments, but was influenced by some other factor. This may be due to the trial date (time of year of the trial/season or their size/stage of maturity), since significantly more spiders remained in Trial 2 (October 1999) (ANOVA:  $F_{1,29} = 3.857$ ,  $P = 0.034$ ), when spiders were smaller than in the other two trials.

## DISCUSSION

Most spider species are solitary and aggressive. As a result, most spiderlings disperse soon after hatching (Foelix 1996). However in social *Stegodyphus* spp., this is not the case. Spiderlings remain together through to maturity, and several successive generations may remain in the original nest (Seibt & Wickler 1988b). Dispersal over short distances may



occur (sociotomy / budding), or periodic dispersal events, by mature males and females, over short or longer distances may ensue (Seibt & Wickler 1988a; Crouch et al. 1998).

We examined one of the proximate factors influencing the decision to emigrate, i.e., access to resources. The effect of access to resources in a social spider colony may be influenced by the mean quantity of resources available, and by variation in the amount of resources. In a previous experiment (Bodasing et al. 2001), we focussed on the influence of variation in the amount of resources on dispersal. Four colony sizes (4, 16, 32 & 64) were set up under a proportional feeding regime. Variance in spider size occurred due to intra-group competition. We expected this variance to be greater and to trigger dispersal in larger colonies, but there was no significant increase in the number of spiders leaving with increasing group size (Bodasing et al. 2001). In the current experiment, some colonies had a mean amount of food available greater than the mean requirements of the colony, and other colonies had a mean amount of food less than the mean amount required by the colony. Those spiders deprived of food would have fewer reserves. If spiders were responding to risk, we expected starving individuals to relocate to find an alternate nest site where they may find food. However, significantly more spiders moved from the fed groups in all three trials (absolute number and relative number based on Day 24 total), while the unfed spiders adopted a risk-averse foraging strategy.

In some spiders, the costs of relocation may be high. There is a cost to silk production (Tanaka 1989; Reichert et al. 1986), the danger of predation either during moving or rebuilding (Vollrath 1985, Reichert et al. 1986, Sundstrum 1994) and the reduced chance of finding a mate (Seibt & Wickler 1988a). These dispersal costs must be compared to the costs of not dispersing, including the cost of inbreeding, which characterizes social spider communities (Johannsen & Lubin 1999). There is also a smaller adult spider size in larger colonies (Reichert et al. 1986; Ward 1986), which would ultimately affect reproduction (Schneider 1996). The costs of smaller size may be countered by prolonged development, rather than building a new web (Vollrath 1985). Even in the fed groups, those remain-

ing were the smaller spiders. These spiders possibly lacked the resources to relocate.

Females may not be able to accumulate sufficient resources to reproduce if they remain in the initial colony, but predation may be higher on migrating individuals. Higher predation during emigration is reported for *Aelosimus eximius* Keyserling 1884 (Christenson 1984). Increased web site relocation may make a spider more prone to predation. Vollrath (1985) reports up to 90% mortality of *Nephila* (males) travelling long distances between webs. Furthermore, information about the new site will not be available without an investment of resources and time and it may not be possible to return to the old site (Vollrath 1985). These costs associated with moving may be more than the costs of smaller size and longer development (Vollrath 1985). In addition, Anderson (1974) points out that many adult spiders may survive starvation by reducing their metabolic rate. Some spiders may also switch to using fat as a catabolic substrate (Tanaka & Ito 1982). It may be preferable to wait in a "safe" retreat rather than risk predation. In some spider species, mean body weight may increase enormously and rapidly when food is available (Miyashita 1991). Although *Neriene radiata* Walckenaer 1842 (referred to as *Linyphia marginata* in reference) do not emigrate when there is a shortage of food, they grow faster when food is available (Wise 1975). Under these circumstances, it may be preferable to wait on the likelihood of better conditions later.

*Nephila*, an orb web spider, moved significantly less in a rich environment, than in a poor environment (Vollrath 1985). Apparently *Nephila* produces an orb web that is more expensive than other orb webs (Vollrath & Houston 1986) and therefore they are less likely to relocate. The sub-social eresid, *S. lineatus* Latreille 1817, decreased web size and some stopped web building when food was supplemented (Pasquet et al. 1999). They suggest that the proximate cue for web relocation is the presence or absence of prey, rather than body condition. While food supplementation in mantids and cursorial spiders resulted in lower dispersal (Moran & Hurd 1997), favorable food conditions have been reported to increase dispersal in other spiders (Ward & Lubin 1993).

Dispersal of better-fed spiders was also



found in an orb web spider and the increased emigration was explained as risk-sensitive foraging (Gillespie & Caraco 1987). If the availability of food is important in the proximate decision to move, and if spiders are acting in a risk-sensitive manner, we predicted that they would move when the mean amount of food available per spider was less than their mean long-term requirements. They should remain at their present nest site if the prey available is more than their mean requirements. However, more spiders that obtained sufficient food showed a propensity to move. Although spiders in the unfed colonies obtained less food than their mean energy requirements, lost weight and many died, they showed little propensity to leave. They showed a preference to sit it out rather than risk moving, i.e., risk-averse behavior. Avilés & Tufino (1998) suggest that the costs of dispersal are so high that colonies of social spiders reach beyond optimal size and crash, rather than disperse.

Social spiders invest a large amount of silk in the production of closely woven retreats and in many sheets of capture web. Nests of *S. mimosarum* consist of a central retreat with numerous tunnels opening onto the lower surface, and a capture web of cribellate silk, which radiates out from this retreat. Under normal circumstances, in a social spider colony with its complex retreat and capture web, a number of spiders share these costs, so that the cost per spider is usually reduced. Silk is extremely expensive to produce and cribellate silk is more costly than sticky orb web silk (Tanaka 1989; Opell 1998). Non-adhesive webs are known to be costly to produce compared to sticky orb webs (Opell 1998; Tanaka 1989), and the webs of spiders that resorb silk (Opell 1998). Further, there is the cost of building a retreat. Studies on *S. lineatus*, a subsocial eresid, indicate that they lost 8% of their body mass and spent about six hours rebuilding webs (Pasquet et al. 1999). Spiders with more costly webs do not relocate often (Tanaka 1989). Emigrating social spiders may only have sufficient resources to relocate and build an energetically expensive nest under conditions of high prey availability. The spiders in our unfed colonies, without adequate food resources may remain in a site with little prey because they do not have the reserves required for relocating and rebuilding.

We know that *S. dumicola* may have a sol-

itary or social lifestyle (Henschel 1991), and single *S. mimosarum* do occur (Crouch et al. 1998). Individual spiders are therefore capable of initiating a new nest. However, the cost of setting up a new nest may be too high for spiders that are living at a low rate of food intake, and only well fed spiders may have the resources required to relocate. Well nourished individuals would therefore drive medium to longer distance dispersal.

High concentrations of food are thought to have resulted in gregarious behavior and an abundant food supply has been considered a major prerequisite influencing colony formation and the evolution of sociality (Rypstra 1986). However, in our experiment spiders did not reverse their sociality in response to starvation. We conclude that some factor other than mean amount of food available is more likely to trigger dispersal in these spiders. When food is abundant, they increase mass, and may emigrate if other factors (time of year, environmental conditions, spider size) are appropriate. In a previous experiment, significantly more spiders left during spring and when spiders were larger (Bodasing et al. 2001). However, when food is scarce, they stay to try to survive short-term changes. It would be less costly to remain especially if the retreat is intact and can provide some shelter, protection and prey.

#### ACKNOWLEDGMENTS

Specimens were collected under permit no. 244/1997 of the Natal Parks Board, to Dr. T. Crouch. We appreciate the field help provided by Kumar, Tarik and Jarrad Bodasing; and the laboratory help provided by Simon Shezi. This study was supported by NRF grant 2037182 to R. Slotow.

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*Manuscript received 27 August 2001, revised 12 April 2002.*





Bodasing, Marilyn, Crouch, Tanza E., and Slotow, Rob. 2002. "THE INFLUENCE OF STARVATION ON DISPERSAL IN THE SOCIAL SPIDER, STEGODYPHUS MIMOSARUM (ARANEAE, ERESIDAE)." *The Journal of arachnology* 30(2), 373–382. [https://doi.org/10.1636/0161-8202\(2002\)030\[0373:tiosod\]2.0.co;2](https://doi.org/10.1636/0161-8202(2002)030[0373:tiosod]2.0.co;2).

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