

Limited male dispersal in a social spider with extreme inbreeding

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Cooperatively breeding animals commonly avoid incestuous mating through pre-mating dispersal. However, a few group-living organisms, including the social spiders, have low pre-mating dispersal, intra-colony mating, and inbreeding. This results in limited gene flow among colonies and sub-structured populations. The social spiders also exhibit female-biased sex ratios because survival benefits to large colonies favour high group productivity, which selects against 1 : 1 sex ratios. Although propagule dispersal of mated females may occasionally bring about limited gene flow, little is known about the role of male dispersal. We assessed the extent of male movement between colonies in natural populations both experimentally and by studying colony sex ratios over the mating season. We show that males frequently move to neighbouring colonies, whereas only 4% of incipient nests were visited by dispersing males. Neighbouring colonies are genetically similar and movement within colony clusters does not contribute to gene flow. Post-mating sex ratio bias was high early in the mating season due to protandry, and also in colonies at the end of the season, suggesting that males remain in the colony when mated females have dispersed. Thus, male dispersal is unlikely to facilitate gene flow between different matrilineages. This is consistent with models of non-Fisherian group-level selection for the maintenance of female biased sex ratios, which predict the elimination of male dispersal. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society* 2009, 97, 227–234.

ADDITIONAL KEYWORDS: breeding system – gene flow – matrilineages – movement – sex ratio.

INTRODUCTION

Cooperatively breeding animals commonly avoid incestuous mating through pre-mating dispersal. For example, in ants and termites, outbreeding is ensured by swarming of alates from different nests, and in group-living mammals and birds, by obligate pre-mating dispersal of one of the sexes (Johnson & Gaines, 1990; Cook & Crozier, 1995; Husseneder *et al.*, 1998; Lehmann & Perrin, 2003). However, a few group-living organisms are characterized by low pre-mating dispersal, intra-colony mating, and inbreeding (naked mole rats: Jarvis *et al.*, 1994; ambrosia beetles: Peer & Taborsky, 2007; gall thrips:

Chapman *et al.*, 2000; McLeish *et al.*, 2006). In the cooperatively breeding ('social') spiders, males and females of a cohort mate within the parent colony and their offspring mature and again mate within the same colony, producing inbred colonies that may last for several generations (Lubin & Bilde, 2007).

The social spiders also exhibit primary female-biased sex ratios (Aviles, 1993; Lubin & Bilde, 2007). Large colonies have increased survival (Bilde *et al.*, 2007) and colonies with a female-biased sex ratio will grow rapidly to reach the threshold size necessary to produce dispersing propagules (Aviles, 1993). The female-biased sex ratio combined with limited migration among colonies are necessary pre-conditions for group-level selection that acts against the Fisherian 1 : 1 sex ratio (Wilson & Colwell, 1981). The

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conditions favouring a female-biased sex ratio should also select against male dispersal because reproductive benefits to males resulting from their dispersal should favour the evolution of an equal sex ratio (Fisher, 1930). In the present study, we ask whether the condition of limited migration by males is met in the social spider *Stegodyphus dumicola* Pocock (Eresidae).

The inbred population structure in social spiders is perpetuated by the mode of propagation and establishment of new colonies. This is either by propagule dispersal, which is accomplished by single females (or, in some species, small groups of females) that leave the parent colony after mating to establish an incipient nest, or by budding or fission of the parent colony to form one or more sub-nests (Lubin & Bilde, 2007). Both modes of colony establishment occur in *S. dumicola*, where propagule dispersal is accomplished by ballooning females (Wickler & Seibt, 1986; Henschel, 1998; Schneider *et al.*, 2001). Although propagule dispersal of mated females could occasionally lead to limited gene flow, little is known about the role of male dispersal. Males were observed joining incipient colonies of *S. dumicola* in Namibia and, in some incipient colonies that were established by sub-adult females, these females later molted to adult and produced an egg sac (Henschel *et al.*, 1995). This indicates that they mated after dispersing from the parent colony, which could happen only if a male had joined the nest.

Both budding and propagule dispersal can produce local populations of colonies of a single maternal lineage (matrilineage), with little gene flow between lineages. Population genetic studies show that social spiders are genetically similar within colonies and within clusters of colonies in the same area (Lubin & Crozier, 1985; Smith, 1986; Smith & Engel, 1994; Smith & Hagen, 1996; Johannesen *et al.*, 2002). In *S. dumicola*, most colonies were monomorphic for mitochondrial DNA haplotypes and only 13% of colonies had two haplotypes (Johannesen *et al.*, 2002). Haplotypes that differed within or between neighbouring colonies came from the same haplotype lineage, indicating little or no mixing between different populations. However, analysis of nuclear DNA markers in this species showed that on average 15% of loci within a colony were polymorphic (Smith *et al.*, in press). These nuclear DNA data suggest that male dispersal could contribute to the occurrence of a small amount of within-colony genetic variation.

Although the field observations suggested that males can move from their natal colony into other colonies (Henschel *et al.*, 1995), population genetic structure and selection for a female-biased sex ratio lead us to predict that male mating dispersal is limited and does not contribute to gene flow in social

spider colonies. To resolve these questions, we assessed the extent of male movement between colonies of *S. dumicola* in natural populations in Namibia and South Africa, both experimentally and by studying the change in the proportion of males in colonies over the mating season. The primary sex ratio in *S. dumicola* is female-biased (Aviles *et al.*, 1999), but males mature before females (Henschel *et al.*, 1995) and the adult sex ratio will vary over time in the mating season. If males do not disperse, we predict a lower female bias (larger male/female ratio) at the end of the mating season as adult mated females disperse to establish new colonies.

MATERIAL AND METHODS

STUDY SITES AND NATURAL HISTORY

The data are derived from four study sites: two in Namibia (Rooisand Desert Farm at the eastern edge of the Namib Desert and Opumbamewa Cattle Farm near Seeis) and two in South Africa [Weenen and Spioenkop Game Reserves, KwaZulu-Natal (KZN) Province]. The characteristics of these sites are shown in Table 1.

Although we use the terms 'colony' and 'nest' interchangeably throughout, nest is used more often to denote the physical structure housing the colony. At all sites, nests of *S. dumicola* were found mainly at distal ends of branches of spiny *Acacia* spp. shrubs or trees, and more infrequently on other shrub or tree species. At Spioenkop and Weenen Game Reserves and at Seeis, *S. dumicola* nests were found in shrubs < 1.5 m above ground but, at Rooisand Desert Farm, they usually occurred in larger trees \geq 2 m above ground (Lubin & Crouch, 2003; Bilde *et al.*, 2007) (Table 1).

Colonies of *S. dumicola* exhibit strong seasonality, with some differences in timing at the different sites: adult males and females are present generally in December, egg sacs are produced in January/February and the young emerge from the egg sacs in March. In the winter months (May to August), activity is much reduced. Thus, there is only a single generation a year and the parent and offspring generations overlap only during juvenile stages of the offspring.

FIELD EXPERIMENTS TESTING MALE MOVEMENT

Three experiments in the field tested the movement of males between nearby nests: Two field experiments were conducted on Rooisand Desert Farm, Namibia, in 2003 to determine whether males will move away from a source nest into a recipient nest that contains sub-adult or unmated adult females. A third experiment, performed at Opumbamewa Farm, Seeis,

Table 1. Characteristics of the *Stegodyphus dumicola* study sites: location, annual rainfall, main habitat type, and approximate density of colonies of *S. dumicola* during the study period

Location	Annual rainfall (mm)	Habitat type	Total number of colonies surveyed (Number per km ²)	Study date
Rooisand Desert Farm, Namibia (23°17S, 16°06E)	200–250	Savanna-transition to desert: grassland with sparse shrubs and trees	128 (31)	December 2002 to May 2003; December 2003
Opumbamewa Farm, Seeis, Namibia (22°33S, 17°34E)	350–400	Grassland with scattered shrubs and acacias; heavily grazed	222 (78)	December 2003 to February 2004; November 2004
Weenen Game Reserve, KwaZulu-Natal, South Africa (27°11S, 22°70E)	c. 800	Wooded grassland	60 (4.9)	December 2007 to February 2008
Spioenkop Game Reserve and Spioenkop Lodge, KwaZulu-Natal, South Africa (28°40S, 29°30E)	825 (Crouch & Lubin 2003)	Grassland with scattered acacia trees and thickets	32 (4.8)	December 2007 to February 2008

Habitat descriptions and rainfall for Rooisand Desert Farm and Opumbamewa Farm (Seeis) are from Bilde *et al.* (2007). Colony density was estimated for the two sites in Namibia from Global Positioning System data.

Namibia, in 2004 examined movement of marked males between naturally-occurring sub-nests.

Artificial source and recipient nests

Source and recipient nests were established in the laboratory from colonies collected in the Rooisand area. Each source nest ($N = 8$) comprised of 15 mated females and 12 males. We chose this ratio of males to females because, owing to protandry, the operational sex ratio at the time of mating is close to equal (Henschel *et al.*, 1995) and, at the end of the mating season, some mated females disperse from the colony. Hence, we aimed at simulating the sex ratio at the end of the mating season because this is the time when we expected male dispersal to be favoured. All males were marked on the abdomen or legs with a nest-specific colour dot of water-based paint. Recipient nests ($N = 3$ per source nest) were placed at 0.5, 1, and 2 m from each source nest. These distances were similar to those found between closely occurring natural colonies, and we selected these relatively short distances to increase the likelihood of observing dispersing males at all. Each recipient nest had ten sub-adult or virgin adult females. Source and recipient nests were created by providing spiders with an acacia twig and wrapping spiders and twig with mesh cloth to prevent escape until the spiders had produced webs. These nests were maintained in the laboratory at natural temperature and photoperiod for several days until they had established webs. On 1 February 2003, the source and recipient nests were attached by

wire to branches on the east side of Acacia trees (the preferred orientation of nests in the field) and the mesh was opened to allow movement in and out of the colony. The nests were monitored on days 2 and 3 of the experiment, and all recipient nests were collected on day 6.

Natural source and artificial recipient nests

Recipient nests ($N = 22$) were created with 6–10 virgin females each and kept in the laboratory (as above) until the spiders had constructed capture webs. At the beginning of February 2003, each recipient nest was placed on a tree or shrub up to 5 m distance from a naturally-occurring *S. dumicola* colony. Male density in the natural source nests was not known because nests cannot be taken apart to count spiders without being completely destroyed. The aim was to examine whether males would move out of a natural nest at all and to control for the manipulation effects in experiment 1. We increased the distance to the recipient nests compared to experiment 1 to gain additional information about male dispersal ability. The recipient nests were monitored once a week for a month for the presence of a male in the nest and for the presence of egg sacs (i.e. an indication that the females had mated).

Male movement between adjacent sub-nests

We used five pairs of sub-nests that were connected by capture web to determine whether males moved readily between the connected sub-nests. On 23

Januray 2004, five males in each sub-nest were marked for individual recognition. On five dates over a period of 10 days, 20-min observations were conducted during the middle of the day (when males were active outside the nests) on each pair of sub-nests. We recorded the presence of marked males at each nest. The distances between the sub-nests in each pair were 0.17–1.05 m (median = 0.6 m). All sub-nests contained sub-adult and/or adult females and no egg sacs were seen in the nests.

MALE MOVEMENT INTO INCIPIENT NESTS

Naturally-occurring incipient nests containing one or a few females were monitored for the presence of males. At Rooisand Desert Farm, Namibia, newly-established nests were monitored bimonthly from 27 January to 15 May 2003. In Weenen and Spioenkop Game Reserves, KZN Province, South Africa, we surveyed incipient nests during December 2007 to February 2008.

COLONY SEX RATIOS

Nests were opened at two sites in Namibia, Seeis ($N = 26$ nests) and Rooisand ($N = 47$ nests) and at Spioenkop and Weenen Game Reserves (KZN) in South Africa ($N = 19$ combined). Colonies at Seeis were opened earlier in the reproductive season (November to December 2004) than those at Rooisand (December 2003 to January 2004) and KZN (December 2007 to January 2008). We counted numbers of juveniles, sub-adult females, sub-adult males, and adult males and females. Egg sacs were not present in any of the nests at this stage. We constructed frequency distributions of the proportion of males and correlated these proportions to total colony population size. Proportions were analysed using arcsine \sqrt{p} transformation and numbers of individuals were log-transformed when necessary.

We looked for changes in the proportion of males over the mating season. However, because the samples were from different populations, differences between the sites could contribute to the observed variation.

RESULTS

FIELD EXPERIMENTS

Artificial source and recipient nests

There were a total of 29 observations of marked males in the recipient nests. Marked males moved to recipient nests in seven of the eight replicates, and one unmarked male joined a recipient nest. If all 29 observations were of different males, these would represent 30.2% of the 96 initially marked males.

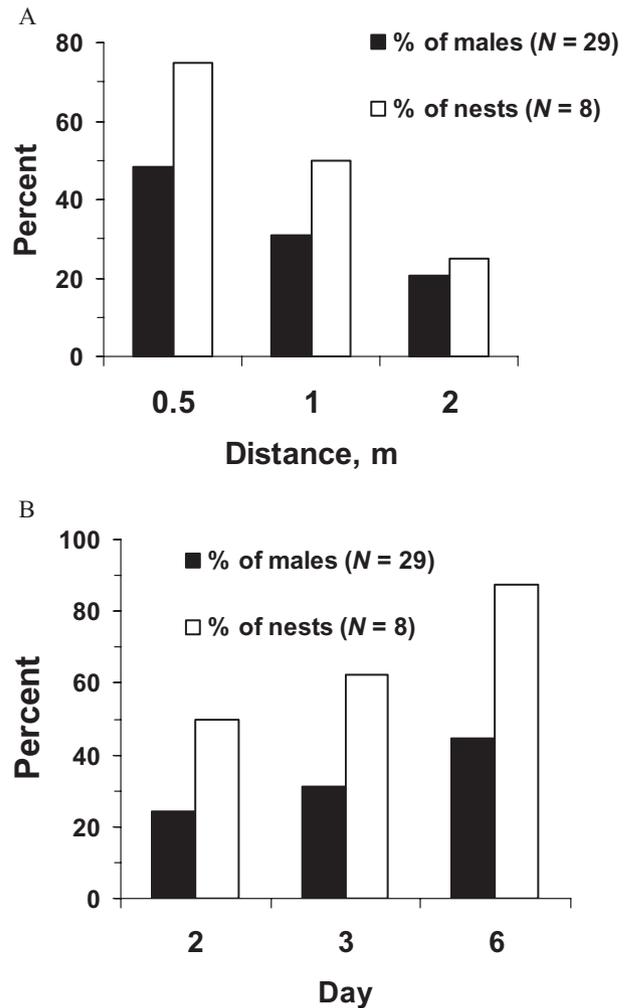


Figure 1. Field experiment 1. Percent of total marked male visits ($N = 29$) observed in recipient nests and percent of nests ($N = 8$) that were visited by marked males in relation to (A) distance of the recipient nest from the source nest (0.5, 1, and 2 m) and (B) day of observation after the release date (days 2, 3, and 6, cumulative percent).

Because males were marked according to colony, and not for individual recognition, the actual number of marked males recovered may have been lower. Discounting four cases in which a marked male was found in a given recipient nest on two successive dates, we estimate that 26% of the 96 marked males moved into recipient nests. Almost 50% of the observations of marked males were in the closest recipient nest (0.5 m) and 24% of the males arrived at a recipient nest on the first day (Fig. 1).

Natural source nests and artificial recipient nests

Of the 22 recipient nests with virgin females that were placed in the field, 13 survived after 1 month.

Table 2. Composition of nests opened at three sites: early in the reproductive season at Opumbamewa Farm (Seeis); in the middle of the season at Spioenkop and Weenen Game Reserves [KwaZulu-Natal (KZN)], South Africa (data from the two sites are combined); and late in the season at Rooisand Desert Farm in Namibia

Season: location (number of nests)	Adult males/total	Adult males/ total males	Adult females/ total females
Early: Seeis ($N = 26$)	0.079; 0.06, 0.1; 0.01–0.23	0.004; 0, 0.012 0–0.11	0.1; 0.025, 0.21 0–0.74
Middle: KZN ($N = 19$)	0.113; 0.08, 0.16; 0–0.23	0.94; 0.8, 1 0.31–1	0.44; 0.28, 0.61 0.03–0.81
Late: Rooisand ($N = 47$)	0.128; 0.1, 0.13; 0–0.46	1	0.8; 0.66, 0.92 0–1

The tabulated data are the proportions (mean; 95% confidence interval; range) of: (1) adult males out of the total colony population; (2) adult males out of the total number of males; and (3) adult females out of the total number of females.

During weekly surveys, we observed six males in four nests (30.8% of nests) and an egg sac was produced in one of these nests. An additional five nests had females that produced egg sacs, indicating that males had visited the nests and copulated with females. Thus, in all, 69.2% of the surviving recipient nests were visited by males.

Male movement between sub-nests

Forty-seven of the 50 marked males were seen on at least one later date. More than 50% moved at least once between the two sub-nests over the six dates of observation; almost 13% moved twice (median number of moves = 1). There was no significant difference among the five pairs of nests in the distribution of number of times males moved. Males were observed on adjacent sub-nests on 1–4 dates (median = 1 date). In four of the five pairs of sub-nests, marked males spent significantly more time at one of the sub-nests (χ^2 tests, $P < 0.05$); the probability of obtaining this result by chance alone is 0.0625. In two instances, the disfavoured sub-nests were large, old nests.

MALE MOVEMENTS INTO INCIPIENT COLONIES

In Rooisand Desert Farm, Namibia, males were observed in three out of 74 incipient nests (4%) in January, and two of 49 nests (4.1%) in February. Distances between these incipient colonies and the nearest colonies that could have been a source of males (i.e. established nests that contained males) were less than 1 m.

In Weenen and Spioenkop Game Reserves, South Africa, we observed four instances of a male in an incipient nest out of a total of 63 such nests that were surveyed (4.8%). The nearest larger nests that contained males were at distances of 2.6–6.6 m

(median = 5 m). Two out of four nests that were joined by males contained sub-adult as well as adult females.

COLONY SEX RATIOS

Colonies in Seeis (Namibia) showed strongly female-biased sex ratios (7.9% males on average; Table 2). The KZN (South Africa) nests from Weenen and Spioenkop combined had 11.3% males on average. At Rooisand (Namibia), the average colony sex ratio was the least female-biased, with 12.8% males on average, and the colonies also had the greatest variation in sex ratio from no males at all to 50% males (Fig. 2). The distribution of colony sex ratios was significantly different between Seeis and KZN ($\chi^2 = 11.39$, $P = 0.044$, d.f. = 5) and between Seeis and Rooisand ($\chi^2 = 17.671$, $P = 0.003$, d.f. = 5), but not between KZN and Rooisand (sex ratio categories > 0.2 were combined for the analysis).

Colonies at Seeis were opened early in the reproductive season, at the stage when males and females were just beginning to mature. These colonies contained a large proportion of juveniles (mean 69% of the total population) that could not be sexed (Table 2). Only 0.4% of all males were adult and 1% of all females were mature. Two colonies, containing 98 and 335 juveniles, respectively, had no sub-adult or adult females, and males in these two nests were all sub-adults. There were no incipient nests in the population at this time.

At KZN and Rooisand, nests were opened later in the reproductive season. At the time of collection, many small incipient colonies were present in the population, indicating that dispersal of females was occurring. Female dispersal had just begun at the KZN sites (R. Berger-Tal, pers. observ.); 94% of males were adult, but only 44% of the females were mature.

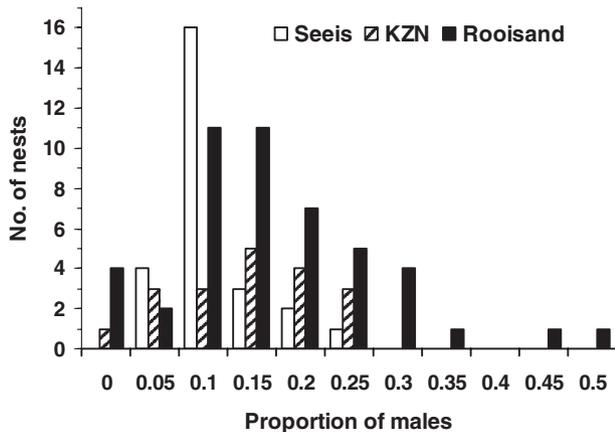


Figure 2. Proportion of males out of all spiders in nests collected from three sites at different times in the mating season: early, Seeis, Namibia (white bars, $N = 28$); middle, KwaZulu-Natal (KZN), South Africa (diagonal striped bars, $N = 19$); and late, Rooisand, Namibia (black bars, $N = 47$). The mean proportion of males (calculated from arcsin transformed data): Seeis, 0.09 (95% confidence interval = 0.063, 0.101), Rooisand, 0.133 (0.100, 0.171), and KZN, 0.117 (0.078, 0.163). The distribution of proportion of males differs significantly among the three sites ($\chi^2 = 2.28$, d.f. = 10, $P = 0.014$; categories > 0.2 were combined).

In Rooisand, nests had adult males; no juveniles or sub-adult males were present and 80% of females were adult. At Rooisand, there was a positive correlation between the proportion of males and the total number of individuals in the colony ($r = 0.335$, $t_{45} = 2.39$, $P = 0.02$), but there was no significant correlation at the other sites. Four small nests at Rooisand contained no males; all four had total population sizes ≤ 32 , well below the 95% confidence intervals for the mean colony population size (mean = 66.5, 95% confidence interval = 50.7, 82.3, $N = 47$ nests), and the three smallest of these nests contained only adult females.

DISCUSSION

We documented the movement of males of the social spider, *S. dumicola*, away from their natal colonies to join other colonies both in natural circumstances and experimentally in the field. From field observations, the probability of a male joining an incipient colony was low at sites with both high and low colony density (Table 1): 4% at the desert site (Rooisand), 4.8% at a mesic site (Weenen), and approximately 10% recorded at another mesic site in Namibia (Henschel *et al.*, 1995). By contrast, male movement was much more frequent in the three experiments. Males were observed to join 25–30% of the nearby recipient nests

in the first two experiments. In the third experiment, half of the marked males moved between sub-nests that were connected by web-silk. In experiment 2, when we added observations of the presence of egg sacs in the recipient colonies to direct observations of male movement, almost 70 percent of recipient nests placed in the same tree as a naturally-occurring nest with males in it received a visit of a male.

The difference between the frequency of naturally-occurring male arrival at incipient nests and at the experimental sub-nests may be unrelated to movement distances, which were similar in both. Males moved less than 5 m in the experiments, and the nearest nests that could contribute males to incipient nests were less than 10 m away. The difference in arrival frequency of males may be explained by differences in the nature of the recipient nests. Within a cluster of connected sub-nests, there is frequent movement of juveniles, males and females, which can occur at any stage of colony development (Y. Lubin, pers. observ.). By contrast, incipient nests are unconnected to any parent nest. Incipient nests arise by propagule dispersal; they are very small and contain usually only a single female or, more rarely, a few adult and sub-adult females (Y. Lubin and R. Berger-Tal, pers. observ.). Encounter rates with such nests will be low. However, if such a dispersing propagule happened to land near an established nest, the incipient nest might be discovered by a male moving in the vicinity. Males and additional females (adult or sub-adult) might be accepted from the neighbouring nest, which is possible because, in social spiders, foreign individuals are not rejected by the host colony (Seibt & Wickler, 1988). Thus, a male arriving at an incipient nest is a rare event by comparison with its movements into adjacent sub-nests.

Does male movement facilitate gene flow? Development within a colony is relatively synchronous (Henschel *et al.*, 1995; Bilde *et al.*, 2007). Once mating opportunities have been exhausted within the colony, dispersing males may increase their reproductive success by mating with maturing virgin females or with previously mated females in adjacent sub-nests. Thus, male movements can be understood in the context of sexual selection on mating opportunities (Andersson, 1994). Nevertheless, it has been demonstrated in several social spider species that sub-nests and adjacent colonies are derived from the same matrilineage and are likely to be genetically identical (Lubin & Crozier, 1985; Smith & Engel, 1994). Indeed, genetic data suggest that most differentiation occurs among populations (Johannessen *et al.*, 2002), whereas the data from the present study show male movements on a scale of a few meters. Thus, male movements over such short distances are unlikely to contribute significantly to within-colony variation in

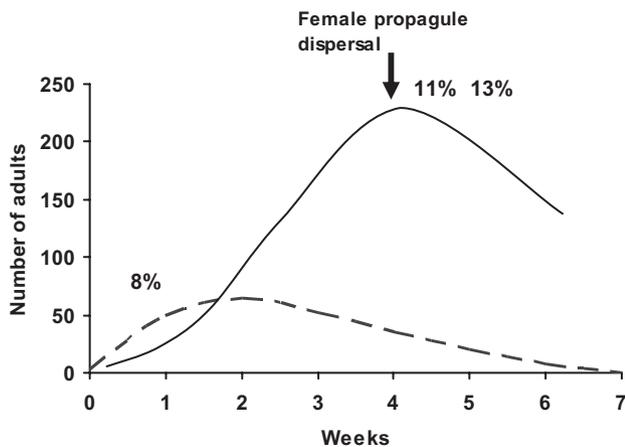


Figure 3. Schematic trajectory of numbers of adult males (dashed line) and females (solid line) in a *Stegodyphus dumicola* colony over the mating season, *sensu* Henschel, Lubin & Schneider (1995), showing the colony sex ratio (% males out of total number of individuals in the colony) early in the season (Seeis) and after female dispersal [KwaZulu-Natal (KZN) and Rooisand].

S. dumicola populations. Only on the rare occasion that a male joins an incipient nest derived from a different matrilineage would there be a possibility of outbreeding.

The results obtained in the present study suggest that selection does not favour long-distance dispersal for outbreeding opportunities in *S. dumicola*. To be most effective, male long-distance dispersal should occur at the beginning of the mating season, when virgin females are available in the population and before males exhaust their resources in mating attempts within the natal colony. Thus, we would expect to see a sharp decline in the proportion of males early in the season. The colony sex ratios we recorded indicate an opposite trend. The timing of maturation and female propagule dispersal may explain the observed changes in colony sex ratios (Fig. 3). The proportion of males in colonies was high during the early part of the mating season because males mature before females (Henschel *et al.*, 1995) and decreased as females matured. In keeping with these observations, we found that males also remained in the colony at the end of the mating season, after the dispersal of mated females. The lack of significant male dispersal was supported by a positive correlation between the proportion of males and colony size in one population examined late in the season (Rooisand). The large number of males remaining in large colonies in this population corresponds to previous observations of a higher frequency of female propagule dispersal from large colonies than from small ones (Henschel *et al.*, 1995; Schneider *et al.*, 2001).

Our data are consistent with the co-evolution of sex-biased dispersal and sex ratio in structured populations predicted by theory (Bulmer & Taylor, 1980; Perrin & Mazalov, 2000; Leturque & Rousset, 2003). The results suggest that male philopatry results from a combination of: (1) no advantage to early dispersal to nearby nests, when suitable females are continuing to mature at home, and (2) a large cost to searching for distant females. The short range movement of males and resulting low frequency of outbreeding, combined with propagule dispersal of females at the end of the mating season, also support the hypothesis of group-level selection favouring a female-biased sex ratio in these social spiders. If long-distance dispersal of males were favoured, equal sex ratios would be expected, as the production of male and female offspring should yield equal fitness. A female-biased sex ratio, however, will enable a rapid increase in colony population size. Subsequently, mated females will disperse from colonies above a threshold size to establish new colonies. The limited dispersal distances of males also suggest that outbreeding is not strongly favoured in *S. dumicola* or, alternatively, if it does provide some benefit, female long-distance dispersal will be the means of obtaining outbreeding, and not male dispersal.

Social spider species that have been studied to date demonstrate a constellation of behavioural, life history and demographic traits that, taken together, suggest that group-level selection plays a major role in their evolution (Lubin & Bilde, 2007). In the present study, we have shown that male dispersal pattern conforms to this hypothesis. However, some questions remain to be resolved in order to understand how the distinctive inbred social system is maintained in social spiders, and perhaps in similar systems in other organisms. First, genetic data from nuclear DNA markers would provide an independent test of gene flow and male versus female dispersal distances and, second, the costs and benefits of inbreeding versus outbreeding are yet to be explored in this system.

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REFERENCES

- Andersson M.** 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.
- Aviles L.** 1993. Interdemic selection and the sex ratio: a social spider perspective. *American Naturalist* **142**: 320–345.
- Aviles L, Varas C, Dyreson E.** 1999. Does the African social spider *Stegodyphus dumicola* control the sex of individual offspring? *Behavioral Ecology and Sociobiology* **46**: 237–243.
- Bilde T, Coates KS, Birkhofer K, Bird T, Maklakov AA, Lubin Y, Aviles L.** 2007. Survival benefits select for group living in a social spider despite reproductive costs. *Journal of Evolutionary Biology* **20**: 2412–2426.
- Bulmer MG, Taylor PD.** 1980. Dispersal and the sex-ratio. *Nature* **284**: 448–450.
- Chapman TW, Crespi BJ, Kranz BD, Schwarz MP.** 2000. High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 1648–1650.
- Cook JM, Crozier RH.** 1995. Sex determination and population biology in the Hymenoptera. *Trends in Ecology & Evolution* **10**: 281–286.
- Fisher RA.** 1930. *The genetical theory of natural selection*. Oxford: Oxford University Press.
- Henschel JR.** 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *Journal of Arachnology* **26**: 61–69.
- Henschel JR, Lubin YD, Schneider J.** 1995. Sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae, Eresidae). *Insectes Sociaux* **42**: 419–426.
- Husseneder C, Brandl R, Epplen C, Epplen JT, Kaib M.** 1998. Variation between and within colonies in the termite: morphology, genomic DNA, and behaviour. *Molecular Ecology* **7**: 983–990.
- Jarvis JUM, O'Riain MJ, Bennett NC, Sherman PW.** 1994. Mammalian eusociality: a family affair. *Trends in Ecology and Evolution* **9**: 47–51.
- Johannesen J, Hennig A, Dommermuth B, Schneider JM.** 2002. Mitochondrial DNA distributions indicate colony propagation by single matri-lineages in the social spider *Stegodyphus dumicola* (Eresidae). *Biological Journal of the Linnean Society* **76**: 591–600.
- Johnson ML, Gaines MS.** 1990. Evolution of dispersal – theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* **21**: 449–480.
- Lehmann L, Perrin N.** 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *American Naturalist* **162**: 638–652.
- Leturque H, Rousset F.** 2003. Joint evolution of sex ratio and dispersal: conditions for higher dispersal rates from good habitats. *Evolutionary Ecology* **17**: 67–84.
- Lubin Y, Bilde T.** 2007. The evolution of sociality in spiders. *Advances in the Study of Behavior* **37**: 83–145.
- Lubin Y, Crouch T.** 2003. Trial by fire: social spider colony demographics in periodically burned grassland. *African Zoology* **38**: 145–151.
- Lubin YD, Crozier RH.** 1985. Electrophoretic evidence for population differentiation in a social spider *Achaearenea wau* (Theridiidae). *Insectes Sociaux* **32**: 297–304.
- McLeish MJ, Chapman TW, Crespi BJ.** 2006. Inbreeding ancestors: the role of sibmating in the social evolution of gall thrips. *Journal of Heredity* **97**: 31–38.
- Peer K, Taborsky M.** 2007. Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. *Behavioral Ecology and Sociobiology* **61**: 729–739.
- Perrin N, Mazalov V.** 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist* **155**: 116–127.
- Schneider JM, Roos J, Lubin Y, Henschel JR.** 2001. Dispersal of *Stegodyphus dumicola* (Araneae, Eresidae): they do balloon after all! *Journal of Arachnology* **29**: 114–116.
- Seibt U, Wickler W.** 1988. Bionomics and social structure of 'family spiders' of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* **30**: 255–303.
- Smith DR.** 1986. Population genetics of *Anelosimus eximius* (Araneae, Theridiidae). *Journal of Arachnology* **14**: 201–217.
- Smith DR, Engel MS.** 1994. Population structure in an Indian cooperative spider, *Stegodyphus sarasinorum* Karsch (Eresidae). *Journal of Arachnology* **22**: 108–113.
- Smith DR, Hagen RH.** 1996. Population structure and interdemic selection in the cooperative spider *Anelosimus eximius*. *Journal of Evolutionary Biology* **9**: 589–608.
- Smith DR, van Rijn S, Henschel J, Bilde T, Lubin Y.** 2009. AFLP fingerprints support limited gene flow among social spider populations. *Biological Journal of the Linnean Society*, in press.
- Wickler W, Seibt U.** 1986. Aerial dispersal by ballooning in adult *Stegodyphus mimosarum*. *Naturwissenschaften* **73**: 628–629.
- Wilson DS, Colwell RK.** 1981. Evolution of sex-ratio in structured demes. *Evolution* **35**: 882–897.