The evolution of social inbreeding mating systems in spiders: limited male mating dispersal and lack of pre-copulatory inbreeding avoidance in a subsocial predecessor

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Cooperation and group living are extremely rare in spiders and only few species are known to be permanently social. Inbreeding is a key characteristic of social spiders, resulting in high degrees of within-colony relatedness that may foster kin-selected benefits of cooperation. Accordingly, philopatry and regular inbreeding are suggested to play a major role in the repeated independent origins of sociality in spiders. We conducted field observations and laboratory experiments to investigate the mating system of the subsocial spider *Stegodyphus tentoriicola*. The species is suggested to resemble the 'missing link' in the transition from subsociality to permanent sociality in *Stegodyphus* spiders because its social period is prolonged in comparison to other subsocial species. Individuals in our two study populations were spatially clustered around maternal nests, indicating that clusters consist of family groups as found in the subsocial congener *Stegodyphus lineatus*. Male mating dispersal was limited and we found no obvious pre-copulatory inbreeding avoidance, suggesting a high likelihood of mating with close kin. Rates of polygamy were low, a pattern ensuring high relatedness within broods. In combination with ecological constraints, such as high costs of dispersal, our findings are consistent with the hypothesis that the extended social period in *S. tentoriicola* is accompanied with adaptations that facilitate the transition towards permanent sociality. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **98**, 851–859.

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INTRODUCTION

Cooperation is an evolutionary paradox because it appears to contradict individual selection. Kin-selection theory states that related individuals more likely cooperate as a result of inclusive fitness gains (Hamilton, 1964). Hence, family groups with parental care and delayed dispersal of juveniles are traits that facilitate the evolution of sociality (Michener, 1958).

The evolution of permanent sociality in spiders is particularly fascinating considering that spiders are infamous for aggressive behaviour and cannibalism and, indeed, only very few species in six families are regarded as social (Lubin & Bilde, 2007). Permanently social species are hypothesized to originate from periodically social (subsocial) ancestors through philopatry and the elimination of dispersal leading to the formation of family groups (the subsocial route) (Wickler & Seibt, 1993; Avilés, 1997). Subsocial spiders show extended maternal care and hence a limited period of cooperation among siblings until the spiders leave the maternal nest to initiate a solitary

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lifestyle. Although all social and subsocial species are described as very peaceful and tolerant towards conspecifics, subsocial spiders beyond their early social phase show aggression towards intruders of the same or opposite sex, whereas permanently social spiders do not (Lubin & Bilde, 2007).

The phylogeny of the genera *Anelosimus* (Theriididae) and *Stegodyphus* (Eresidae) that both contain multiple derivations of social lineages support the hypothesis of transition to sociality via the subsocial route (Agnarsson *et al.*, 2006; Johannesen *et al.*, 2007). The family Eresidae contains three independent origins of sociality, all found within the genus *Stegodyphus* (Kraus & Kraus, 1988; Johannesen *et al.*, 2007). Maternal care and subsocial behaviour is characteristic of all *Stegodyphus* species and appears to be ancestral to the three independently-derived clades showing permanent sociality (Kullmann, 1972).

Unlike eusocial insects or cooperatively breeding vertebrate species, no mechanisms that secure outbreeding are known in permanently social spiders (Riechert & Roeloffs, 1993; Avilés, 1997; Bilde *et al.*, 2005). By contrast, inbreeding is a key characteristic of social spiders (Lubin & Bilde, 2007). The transition to an inbred mating system is a remarkable trait because one of the major forces of evolution is the avoidance of inbreeding to prevent inbreeding depression caused by deleterious recessive alleles or loss of heterozygous advantage (Charlesworth & Charlesworth, 1987). However, according to Hamilton's rule, inbreeding may facilitate the evolution of kin-selected cooperative traits (Breden & Wade, 1981). Inbreeding can be favoured when the costs of inbreeding avoidance are greater than the costs of inbreeding depression (Waser, Austad & Keane, 1986; Avilés, 1997; Kokko & Ots, 2006).

The few subsocial spider species studied to date show pre-mating dispersal that facilitates outbreeding and polyandry (Avilés, 1997; Bilde *et al.*, 2005). Long-term studies on the subsocial *Stegodyphus lineatus* demonstrated that mating is associated with substantial costs for the female and that females aggressively resist multiple mating (Erez, Schneider & Lubin, 2005; Maklakov, Bilde & Lubin, 2005). Female aggression and resistance to re-mating in *S. lineatus* is particularly strong once they guard their egg sacs. This is adaptive because the male will try to remove the egg sac in order to father eggs in a replacement clutch (Schneider & Lubin, 1996). The loss of an egg sac is very costly for the female (Schneider & Lubin, 1996, 1997). An additional disadvantage may arise because multiple paternity reduces relatedness within broods and may negatively effect cooperation (Schneider & Bilde, 2008). A possible benefit of polyandry to balance these costs may be a reduction of the negative effects of inbreeding (Maklakov *et al.*, 2005; Cornell & Tregenza, 2007). During the transition from outbreeding towards regular inbreeding, increased tolerance towards inbreeding is expected.

In the present study, we examined characteristics of the mating system of the subsocial species *Stegodyphus tentoriicola*, a sister species to the permanent social *Stegodyphus dumicola* (Kraus & Kraus, 1988; Johannesen *et al.*, 2007) to gain further insight into life history characteristics that may have facilitated the transition to permanent sociality in hypothetical subsocial predecessors. Lubin & Bilde (2007) report on *S. tentoriicola* nests that contained multiple adult females and their broods. This finding suggests that, compared to other subsocial species in the genus, *S. tentoriicola* is a species showing transitional traits towards a permanently social life style (Lubin & Bilde, 2007). Therefore, in relation to other subsocial congeners such as *S. lineatus*, we hypothesize that measures to effectively promote outbreeding such as polyandry and male mating dispersal are reduced in *S. tentoriicola*.

This is the first study of this transitory species. We studied two populations of *S. tentoriicola* in the field and conducted mating experiments in the laboratory. The study aimed to characterize the species': (1) spatial distribution within populations; (2) male mate search behaviour; (3) male and female natural mating rates; and (4) male and female behaviour during sexual encounters.

MATERIAL AND METHODS

STUDY ANIMALS

Stegodyphus tentoriicola
Stegodyphus tentoriicola (Purcell, 1904) is an eresid spider distributed in South Africa (Kraus & Kraus, 1988). It is a semelparous species (i.e. females invest all resources in a single clutch). Female spiders care for their brood and feed the spiderlings via regurgitation before they are finally consumed by their offspring (matriphagy). Subsequent to matriphagy, spiderlings have a social period within the natal nest prior to juvenile dispersal (Kraus & Kraus, 1988). Males leave their nests after maturation and actively search for females that remain in their nests. The prosoma width of adult female spiders in our populations was 4.01 ± 0.49 mm, and opisthosoma length was 8.95 ± 1.79 mm ($N = 169$). There was a positive correlation between prosoma width and opisthosoma length (Pearson correlation: $r = 0.68$, $P = 0.001$, $N = 169$). Male prosoma width was 3.36 mm ± 0.54 mm. Male opisthosoma length was 5.08 ± 1.0 mm ($N = 50$). Prosoma width and opisthosoma length were posi-

tively correlated (Pearson correlation: $r = 0.86$, $P = 0.001$, $N = 50$). In our study populations, we never found more than one adult female in a nest, *sensu* Lubin & Bilde (2007).

STUDY SITES

The first population was found on 3.12 ha of grassland in the Mountain Zebra National Park (MZNP). The vegetation was dominated by *Pentzia incana* and the area was bordered by *Acacia karoo* trees. The area inside the park was occasionally grazed by game. The second population was found on 4.5 ha of similarly vegetated grassland near Lake Arthur (Glenmore Farm). The area did not belong to the regular grazing land of the surrounding farmland. Only once during our observation period was a herd of cattle driven through the area. The majority of spider-nests in both study areas were found in low vegetation; only a few were found higher than 30 cm above the ground.

MEASUREMENT AND MARKING OF SPIDERS

The survey was carried out from February to April 2008. Spider nests of two populations near Cradock (Eastern Cape, South Africa) were marked with weatherproof tape and their position was mapped with a GPS (Garmin 12 XL) to characterize the spatial distribution. We measured prosoma width and opisthosoma length of every spider with callipers. The prosoma is a sclerotized body part that does not change during an instar and its width is a common measure of body size. After measurement, males and females were marked individually with water colour dots on the dorsal side of the opisthosoma. The small dots were applied with slender blades of grass. Females that moulted were marked and measured again. Male mate search had already begun when our survey was initiated and most of the males were found inside female nests. Hence, it was not possible to distinguish between males that mate locally within their patch of maturation (= resident) and males that immigrated from distant patches. Thus, the existence of inbreeding could only be inferred from what we observed from male mate search behaviour after first sighting.

MALE MATING DISPERSAL AND NATURAL MATING RATES

Every nest was checked daily for the presence of males, and later for the presence of egg sacs, using a pocket mirror to observe the inside of the nest without disturbance of the spiders. We assumed that males move at night and remain inside a female's nest during the day. In *S. lineatus*, males that stayed in a female's nest usually succeeded in mating (Bilde *et al.*, 2005); we assumed the same in *S. tentoriicola* providing us with an approximate measure of male mating success. Squeezing of the nest (a funnel-shaped tube of silk) was occasionally necessary to remove unmarked males or to identify a marked male.

During the daily surveys, we recorded visits of marked male spiders to female nests and measured the covered distances with a tape measure.

MALE AND FEMALE BEHAVIOUR DURING SEXUAL ENCOUNTERS

Mating experiment in the field

In experimental trials in the field, we placed a male on the web of a female guarding an egg sac and observed the nest for 30 min. If no aggressive interactions (biting, chasing the male away) occurred within this time, the male was removed and returned to the nest where he was found. This test examined whether males succeed in removing a female's egg sac and mate with her, forcing her to produce a second clutch that will then contain mixed-paternity brood (Schneider & Lubin, 1996). Such behaviour reduces relatedness among siblings in a brood and subsequently the potential kin-selected benefits of cooperation (Schneider & Bilde, 2008).

Mating experiment in the laboratory

The spiders used in the mating experiment were collected from their natural habitat in South Africa. They hatched between April and May 2008. The juveniles and their mothers were left inside their natal nests and were kept in plastic containers in the laboratory. They were kept under natural daylight and temperature in the range 20–28 °C. A ventilator produced a slight airflow. The spiders were fed with *Calliphora* spp. and *Acheta domesticus*.

Upon maturation around October, spiders were weighed and measured and individually housed in circular perspex-frames (diameter 20 cm). They were randomly assigned to an inbreeding ($N = 10$) or outbreeding ($N = 10$) treatment. Virgin females of the inbreeding-treatment were mated once to a single male from the same brood; females in the outbreeding-treatment were mated once to an unrelated male that stemmed from a population 30 km away.

We placed each male into a female's frame and observed any interactions of the pair for at least 20 min. An observation was terminated after 2 h, or if no activity was observed for 60 min.

Females showed the following presumed levels of aggressiveness: 0 = passiveness; 1 = opistosoma vibra-
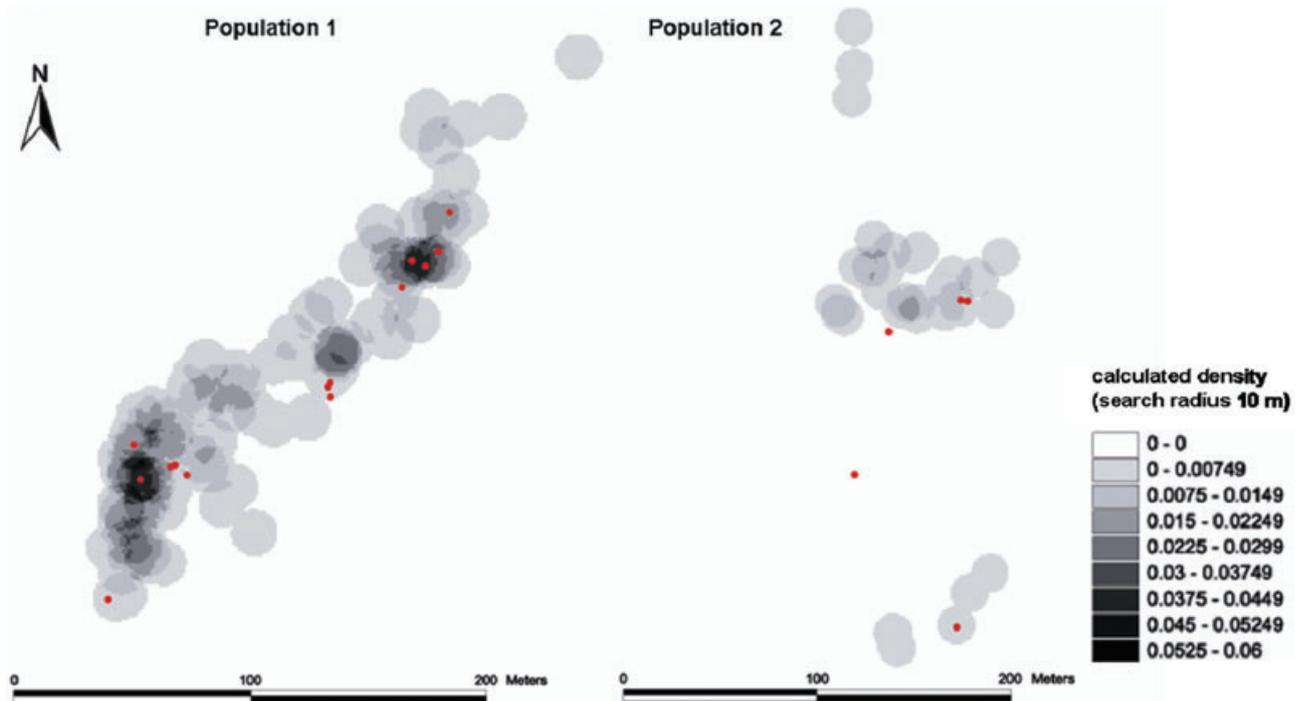
Figure 1. Use of space of the two populations (Mountain Zebra National Park = Population 1; Glenmore Farm = Population 2). Dark areas represent high spider density. Dots indicate deserted, maternal nests of the past season.

tion; 2 = spreading of first pair of legs and pushing the male backwards; 3 – opening of her chelicerae, sometimes followed by biting the male. Observed male behaviours included drumming on the female opisto- soma with the first pair of legs; stroking of the dorsal side of the female's opisthosoma; and the use of the pedipalps to touch the female's epigyne. It was diffi- cult to observe the insertion of pedipalps (copulation) directly. When spiders took up the mating position and the male touched the female's epigyne, this was considered to demonstrate mating.

STATISTICAL ANALYSIS

Data were analysed with JMP 7. All variables were tested for normal distribution (Shapiro–Wilk W-test) and we used nonparametric tests if the requirements for parametric analyses were not fulfilled. Results are given as the mean ± SE. Analyses of population struc- ture and migration distances were performed with ARCVIEW, version 3.1.

RESULTS
SPATIAL DISTRIBUTION

Nests containing mainly mature females were not evenly distributed on vegetation within the popula- tions but mostly occurred in clusters. Nearest neigh- bour distances of nests within the populations

differed significantly from a random distribution (Population 1: Mann–Whitney U-test: $\chi^2 = 44.3$, $N_{random} = 130$, 7.15 ± 0.31 m; $N_{pop1} = 130$, 4.57 ± 0.41 m, $P < 0.0001$, Population 2: $\chi^2 = 19.0$, $N_{random} = 36$, 15.78 ± 1.2 m; $N_{pop2} = 36$, 7.9 ± 0.92 m, $P < 0.0001$). Most of the deserted maternal nests of the past season (dots) were located within the clusters (Fig. 1), suggesting that aggregations might consist of off- spring from a single maternal nest similar to a pattern documented in *S. lineatus* (Johannesen & Lubin, 2001). The mean density of adult females in the study year was 0.42 females per 100 m² in popu- lation 1 (MZNP) (130 females in total, area: 3.12 ha) and 0.08 females per 100 m² in population 2 (Glen- more Farm) (36 females in total, area: 4.5 ha).

MALE MATE SEARCH BEHAVIOUR

We observed 28 male movements between female's nests in total ($N = 12$ spiders). Ten of the 12 observed males exclusively moved within clusters. Males moved from one female to the next within a single night in 19 cases (nine different males) and covered a distance in the range 0.26–13.24 m. The average dis- tance covered was 3.3 m per night (median = 1.8 m, $N = 9$ spiders).

In nine other cases, we did not recapture marked males for several days but, eventually, they appeared in another female's nest after 2–14 days. The
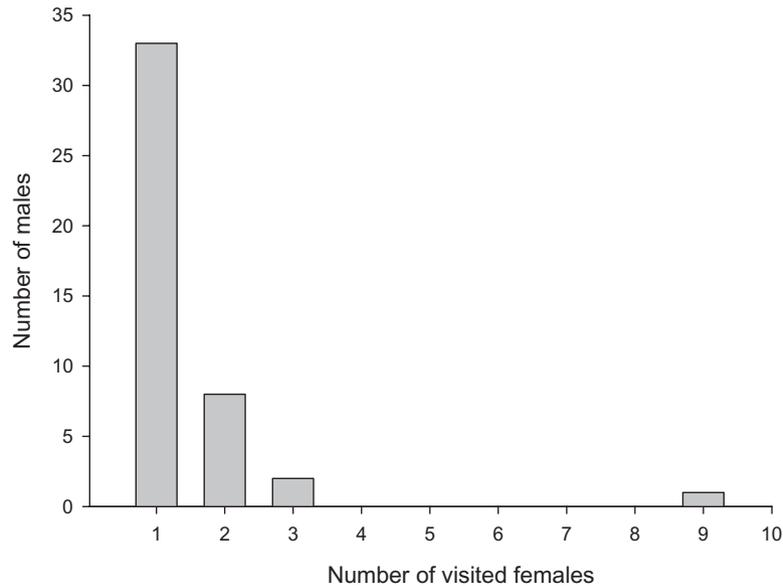
Figure 2. Number of females visited by individually marked males ($N = 44$).

maximal distance that a male walked between two female nests was 68.57 m in eight nights. We have no information regarding where those males stayed in between sightings.

Neither male prosoma width (linear regression, $r^2 = 0.06$, $P = 0.46$; $N = 12$), nor male opisthosoma length (linear regression: $r^2 = 0.07$, $P = 0.41$, $N = 12$) influenced the distance covered during mate search (m day^{-1}).

MALE AND FEMALE NATURAL MATING RATES

Males visited on average 1.5 females (median = 1, SD = 1.28, $N = 44$ males, range 1–9). Thirty-three (75%) of the observed males visited a single female, eight (18.18%) visited two females, two (4.54%) visited three females, and one (2.27%) visited nine females (Fig. 2). Males only found in deserted nests ($N = 5$) or males that were only found with a female that already had produced an egg sac ($N = 4$) were excluded because they had no reproductive success. Females were visited by 1.3 males on average (median = 1, SD = 0.72, $N = 40$ females, range 1–5).

Male size did not influence the number of visited females (logistic regression: $\chi^2 = 1.58$, $r^2 = 0.03$, $P = 0.21$, $N = 44$). Larger females did not attract more males than smaller females (Spearman correlation: $r_S = -0.19$, $P = 0.23$, $N = 40$). The course of the mating season did not affect the number of visited females; earlier males did not visit more or less females than later males (Spearman correlation: $r_S = -0.05$, $P = 0.73$, $N = 44$). The first egg sac was found on 17 February There was an overlap between the mating and the egg-laying season in that males were still active when most of the females had already produced an egg sac (Fig. 3). Males never tried to remove an existing egg sac. We found four female nests with simultaneously cohabiting males but never observed that males behaved aggressively towards other males.

MALE AND FEMALE BEHAVIOUR DURING SEXUAL ENCOUNTERS

Mating experiment in the field

We tested whether a conflict over remating is present in *S. tentoriicola* by putting males on the webs of 13 females with egg sacs. We observed their behaviour and found little evidence for aggressive resistance: ten of 13 males attempted to enter the female's nest. Nine males were peacefully accepted by the females while a single male was chased away (9 : 1, two-tailed sign-test: $P = 0.0215$). We did not observe *S. tentoriicola* males attempting to remove an egg sac.

Mating experiment in the laboratory

In the laboratory, females were presented with either a sibling or an unrelated male. No difference was observed in mating success among inbreeding and outbreeding mating trials. Of the 15 males that reached the mating position, 13 stroked the female and 12 touched the epigyne; males of both treatments were equally likely to stroke the female's opisthosoma (two-tailed Fisher's exact test: $P = 0.49$, $N = 15$) and to touch the epigyne (two-tailed Fisher's exact test: $P = 0.60$, $N = 15$).

Sixteen of 20 females did not show any obvious reaction towards the introduced male. Four females reacted aggressively: three towards a brother and
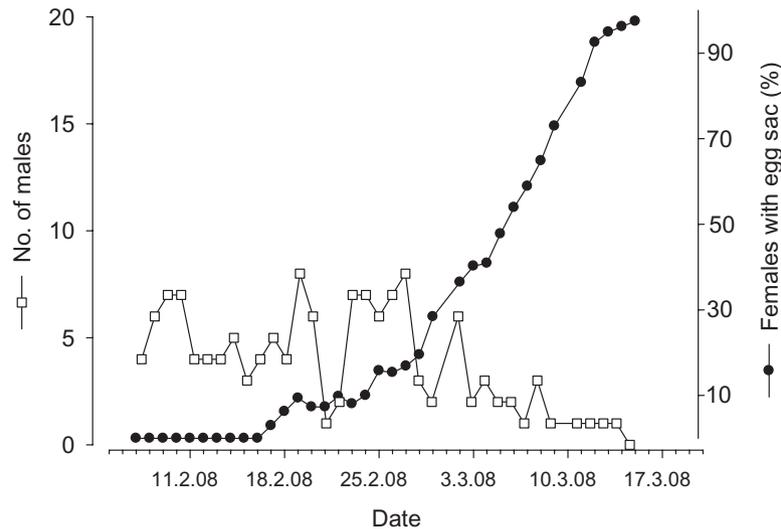
Figure 3. Overlap of the mating and egg-laying seasons of the two observed populations (pooled data). The figure shows the number of active males (□) and the cumulative proportion of females with egg sacs (●).

one towards an unrelated male ($\chi 2 = 1.25$, $P = 0.26$, $N = 20$).

Male opisthosoma vibration occurred in seven inbreeding and in seven outbreeding trials. The time until the male reached the mating position was not influenced by such vibrations (t-test: t = –0.67, $N_{vibrating} = 12$, 22.13 ± 13.57 min; $N_{nonvibrating} = 3$, 15.69 ± 8.73 min, $P = 0.55$). The time until the first male-female contact occurred did not differ between the treatments (Mann-Whitney U-test: $\chi^2 = 0.027$, $N_{inbreeding} = 10$, 4.86 ± 1.64 min; $N_{outbreeding} = 9$, 4.33 ± 2.24 min, $P = 0.87$).

All males of the inbreeding treatment were observed drumming on the female opisthosoma but only six from the outbreeding treatment ($\chi^2 = 5.0$, $P = 0.025$, $N = 20$).

The interval between putting the male onto the web and his reaching of the mating position (t-test: $t = –0.56$, $N_{inbreeding} = 9$, 19.27 ± 15.2 min; $N_{outbreeding} = 6$, 23.19 ± 11.66 min, $P = 0.58$) was similar between the treatments.

Female aggression was not related to male size (logistic regression: $\chi^2 = 0.24$, $r^2 = 0.012$, $P = 0.62$, $N = 20$). Males responded to female aggression with opisthosoma vibration and pushing behaviour. Two of the aggressive females from the inbreeding treatment subsequently allowed the male to assume the mating position.

DISCUSSION

Inspired by the hypothesis that limited dispersal and lack of pre-mating inbreeding avoidance should facilitate the transition to permanent sociality, we exam-

ined whether *S. tentoriicola*, suggested to resemble a transition species between subsocial and social living, would be prone to inbreeding. Consistent with this hypothesis, we found short male movements, low mating rates, and no obvious pre-copulatory inbreeding avoidance. Similar traits were previously documented in another subsocial congener *S. lineatus* (Bilde *et al.*, 2005).

SPATIAL DISTRIBUTION

The distribution of individual nests of *S. tentoriicola* was clumped even though the habitat seemed relatively homogenous. Clusters might be consisting of related individuals, as documented in *S. lineatus* (Johannesen & Lubin, 1999, 2001), because large abandoned maternal nests of the last season were located within these clusters. One cause of the spatially clumped distribution might be short distance dispersal of the young (natal philopatry) (Lubin, Hennicke & Schneider, 1998). If web sites retain their quality over time, remaining near the maternal nest would be a way of ensuring to settle at a suitable site. On the other hand, dispersal might be constrained by high costs such as the risk of predation, starvation, or desiccation during movement. Another cause of a clumped population pattern might be differential mortality and reproduction rates. Spiders that settle at an inferior site either die or are unable to reproduce (Lubin *et al.*, 1998).

MALE MATE SEARCH BEHAVIOUR

We investigated male dispersal to establish whether males search for mates only locally, or move long

distances that would allow them to reach unrelated females. Because of the advanced mating season, however, it was not possible to distinguish with certainty between resident (within population) and immigrant males. *Stegodyphus tentoriicola* males typically covered short distances (3.3 m day^{-1} on average) and usually made these movements within a cluster (i.e. a potential sibling group). Distances measured are similar to those reported from *S. lineatus* males ($\leq$ 5 m) (Bilde *et al.*, 2005). During the observation period, most *S. tentoriicola* males encountered only a single female, usually from within the same cluster. If nest clusters consist of siblings, mating between close kin may be common. In general, a high risk of encountering kin during mate search is expected to select for inbreeding avoidance (Émlen, 1991; Cook & Crozier, 1995; Cockburn, 1998). Exceptions from this rule arise, however, when the costs of lost mating opportunities, or high mortality rates during dispersal, exceed the costs of inbreeding (Waser *et al.*, 1986). Short male movements that result in mating with kin may be the first step towards inbred sociality (Lubin & Bilde, 2007).

MALE AND FEMALE NATURAL MATING RATES

Males visited on average 1.5 females and there was variation in mating success (range 1–9), and females were visited by 1.3 males (range 1–5). Later males did not appear to compensate the risk of encountering a mated female by visiting more females in total. However, the fieldwork was conducted during the advanced mating season. Hence, it is possible that some males had already visited females before the observation began.

Our field data suggest that natural mating rates are low, male movements short and encounters between potentially related mates are likely. Field observations as well as observations in the laboratory suggest that there is a lack of pre-mating discrimination against related mates. This is a suite of traits that may result in a partially inbreeding mating system and possibly inbreeding tolerance (Bilde *et al.*, 2005), consistent with the expectations from the subsocial route to inbreeding social mating systems through philopatry and delayed dispersal.

MALE AND FEMALE BEHAVIOUR DURING SEXUAL ENCOUNTERS

Female intersexual aggression in *S. tentoriicola* was rare and independent of mating status or male relatedness. Unlike in *S. lineatus* (Schneider & Lubin, 1996, 1997), there was no evidence for infanticide in *S. tentoriicola*. The absence of this threat to females might explain why even females that had already produced their eggs, and were uninterested in mating, admitted males into their retreats. It may appear surprising that males do not attempt to remove the present egg sac to enforce copulation, as observed in *S. lineatus* (Schneider & Lubin, 1996, 1997).

The results of the mating experiment in the laboratory indicate that female *S. tentoriicola* exhibit no behavioural mechanism to prevent mating with close relatives. One possible mechanism could have been aggression towards related males. Resistance behaviour was rare, but occurred in both treatments, and was independent of male size. This implies that females are either unable to identify a related male or that they do identify but accept a related male.

Male behaviour did not differ between the treatments, except that drumming on female's opisthosoma occurred more often in the inbreeding than in the outbreeding treatment. However, drumming did not result in higher rates of reaching the mating position and did not inhibit aggressive female behaviour. Male opisthosoma vibration, which is probably courtship behaviour, did not differ between the treatments. The vibration did not shorten the time until reaching the mating position, as was found in *S. lineatus* (Maklakov, Bilde & Lubin, 2003). Male as well as female behaviour suggest a lack of pre-mating inbreeding avoidance in *S. tentoriicola*. In the absence of pre-mating inbreeding avoidance, polyandry may provide a potential for outbreeding if females preferentially bias paternity towards unrelated males (Arnqvist & Nilsson, 2000; Tregenza & Wedell, 2002). In *S. lineatus*, multiple mating is common and results in mixed paternity (Schneider & Lubin, 1996, 1998). However, the majority of the observed *S. tentoriicola* females were monandrous, which diminishes the potential for post-mating inbreeding avoidance (Tregenza & Wedell, 2002). Data concerning inbreeding effects on fitness in *S. tentoriicola* are lacking, but it is possible that monandry and mating among kin favours inbreeding tolerance (Bilde *et al.*, 2005). According to Hamilton's rule, one potential benefit of inbreeding might be favouring the evolution of kin-selected cooperative traits through an increase in the coefficient of relatedness (Breden & Wade, 1981; Schneider & Bilde, 2008). Higher cooperation within the brood among other factors such as high dispersal mortality (Lubin *et al.*, 2009) may lead to prolonged associations of juveniles in this species. Delayed juvenile dispersal was found to benefit females and their offspring in another subsocial species, *Anelosimus studiosus* (Jones & Parker, 2002). In the same species, communal or solitary breeding was found to be an alternative reproductive strategy depending on environmental conditions (Jones & Riechert, 2008). Similar factors may be operating in *S. tentoriicola*

providing an explaination as to why, unlike that previously reported in Lubin & Bilde (2007), females in the previous study were not found to breed communally.

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