

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

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ABSTRACT. The costs and benefits of group living vary with group size, and competition for resources increases with increasing group size. In the social spider, *Stegodyphus mimosarum*, individuals attain smaller sizes, and survival is lower in larger colonies. In this study we assess whether group size influences the decision to leave a colony—or disperse. Four colony sizes (8, 16, 32 and 64) of *S. mimosarum* were set up under a proportional feeding regime in a laboratory experiment. We expected more spiders to leave large colonies due to intra-group competition. However, there was no significant increase in the number of spiders leaving with increasing group size. Significantly more spiders left a colony during spring and when spiders were larger (at a more advanced stage of development). Variability in access to resources does not promote dispersal, but season and spider size does influence dispersal.

Keywords: Group size, intragroup competition, dispersal, social spiders, *Stegodyphus mimosarum*

The trade-off between the costs and benefits of group living changes with group size (Ranala & Brown 1994; Uetz & Hieber 1997). Social animals interact in groups of sizes that maximize the fitness of the individual (Caraco & Wolf 1975; Sibly 1983; Kramer 1985; Giraldeau & Gillis 1988; Packer & Ruttan 1988; Avilés & Tufino 1998). There is a stable group size, larger than the optimal group size, where the mean inclusive fitness of joining is larger than if the individual remained alone (Sibly 1983; Giraldeau & Gillis 1985; Zemel & Lubin 1995). If the optimal group size cannot be reached, it is preferable for an individual to be in a group larger than optimal rather than a smaller group (Sibly 1983; Giraldeau & Gillis 1985), and most groups in nature are larger than optimal (Sibly 1983; Giraldeau & Gillis 1985; Ward & Enders 1985; Zemel & Lubin 1995). An animal should join a group of supraoptimal size if its fitness would be greater than if it remained alone. Beyond the stable group size, the benefits are too small or the cost levels too high to outweigh the advantages of sociality; and individuals should disperse from this group (Kramer 1985).

In social spiders, there may be advantages to emigration before reproduction or when

there is a large increase in numbers in the colony, such as soon after juveniles are born/hatch out, and when the predation effects or parasite loads are too high. In addition, the low genetic diversity in social spider colonies may make dispersal imperative (Smith & Engel 1994). These are the ultimate reasons why animals disperse.

However, the proximate reasons driving the decision to disperse from colonies includes access to resources (Ward 1986), season and size of the animal (Miller & Miller 1991). Resources in a particular area become depleted, and it is advantageous for an animal or a group of animals to find another location before the resources are completely finished. In social animals there may be increased intra-group competition when resources are diminished (Ward 1986).

There are two main aspects to examine with respect to access to resources. First, intra-group competition results in a greater variability in individual access to resources (Ulbrich et al. 1996). In most large social spider nests, competition for resources increased with increasing group size and spiders were less competitive in smaller nests (Ward 1986; Seibt & Wickler 1988a). If the quantity of

prey obtained is proportional to the size of the colony, some individuals may get a higher quantity of food, resulting in a range of individual body sizes within the colony (Ulbrich et al. 1996; Ward 1986). Although the mean mass of spiders is lower in larger colonies, there is no clear indication whether the variance in body mass correlates with colony size (Seibt & Wickler 1988a; Ward 1986). The decision on whether to leave or remain in a group may depend on risk-sensitivity (Uetz 1988). If there is more prey available than the individual needs, remaining in a group reduces the risk of starvation by reducing the variance in the food intake (i.e., foraging in a risk-averse manner). However, when resources are less than the individual requirements (i.e., there is a negative energy budget), it is preferable to move to improve the chance of obtaining resources (i.e., foraging in a risk-prone manner) (Uetz 1988; Lawes & Perrin 1995). This should also apply when there is less access or more competition for food, as is the situation for the disadvantaged spiders in larger nests. Contest competition gives the larger spiders an advantage over the smaller ones (Ulbrich et al. 1996; Ward 1986; Whitehouse & Lubin 1999). Spiders should then leave the larger nests as competition for resources increases, and the smallest spiders should leave.

Second, mean access to resources may also trigger dispersal. The mean food intake per spider decreases with increasing group size, spiders take longer to extract the same amount of food (Ward & Enders 1985) and spiders attain smaller sizes in larger nests (Ward 1986; Seibt & Wickler 1988a, b). Ultimately, competition for resources would have an impact on adult spider size and time of maturity. This should result in spiders dispersing more from larger nests. Dispersal would then be important since it acts as a stabilizing factor by spreading the risk of starvation (Kuno 1980). In addition, in an experiment to test survival rates, more spiders survived from smaller nests than from larger nests (Ward 1986; Seibt & Wickler 1988a). This also suggests that more spiders should leave the larger nests.

We postulated that there would be more intra-group competition in larger colonies. Under conditions of proportional food availability per individual, this would result in a range of individual access to food within each col-

ony with some spiders being disadvantaged. This variability would be greater in larger colonies and the more disadvantaged spiders are expected to leave these colonies.

In this experiment, we tested the influence of variability in the access to resources on dispersal in different colony sizes. We used four group sizes of *S. mimosarum* Pavesi 1883 (Araneae, Eresidae) to test if spiders were more likely to disperse from small groups (low variability in food intake) or large groups (high variability in food intake). We also examined the influence of spider size and the season at which dispersal occurs by conducting the experiment at intervals throughout the year. The influence of mean access to resources will be tested in a subsequent experiment.

METHODS

Twelve nests of *S. mimosarum* were collected from Weenen Nature Reserve, South Africa (28°50'S, 29°51'E) during March 1997, five in June 1997, six in December 1997 and eight from Itala Game Reserve, South Africa (27°31'S, 31°22'E) in April 1998. *Stegodyphus mimosarum* are social spiders, with a life cycle of approximately one year; young spiders emerge from eggs sacs in late summer (February to March) and the adult spiders are found from spring to midsummer (October to January). Data on the growth rate of *S. mimosarum* from Richmond, Kwazulu-Natal is described elsewhere (Crouch & Lubin 2000). Voucher specimens were deposited at the Durban Natural Science Museum.

Nests were maintained in the School of Life and Environmental Sciences, University of Natal, Durban, South Africa under controlled conditions: at 28 °C, on a 12/12 h light/dark cycle to control for seasonal changes in day length. The spiders were fed on a diet of adult mealworms, *Tenebrio molitor*, and mist-sprayed with water once a week. Nests were housed on *Acacia robusta* plants in cages of plastic mesh on a metal frame (1 m diameter × 0.5 m or 1 m high). Each cage had a removable wooden base on a metal stand. The stand could be immersed in water to prevent predation by ants. A tie-up opening at the top of each cage allowed access for feeding.

During preliminary experiments (1996–1997) we found that groups of two and four spiders either did not survive, or did not produce sufficient silk and had difficulty in the

Table 1.—Mean body length and mass of spiders for each of the four trials. Note that the spiders used in the April 1998 trial are closer in size to those used in the October 1997 trial than to those used in the April 1997 trial.

Trial number Month Season	Colony size	Mean body length of colony \pm SE (mm)	Mean body length for trial \pm SE (mm)	Mean mass (mg)
1 April 1997 Autumn	8	3.44 \pm 0.65	3.32 \pm 0.08	6.7
	16	3.24 \pm 0.79		
	32	3.31 \pm 0.94		
	64	3.32 \pm 0.72		
2 July 1997 Winter	8	3.96 \pm 0.80	3.62 \pm 0.34	6.5
	16	3.85 \pm 0.70		
	32	3.67 \pm 0.71		
	64	3.79 \pm 0.59		
3 October 1997 Spring	8	4.55 \pm 0.63	4.38 \pm 0.17	13.8
	16	4.4 \pm 0.71		
	32	4.16 \pm 1.01		
	64	4.53 \pm 0.93		
4 April 1998 Autumn	8	3.93 \pm 1.39	3.97 \pm 0.24	12.6
	16	3.71 \pm 1.49		
	32	3.94 \pm 0.71		
	64	4.29 \pm 0.71		

capture and immobilization of adult mealworms. We therefore selected colonies of 8, 16, 32 and 64 spiders for this experiment; to represent small (8), intermediate-sized (16 and 32) and large colonies (64). The selected group sizes of spiders mainly reflected those collected in the field ($\bar{x} \pm SE = 43.08 \pm 31.42$, $n = 12$) although some field nests contained more than 100 spiders.

Spiders removed from nests from both localities (Weenen Nature Reserve and Itala Game Reserve) were randomly allocated into groups to eliminate any source effects. *Stegodyphus mimosarum* individuals from different nests can be combined as they readily accept conspecifics (Seibt & Wickler 1985). At each trial, four replicates of each group size were created, giving a total of 480 spiders in 16 colonies. No spiders were reused in successive trials. The experiment was repeated four times, in April 1997, July 1997, October 1997 and April 1998, to give a range of seasons, spider sizes and levels of maturity. All the spiders used in these trials were immature, i.e., either juvenile or subadult.

The total body length of a sub-sample of spiders was measured from every colony. Every second, third or fourth spider was selected, with a total of 4–14 individuals measured,

depending on the colony size. The average body length was calculated for each colony (Table 1). The mass for each group was measured to four decimal places, on a Mettler AE240 balance, and the average mass of each spider was calculated (Table 1). We preferentially use body length as an indicator of body size (rather than body mass) since it is less affected by the momentary feeding status of the spider. We created a unique color marking for each colony by painting every spider in the colony with two colors of water-based poster paints on the dorsal surface of the abdomen.

Forty-nine *A. robusta* plants (600–700 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 a grid of seven rows, and each row contained seven plants. The pot saucers (outer diameter = 240 mm) were used for the first trial (April 1997), but these were omitted in subsequent trials. 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

light bulbs of 60 W each, mounted on a metal frame suspended from the ceiling (except for Trial 1, where 8 light bulbs were used on a free-standing frame). The allocation of nests on plants was random. However, no nests were placed on the plants adjacent to the walls, to prevent any edge effect from the proximity of the walls. Each colony was placed on a tree, and enclosed with fine netting, which was tied onto the branch with string. There was sufficient space inside the netting for the spiders to construct a retreat and capture web. Two days later (i.e., Day 0 of the experiment), the netting was removed.

During the experiment, each colony was fed twice weekly—on days 2, 5, 9, 12, 16 and 19 of each trial. Feeding was proportional to the number of spiders in the colony: colonies of eight were fed one prey item per feeding event, colonies of 16 were fed two prey items, colonies of 32 were fed four prey items and colonies of 64 were fed eight prey items.

All movements of spiders were noted daily and 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 the number of spiders present. Information was recorded on the source of the spiders based on color, the number of spiders and their destinations. The spiders were removed from their new locations each day.

After the first five days, the nests were taken apart, the spiders were counted and the number in each colony was recorded. Spiders that had molted were repainted. Some spiders could not be located and the missing individuals (excluding any dead spiders, since we could not determine the cause of mortality) were replaced so that the original numbers were re-instated. This initial period was termed the Early Trial (1a, 2a, etc.). The colonies were then covered in netting for a further two days, after which the netting was removed. Fourteen days of daily observations then followed. At the end of this period, the nests were again taken apart, all spiders counted and their source noted. This part of the experiment was called Trial 1b, 2b, etc., or the Late Trial. The separate early and late parts of each trial were compared using a Wilcoxon Paired Ranks test, and since no influence of early vs. late trials was found ($Z = -1.903$, $P = 0.056$), the two sections were combined and

averaged. All subsequent analyses were on the combined averaged trials, which increased the internal validity of the data from each colony.

The total number leaving each colony was used to calculate the relative number of spiders that moved (i.e., total number that moved divided by the number in the colony). The data were normalized using an arcsine [square root] transformation and the transformed data were used for all analyses. An analysis of covariance, with a *post-hoc* Bonferroni test, was carried out on each separate section of the experiment (i.e., 1a, 2a, 1b, 2b, etc.). ANCOVA was used to remove the effect of trial date or body size. Arcsine [square root] (relative number moving) was the dependent variable, with colony size (8, 16, 32 and 64) as the factor and trial number or body length as the covariate. The assumptions of the ANCOVA were verified using a Kolmogorov-Smirnoff test to check that the data and residuals were normally distributed, and a Bartlett's Box F -test was used to check for homogeneity of the variances. The assumptions of the parametric tests were met in all cases ($P > 0.05$).

RESULTS

We tested the effect of the mean body size of the spiders on dispersal, for the four trials. The relative number of spiders leaving increased significantly with increasing body length (Linear Regression: $F_{1,62} = 11.45$, $P = 0.001$) (Fig. 1), and with increasing spider mass (Linear Regression: $F_{1,62} = 8.21$, $P = 0.006$).

The absolute number of spiders moving increased with increasing colony size (Fig. 2) (ANOVA: $F_{3,63} = 19.985$, $P < 0.001$). More spiders left the largest colonies (64) compared with the smaller colonies, and this was especially marked during the October 1997 trial. Significantly more spiders left the colonies of 32 in the October 1997 and April 1998 trials compared with the earlier trials. We compared the absolute number of spiders moving with the relative number of spiders moving in each trial (Fig. 3). The relative number of spiders moving increased over the first three trials, ($F_{3,63} = 8.32$, $P < 0.001$).

We then tested the relative numbers of spiders moving in each colony size. We removed the influence of body length using an ANCOVA, with body length as the covariate (Fig. 4). The trend was for more spiders to leave

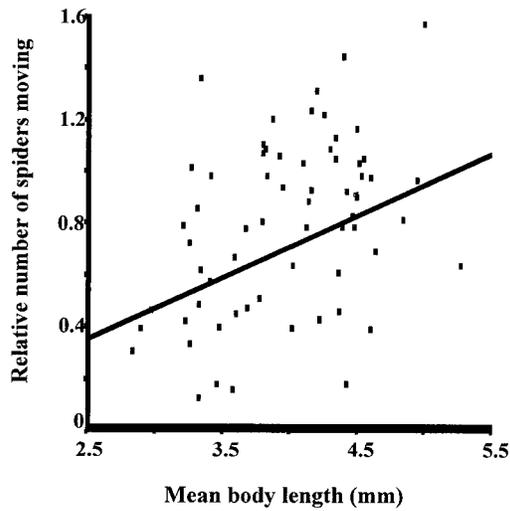


Figure 1.—The influence of body size of spiders on their propensity to move. We plotted the relative number of spiders moving (arcsine square root transformed) against the mean spider body length (mm) for each replicate. The relative number was calculated as the number moving divided by initial colony size.

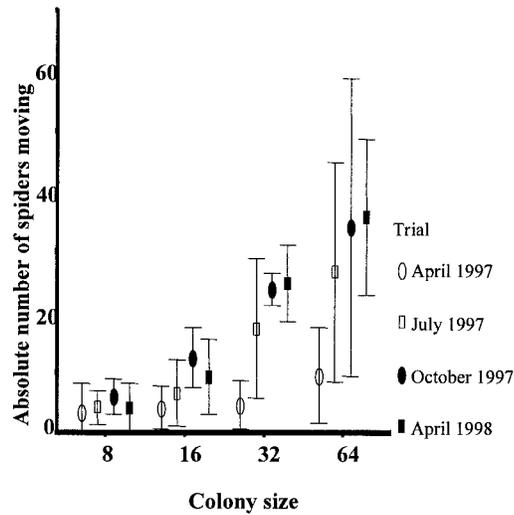


Figure 2.—The influence of colony size on the propensity to move. The absolute number of spiders moving is plotted against trial. Note that all other analyses presented are on the relative number of spiders moving.

the smaller group sizes, but these results were not statistically significant ($F_{3, 63} = 1.34$, $P = 0.271$). Similar results were obtained using spider mass as covariate ($F_{3, 63} = 0.82$, $P = 0.486$). We found no influence of colony size on the dispersal of spiders in any of the individual early or late trials or in the combined and averaged early and late trials (in all cases $F_{3, 63} < 2.56$, $P > 0.104$). The results for all trials therefore confirm the null hypothesis that group size does not influence dispersal in the group sizes tested.

The numbers of spiders leaving increased over the first three trials with more spiders leaving later in the year (Fig. 2, Fig. 5). Trial date had a statistically significant effect ($F_{3, 63} = 11.91$, $P < 0.001$) with significantly more spiders leaving during the October trial than either the April or July trials. The first and fourth trials were both run in the same month of different years, i.e., April 1997 and April 1998. The numbers of spiders leaving during the two April trials are significantly different, with more spiders leaving during the April 1998 trial. Despite this difference, when the two April trials are considered as the same season (autumn), there is still a significant seasonal effect (ANOVA: $F_{2, 63} = 6.64$, $P =$

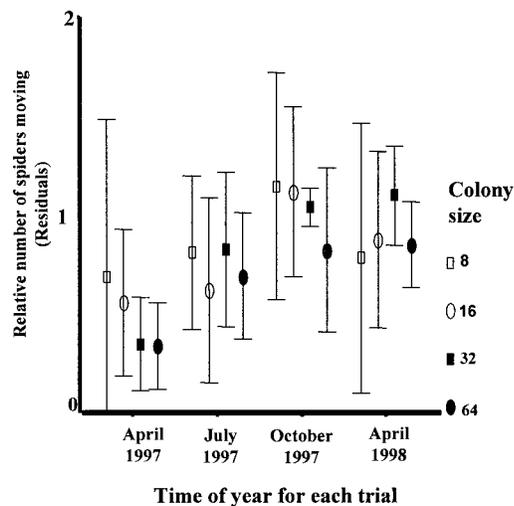


Figure 3.—The influence of colony size on the propensity to move. The effect of mean body length was removed by using the residuals from the regression of the relative number moving (arcsine square root transformed) against spider size. The relative number was calculated as the number moving divided by number in the colony. We plotted the residuals against trial date.

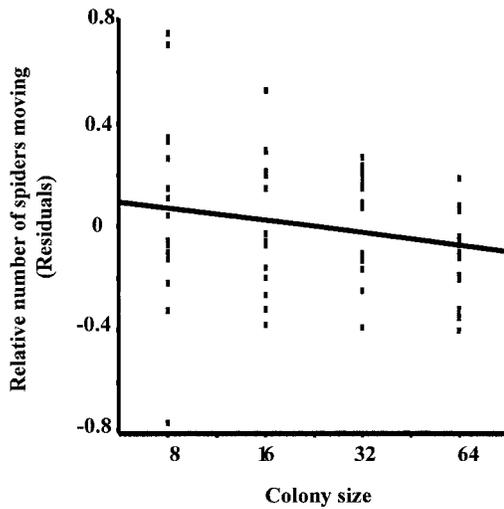


Figure 4.—The influence of colony size on propensity to move. The effect of mean body length was removed by using the residuals of the regression of the relative number moving (actual number moving divided by the number in the colony, arcsine square root transformed) against spider size. We plotted the residuals against colony size. The results were not statistically different ($F_{3,63} = 1.34$, $P = 0.271$). Sample size for each mean = 16 colonies.

0.002) with most spiders leaving during the spring (October) trial (Fig. 4). The relative number of spiders leaving for each season was still significantly higher in spring (October) when the effect of body length and mass were removed (ANCOVA: $F_{2,63} = 3.16$, $P = 0.050$; body length and mass as covariate).

We tested the combined effect of colony size and season on the number of spiders moving, in a two-way interaction between the mean number of spiders emigrating in the different colony sizes, with season. We used body length as covariate to remove the effect of body length. We found that there was a significant difference in the effect of mean spider size on the relative number of spiders moving in each trial (Fig. 6). In the April 1997 trial, the number of spiders leaving increased with increasing spider size, while this trend reversed in the subsequent trials despite the larger mean size of the spiders in the later trials. There was a significant interaction effect on the mean number of spiders moving (ANOVA: interaction of colony size and trial:

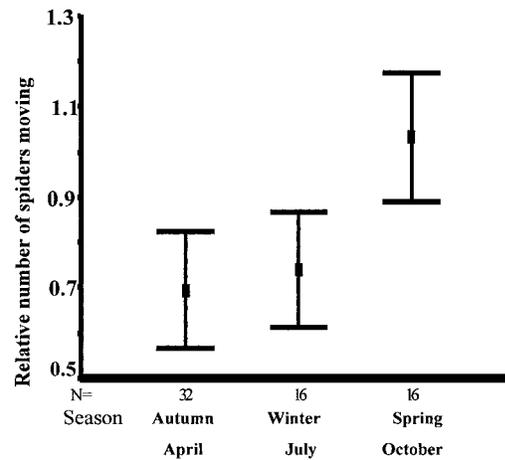


Figure 5.—The influence of season on the propensity to move. Variability in spider size was controlled by using the residuals from the regression of the relative number moving (arcsine square root transformed) against spider size. We present the mean \pm 95% confidence intervals for each trial. Significantly more spiders moved during the spring trial. Note that the two autumn trials are combined (i.e., $n = 32$ colonies; all others $n = 16$ colonies).

$F_{9,63} = 2.887$, $P = 0.008$, body length as covariate).

The size of the colony alone did not influence dispersal but there was a combined effect of colony size and season. The dispersing spiders were found on other plants, the walls, ceilings and corners of the experimental room. Most spiders moved during October (spring). Although relative movement from colonies increased with increasing spider size, the mean number moving in each of the later trials decreased.

DISCUSSION

In most large social spider nests, spider size decreases with increasing group size (Ward 1986; Seibt & Wickler 1988a, b). Under conditions of a proportional food supply, intra-group competition results in variability in the individuals' access to resources. We expected this variability to be greater in larger colonies. This should result in relatively more spiders leaving the larger colonies since ultimately such competition would impact on spider size and time of maturity. We found that spider group size alone did not influence dispersal in the group sizes tested.

Other components of fitness (e.g., related-

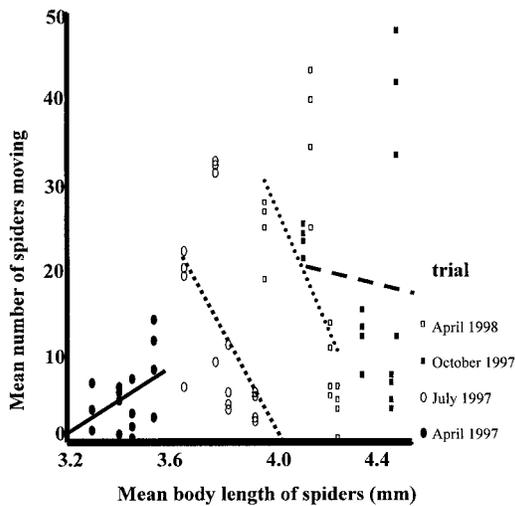


Figure 6.—The influence of the mean size of spiders and the time of year on their propensity to move. We plot the mean number of spiders moving against the mean body length for each colony size in each of the four trials. Note the increasing trend in the number of spiders moving with increasing spider size in the April 1997 trial and the decreasing trend in subsequent trials.

ness of kin) may make it acceptable to have a larger than optimal group size (Rannala & Brown 1994). Very small spiders would not survive outside the nest (Ward 1986). Even with increased competition, it may benefit an individual to stay in a larger nest since variance in body weight may be less in larger colonies (Seibt & Wickler 1988a; Ward 1986). Fitness losses are greater on splitting into groups that are smaller than optimal than they are for remaining in a group that is larger than optimal (Giraldeau & Gillis 1985). Dispersal would only replace intra-group competition with inter-group competition (Zemel & Lubin 1995). The costs of dispersal may also discourage spiders from moving (Aviles & Tufino 1998).

An abundance of insects should be available after the spring rains have fallen and when the trees, on which the spider nests occur, are in flower. Most spiders dispersed during the October (spring) trial, which represents the time when insects would be abundant.

The number of spiders moving increased consistently over the year, with increasing spider size. The influence of body size is most

important in the October 1997 and April 1998 trials. Spiders mature from October onwards and dispersal may be influenced by the sexual maturity associated with the larger size. Burrowing wolf spiders dispersed during spring and autumn and the size of the dispersing spiders determined their survival (Miller & Miller 1991). Field observations on *S. mimosarum* showed dispersal by mature males and females during midsummer (Crouch et al. 1998). Also, dispersal of *Anelosimus eximius* Simon, 1891 (Araneae, Theridiidae) occurs only in inseminated adult females (Vollrath 1982) and *S. mimosarum* adults occur from October through February. Our results show increased dispersal in spring (October), when spiders are larger and adults occur. The larger size of spiders in the April 1998 trial may be attributed to spiders that were laboratory raised for a few months prior to the experiment and hence larger than those in the field at this time.

Although there was an overall increase in the number of spiders moving with increasing spider size, in the later trials this trend reversed. It appears then that for *S. mimosarum*, the influence of spider body size, level of maturity and the time of year (season) with its particular set of environmental conditions, is more important than variability in the access to resources in driving dispersal.

The mean amount of food obtained by each spider is less in larger nests (Ward 1986; Seibt & Wickler 1988a). This would influence adult spider size and ultimately, reproduction. It is then preferable to move to improve the chance of obtaining resources (i.e., foraging in a risk-prone manner) if the amount of food obtained is less than the mean requirements (Uetz 1988; Lawes & Perrin 1995). We are presently testing the influence of mean access to food on dispersal in colonies of *S. mimosarum*, by comparing colonies that have been adequately fed with those that have not been fed.

ACKNOWLEDGMENTS

Specimens were collected under permit #244/1997 of the Natal Parks Board, to Dr. T. Crouch. We appreciate the field help provided by the Natal Parks Board, Navashni Govender and Komalan Govender; and the laboratory help provided by Simon Shezi. This study was supported by NRF grant #2037182 to R. Sloatow.

LITERATURE CITED

- Avilés, L. & P. Tufino. 1998. Colony size and individual fitness in the social spider, *Anelosimus eximius*. *American Naturalist* 152:403–418.
- Caraco, T. & L.L. Wolf. 1975. Ecological determinants of group sizes of foraging lions. *American Naturalist* 109:343–352.
- Crouch, T., Y. Lubin & M. Bodasing. 1998. Dispersal in the social spider *Stegodyphus mimosarum* Pavesi, 1883 (Araneae: Eresidae). *Durban Museum Novitates* 23:52–55.
- Crouch, T. & Y.D. Lubin. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae) *Journal of Arachnology* 28:158–168.
- Giraldeau, L. & D. Gillis. 1985. Optimal group size can be stable. A reply to Sibly. *Animal Behaviour* 33:666–667.
- Giraldeau, L. & D. Gillis. 1988. Do lions hunt in group sizes that maximize hunters' daily food returns? *Animal Behaviour* 36:611–613.
- Kramer, D.L. 1985. Are colonies supraoptimal groups? *Animal Behaviour* 33:1031–1032.
- Kuno, E. 1980. Dispersal and persistence of populations in unstable habitats. A theoretical note. *Oecologia* 49:123–126.
- Lawes, M.J. & M.R. Perrin. 1995. Risk-sensitive foraging behaviour of the round eared elephant shrew (*Macroscelides proboscideus*). *Behavioral Ecology & Sociobiology* 37:31–37.
- Miller, P.R. & G.I. Miller. 1991. Dispersal and survivorship in a population of *Geolycosa turricola* (Araneae, Lycosidae). *Journal of Arachnology* 19:49–54.
- Packer, C. & L. Rutan. 1988. The evolution of cooperative hunting. *American Naturalist* 132:159–198.
- Rannala, B.H. & C.R. Brown. 1994. Relatedness and conflict over optimal group size. *TREE* 9:117–119.
- Sibly, R.M. 1983. Optimal group size is unstable. *Animal Behaviour* 31:947–948.
- Seibt, U. & W. Wickler. 1985. Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. *Animal Behaviour* 35:1903–1905.
- Seibt, U. & W. Wickler. 1988a. Bionomics and social structure of “family spiders” of the genus *Stegodyphus*, with special reference to the African species, *S. dumicola* and *S. mimosarum*. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 30:255–303.
- Seibt, U. & W. Wickler. 1988b. Why do “Family spiders,” *Stegodyphus* (Eresidae), live in colonies? *Journal of Arachnology* 16:193–198.
- Smith, D.R. & M.S. Engel. 1994. Population structure in an Indian cooperative spider, *Stegodyphus sarasinorum* Karsch (Eresidae). *Journal of Arachnology* 22:108–113.
- Uetz, G.W. 1988. Risk sensitivity and foraging in colonial spiders. Pp. 353–377. *In The Ecology of Social Behaviour* (C.N. Slobodchikoff, ed.). Academic Press, London.
- Uetz, G.W. & C.S. Hieber. 1997. Colonial web-building spiders: Balancing the costs and benefits of group living. Pp. 458–475. *In The Evolution of Social Behaviour in Insects and Arachnids* (J.C. Choe & B.J. Crespi, eds.) Cambridge Univ. Press, Cambridge.
- Ulbrich, K., J.R. Henschel, F. Jeltsch & C. Wissel. 1996. Modelling individual variability in a social spider colony in relation to food abundance and its allocation. *Proceedings of the International Congress of Arachnology, Revue Suisse de Zoologie*. Vol. hors Serie 13:661–670.
- Vollrath, F. 1982. Colony foundation in a social spider. *Zeitschrift für Tierpsychologie* 60:313–324.
- Ward, P.I. 1986. Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. *Behaviour* 97:213–225.
- Ward, P.I. & M.M. Enders. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. *Behaviour* 94:167–182.
- Whitehouse, M.E.A. & Y. Lubin. 1999. Competitive foraging in the social spider *Stegodyphus mimosarum*. *Animal Behaviour* 58:677–688.
- Zemel, A. & Y. Lubin. 1995. Inter-group competition and stable group sizes. *Animal Behaviour* 50:485–488.

Manuscript received 28 January 2000, revised 11 July 2000.