



High mortality and female-biased operational sex ratio result in low encounter rates and moderate polyandry in a spider

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Mating systems are shaped by ecological factors such as timing of maturation, spatiotemporal distribution of individuals, and the operational sex ratio. These factors influence male–female encounter rates, which shape the intensity and form of inter- and intrasexual competition. Whereas knowledge of natural encounter rates is vital for understanding the evolution of mating systems, data from the wild are difficult to obtain. We present data on the ecology and natural history of the subsocial spider *Stegodyphus bicolor* (Eresidae) with the aim of assessing its mating system. We investigated male mate search in relation to female spatial distribution, the timing of maturation of individuals, and the operational sex ratio, which may affect male–male competition and be used to predict mating strategies. We recorded male visits and cohabitation patterns with females of different reproductive state (immature and adults) to investigate evidence for mate choice as an indicator of sperm priority patterns. Finally, we used male visiting rates as a proxy for female natural mating rates. Both sexes matured synchronously: 51% of the females mated and received on average 1.2 visiting males. With increasing female availability male cohabitation time decreased. Preference for adult females, a decline in the occurrence of cohabitation with increasing female availability, and a lack of male protandry suggest that males do not employ strategies to protect paternity. Indeed, female-biased operational sex ratio throughout the mating season and high mortality may result in low male visitation rates. We suggest that ecological constraints shape a moderately polyandrous mating system in this species. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, 107, 910–919.

ADDITIONAL KEYWORDS: Eresidae – mate search – mating systems – natural mating rates.

INTRODUCTION

The ecology and life history of species provide insights to the selective forces driving the evolution of mating systems. Because of the differential investment in reproduction between the sexes, females are the limiting sex for which males generally compete (Bateman, 1948; Trivers, 1972). In most systems males move in search of females (Andersson, 1994; Kokko & Wong, 2007; but see Aisemberg, Viera & Costa, 2007), and their reproductive success is largely predicted by the number of mating partners achieved

(Bateman, 1948). The rate at which males encounter potential mating partners within a population is limited by ecological factors, such as the spatiotemporal distribution of individuals and the operational sex ratio (OSR) of the population, i.e. the average ratio of sexually active males to sexually active females (Emlen & Oring, 1977; Ims, 1988; Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjö, 1996).

Male searching ability will depend on several factors, such as locomotive performance (i.e. ability to move through space) or cognitive processes (i.e. visual or olfactory cues), and their success will also depend on the distances that they are required to cover to reach females, on the timing of maturation to adulthood (i.e. female sexual maturity), and their spatial

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distribution. For instance, if females are randomly distributed or mature synchronously, the chances that males reach many mating partners is expected to be low (Ims, 1988). The mortality of individuals is also a significant source of variation in male–female encounter rates. Males generally suffer from higher mortality rates because of the costs associated with searching for a mate, such as predation risks and energetic expenses (Gwynne, 1987; Vollrath & Parker, 1992; Kotiaho *et al.*, 1998; Byers, Byers & Dunn, 2006; Kasumovic *et al.*, 2007; Kokko & Wong, 2007; but see De Mas, Ribera & Moya-Laraño, 2009). Hence, biases in the operational sex ratio should shape the adopted male mating strategy (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996; Weir, Grant & Hutchings, 2011). When there is a female-biased operational sex ratio ($OSR < 1$), females face very low chances of encountering a second male. Males are thus expected to experience a reduction in male–male competition for mating partners and achieve full paternity of the offspring from each mating. Males would benefit from increased reproductive success by searching for new mating opportunities rather than investing all of their resources in a single mating partnership (Fromhage, McNamara & Houston, 2008; Berger-Tal & Lubin, 2011). In contrast, a male-biased operational sex ratio ($OSR > 1$) would imply an elevated risk of competition among males. Males should therefore invest in paternity protection, for example via contests or mate guarding, rather than investing in multiple matings (Enders, 1993; Dick & Elwood, 1996; Segoli, Harari & Lubin, 2006; Kasumovic *et al.*, 2007).

The number of mating partners a female achieves in her lifetime, i.e. one (monandry) or several mates (polyandry), may have broad implications for inter- and intrasexual competition. In a polyandrous context, male mating strategies will also be shaped by sperm priority patterns (Parker, 1970; Austad, 1984; Simmons, 2001; Uhl, 2002). If fertilization success is biased towards the first male to mate, selection should favour males that mature early and that are able to seek and guard immature or virgin females before mating. Whereas under conditions in which sperm from the last male to mate with the female takes precedence, males should seek and guard mature females after mating, and aim to be the last male to mate because of sperm competition (Bonduriansky, 2001; Wedell, Gage & Parker, 2002). Thus, the timing of maturation over the season, male mate choice for females differing in their sexual maturity or mating status, and mate guarding behaviour may reveal important information about the intensity of sperm competition and fertilization patterns. Factors such as parental investment in offspring or male provisioning of females further contribute to shaping

the mating system in a predictable way. For instance, a high frequency and degree of polyandry may be expected when females gain direct benefits (i.e. food or sperm supply) from mating (Arnqvist & Nilsson, 2000). Studies of male and female behaviours and life-history traits in the wild can therefore provide insights into the mating system of a species.

Here, we report data from a field study of a natural population of the subsocial spider *Stegodyphus bicolor* (O. Pickard-Cambridge, 1869) (Eresidae) with the aim of gaining insights into the life history and the mating system of this species. The reproductive biology of *S. bicolor* is unknown. To our knowledge, the only records available for this species concern its taxonomic and phylogenetic description: *S. bicolor* occurs in Southern Africa (Namibia, Botswana, and South Africa) and is phylogenetically grouped with two sister species, the subsocial *Stegodyphus dufuori* (Audouin, 1826) and the permanently social *Stegodyphus sarasinorum* Karsch, 1891 (Kraus & Kraus, 1988; Johannesen *et al.*, 2007). Spiders of the Eresid family are semelparous, and invest all their resources into a single clutch, as females provide extreme maternal care until they are eventually eaten by their young (Kullmann, Sitterz & Zimmermann, 1971). Subsocial *Stegodyphus* spiders are further characterized by a temporary cooperative stage in which juveniles cohabit and cooperate in prey capture, followed by philopatric dispersal and the establishment of a solitary lifestyle (Lubin, Hennicke & Schneider, 1998; Johannesen & Lubin, 1999, 2001). During the breeding season adult males abandon their nest in search of sedentary females (Schneider, 1997; Ruch *et al.*, 2009). These features appear to be shared by all subsocial species of the genus *Stegodyphus* (Kullmann, 1972; Kraus & Kraus, 1988).

We investigated aspects of the reproductive biology of a wild Namibian population of *S. bicolor* by addressing ecological factors that affect encounter rates, such as spatiotemporal distribution of individuals, sex ratio during the breeding season, and survival rates. We monitored the population during the breeding season and recorded the timing of maturation of spiders, male visits to females that differed in their reproductive state (immature versus mature), and duration of cohabitation with the females. The duration of cohabitation with females may represent an indicator of the intensity of male–male competition. Hence, pre- or post-copulatory cohabitation might be expected under the risk of sperm competition, depending on whether there is first or last male sperm priority (Schneider, 1997; Uhl, 2002; Maklavov, Bilde & Lubin, 2004). Alternatively, males could occupy female nests to steal food captured by the female web (Erez, Schneider & Lubin, 2005), or to benefit from shelter and avoid the risk of searching

for other females because of the mortality costs associated with searching for a mate (Kokko & Wong, 2007; Berger-Tal & Lubin, 2011). We estimated male visitation rates to females as a proxy for female natural mating rates to examine the mating system of *S. bicolor*, as male encounter rate may be considered a reliable measure of female mating rate (Moya-Laraño, Pascual & Wise, 2003; Maklakov & Lubin, 2004; Bilde *et al.*, 2005; Berger-Tal & Lubin, 2011). Finally, we estimated female reproductive fitness with the aim of understanding the economics of the mating system.

MATERIAL AND METHODS

STUDY LOCATION

We conducted a field survey on a study population (site 1) found in a 7.2-ha grassland belonging to the Huttenhof Farm, close to Otavi, in Namibia (19°28'50"S, 17°11'39.6"E). Spiders were found inside nests that consist of a funnel-shaped tube of silk (approximately 4–8 cm in length) placed with the entrance facing the ground. An irregular shaped capture-web generally radiates from the entrance of the nest and runs on one of the lateral sides of the nest. Nests were attached to grass and low vegetation (at approximately 30–40 cm above ground) consisting of annual shrubs and grasses typical of the Southern African savannah Bushveld biome. The study area bordered a country road: it was unfenced and therefore subject to potential animal grazing.

FIELD SURVEY

Starting from 11 January 2010 (day 1), the population was monitored every 4 days for 48 days, with the only exception being day 44 where observations were prevented by rain. A total number of 109 spider nests were individually marked with weatherproof tape and were assigned GPS coordinates to characterize the spatial distribution of the population. At the beginning of the survey each nest hosted one resident individual, and the reproductive state of each individual was described (immature, adult female, or adult male). Immature spiders were not sexed because of the lack of visible morphological traits to differentiate between males and females. Adult individuals were those for which we recorded a moult. We classified adult males based on the occurrence of pedipalps (spiders' secondary sexual organs), whereas adult females were classified a posteriori because of the difficulties in visually distinguishing them from subadult females. Therefore, we classified females as adults if we did not observe a second moult and/or if an egg sac was produced after a visit from a male. During each observation we recorded the reproductive

state of the resident spider, the occurrence of moults inside or at the entrance of the nest, the presence of males visiting females inside or on the nest, the occurrence of mating pairs, and the presence of egg sacs. In order to avoid any disturbance of the spiders we checked the inside of the nests using a pocket mirror. If spiders were out of sight we would squeeze the nest gently from the peak opposite to the entrance, which made the spider move towards the observer. Nests that were found deserted or that disappeared altogether were used as an indication of female mortality because adult females rarely move (R. Berger-Tal and C. Tuni, pers. observ.), as in other *Stegodyphus* species (Schneider, 1997; Ruch *et al.*, 2009; Berger-Tal & Lubin, 2011). Our experimental design did not allow us to distinguish between resident and immigrant males. Although male mating dispersal is known to be limited in other *Stegodyphus* species (Bilde *et al.*, 2005; Ruch *et al.*, 2009; Berger-Tal & Lubin, 2011), we considered the number of immigrants to equal the number of emigrants.

Each male found visiting a female inside her nest was marked individually with non-toxic watercolour dots on the dorsal side of the opisthosoma in order to distinguish among subsequent visiting males (i.e. if it was the same male found in the nest on subsequent days of observation or a new male). Males of *Stegodyphus lineatus* (Latreille, 1817) that are found inside a female's nest always succeeded in mating, as females later produce fertilized eggs (Maklakov & Lubin, 2004; Bilde *et al.*, 2005), and hence we used male visitation rate as a proxy for female natural mating rate.

FEMALE FITNESS

In order to investigate female fitness in relation to natural mating rates we conducted the last inspection of nests on day 60 (15 March 2010) and collected all surviving females to reproduce in captivity. Females were housed in small plastic cups with a mesh lid, and were kept inside their nest where they laid egg sacs. We kept them under natural daylight and temperature (mean \pm SD, 24.5 ± 1.4 °C) conditions for 1.5 months. Afterwards, to prevent the unsuccessful hatching of eggs, we placed them under light bulbs for 3 hours per day around noon, which raised the temperature to 27.2 ± 1 °C (mean \pm SD) to simulate a natural increase of temperature and enhance the hatching success of eggs. Females were fed once a week with small crickets (*Acheta domestica*) and blowflies (*Calliphora* sp.), and were monitored for the production of new egg sacs and the emergence of hatchlings on the day of feeding. Once egg sacs hatched we counted the number of spiderlings and preserved them in 70% ethanol. We measured the

prosoma width of adult females with calipers as a measure of body size. Prosoma width is a standard measure of body size in spiders, as the exoskeleton is sclerotized, and therefore does not change in size during the adult life of the individual (Foellmer & Moya-Laraño, 2007). The prosoma width of adult females was 4.42 ± 0.06 mm ($N = 70$), and was 3.83 mm for the single male collected. One of the females hosted a visiting male inside the nest on the day of collection, which was raised and measured.

ADDITIONAL COLLECTION FROM SITE 2

Once the field survey at site 1 was terminated, we assigned GPS coordinates to 63 additional nests found from a second study population (site 2) from the same area ($19^{\circ}29'22.3''S$, $17^{\circ}11'28.5''E$) to characterize their spatial distribution and compare it with the distribution of individuals sampled from site 1. The study population from site 2 was 650 m distant from site 1, and consisted of 2.8 ha of grassland. All nests that were occupied by adult females were collected and kept in the laboratory (as described above) to measure their reproductive output.

STATISTICAL ANALYSIS

Data were analysed using JMP 7 (SAS Institute). Continuous variables were tested for normal distribution (Shapiro–Wilk W -test) and variances for homogeneity (Levene’s test). Non-parametric tests were used if the requirements for parametric analyses were not fulfilled. Results are given as means \pm SEs. Spatial distribution analysis was conducted using the ArcGIS 9. Nearest-neighbour analysis was performed using Clark and Evans’ random spatial index, R , which calculates patterns of distribution (Krebs, 1989), and its value indicates random ($R = 1$), clumped ($R < 1$), or regular ($R > 1$) patterns.

RESULTS

SPATIAL DISTRIBUTION OF SPIDERS

Spider nests were not evenly distributed within the two study populations, but occurred in clusters, as shown in Figure 1. The nearest distance of nests differed significantly from a random distribution, and indicated a clumped distribution in both study populations (site 1, $R = 0.41$, $z = -5.58$, $P < 0.0001$; site 2, $R = 0.36$, $z = -12.21$, $P < 0.0001$). The mean density of

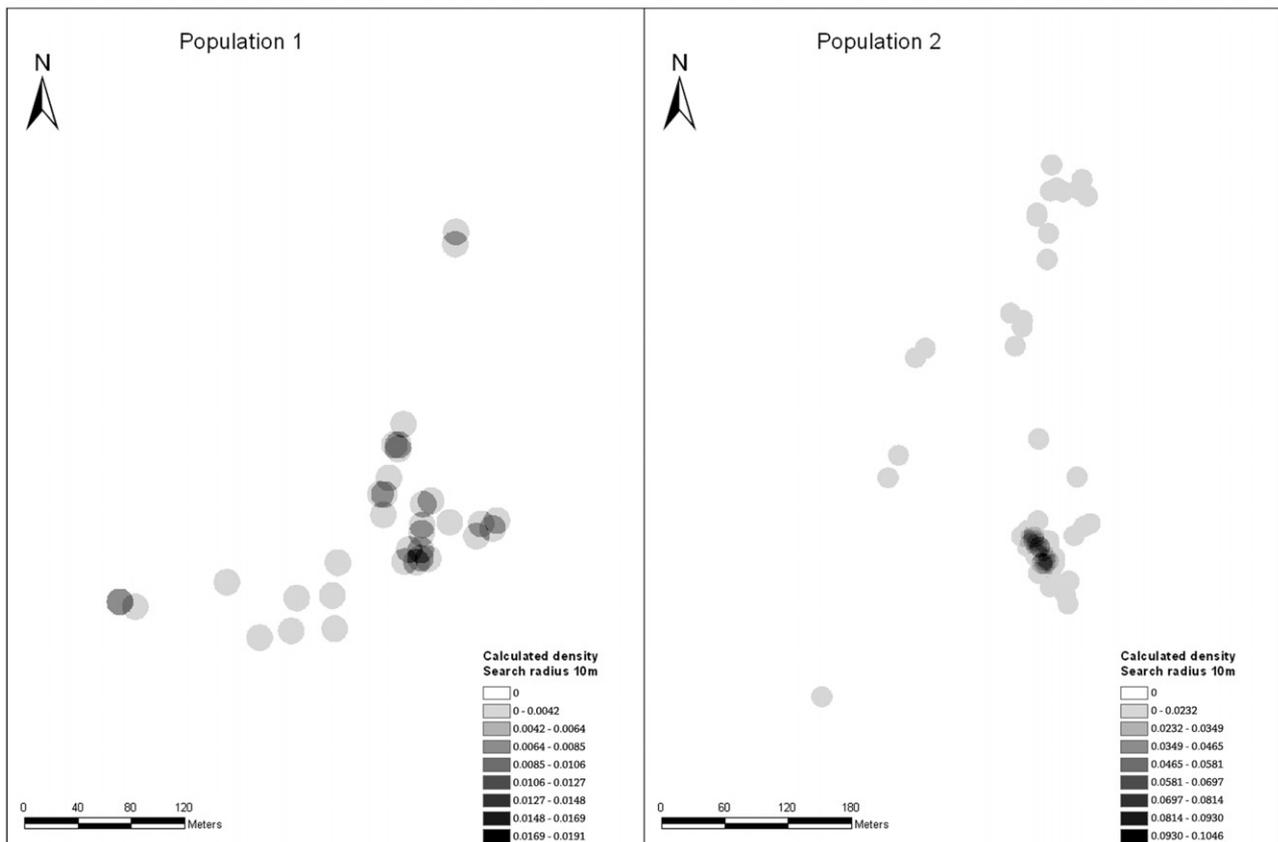


Figure 1. Spatial distribution of nests from collection sites 1 and 2. Darker areas represent higher densities of spiders.

spider nests was 0.0014 spiders m^{-2} in site 1 (with a maximum of 0.019 spiders in a 10-m radius), and 0.0073 spiders m^{-2} in site 2 (with a maximum of 0.100 spiders in a 10-m radius).

TIMING OF MATURATION, COHABITATION, SEX RATIO, AND MALE VISITATION RATES

During the entire period of the field survey (site 1) we recorded a total of 49 adult females, 14 adult males, and 46 immature individuals inside their nests. At the beginning of the season spiders were predominantly subadult at their penultimate instar, from which they gradually matured to adulthood (Fig. 2). The mortality rate was high, and only 12.8% ($N = 14$) of the adult females survived to the last day of the field survey (Fig. 2).

Mature females were already found during the first days of the survey (from 11 January), whereas adult males were first observed at the end of January, and continued to mature until 18 February (day 40 of observation), when all males had abandoned their nests. Although adult females seemingly appeared earlier in the season than adult males, there was no significant difference in the timing of maturation between the sexes measured as the day of observation in which adults appeared (females, 22 ± 1.6 days of observation; males, 26 ± 1.7 days of observation; Wilcoxon two-sample test, $Z = 1.1$, $P = 0.3$). From after moulting to adulthood, all males dispersed from their nests in search of females. The occurrence of adult males in the field reached a peak number of 15 individuals on day 36 (15 February), and their numbers declined until the end of the survey (Fig. 2).

The average sex ratio during the field survey was 0.22 ± 0.05 adult males to adult females; the variation in the operational sex ratio over the mating season is shown in Figure 3. As individuals began to mature the sex ratio ranged between 0.10 and 0.34, whereas between 13 and 18 February (days 32–40), when most of the males and females had matured, the ratio increased to a maximum of 0.65 (Fig. 3).

Males were much more likely to be found in the nests of adult females ($N = 20$) than in those of subadults ($N = 2$) or inside deserted nests ($N = 6$) (chi-square test, $\chi^2_{2,26} = 20.5$, $P < 0.001$). To test whether male visits to adult females depend upon their higher availability in the field as the season progressed, we performed a logistic regression analysis taking into account male visits to females (adult females = 1; subadult females = 0) in relation to the ratio of available adult females (number of adult females/total number of females) in the field at the time of the visit. Adult females with a cohabiting male were excluded from the analysis. Male visits to adult females did not depend on the availability of adult females in the field (logistic regression: $F_{1,23} = 3.1$, $R^2 = 0.15$, $P = 0.1$).

We used the number of consecutive observations in which males were found inside the female nest to estimate the duration of cohabitation. As males found during a single observation may have been in the female nest for 4–8 days (4 days before and 4 days after the observation), we estimated the average number of days a male spent in the nest as 4 days per observation. Males cohabited with females for an average of 6.3 ± 0.8 days (range 4–16 days), although the majority (76.2%) of the males were found in females' nests only once. Although low sample size prevented any statistical comparison, males appeared

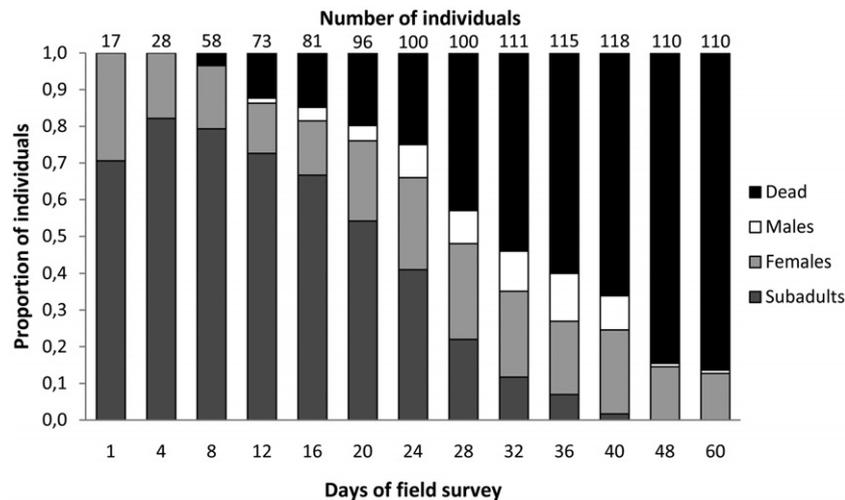


Figure 2. Occurrence of subadult individuals (immature), adult males, and adult females during the mating season (11 January–15 March). Black bars indicate mortality rates.

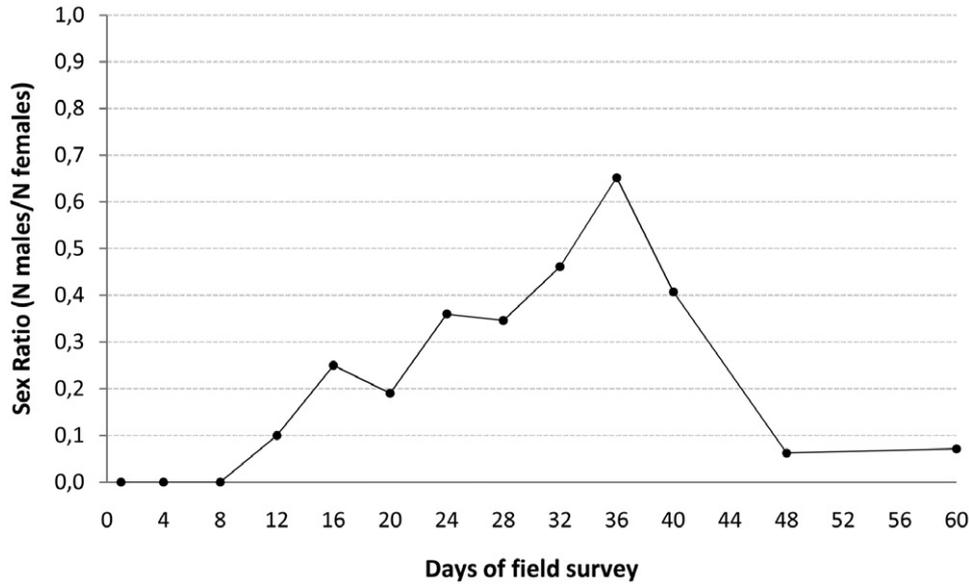


Figure 3. The operational sex ratio (number of adult males/number of adult females) during the field survey.

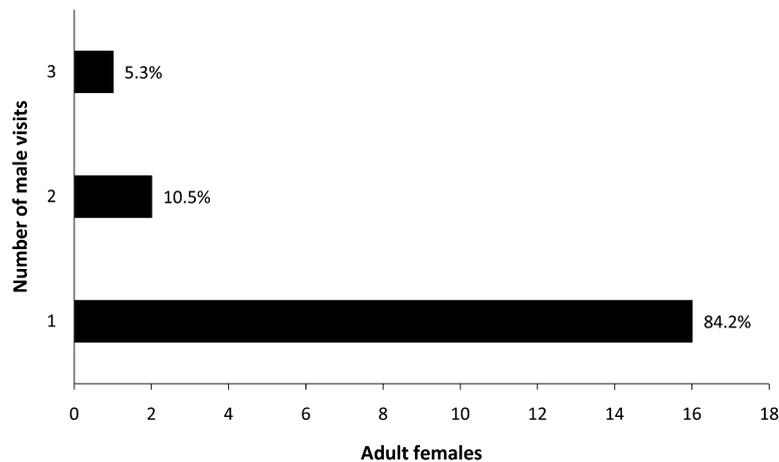


Figure 4. Frequency distribution of the number of males visiting adult females.

to spend substantially longer time in the nests of subadult females than in the nests of adult females (subadult females, 16 ± 2.6 days, $N = 2$; adult females, 5.9 ± 0.8 days, $N = 21$). In one case we observed female moulting in the presence of the male; in another, we recorded a female moult on the nest while the male was still inside. The duration of cohabitation decreased as the season progressed (pairwise correlation, $r = 0.5$, $P = 0.016$, $N = 23$) and as the number of available adult (mated and virgin) females in the field increased (pairwise correlation, $r = 0.6$, $P = 0.005$, $N = 23$). The distance to the nearest female did not affect the duration of cohabitation with females (pairwise correlation, $r = 0.06$, $P = 0.7$).

Among the total number of adult females, 38.7% ($N = 19$) experienced one or more male visits, and

were therefore considered to have mated. Most females were visited by one male, and received on average 1.22 ± 0.12 males (range 1–3 males) (Fig. 4). Males on their first visit did not cohabit with females for longer than subsequent males (first male, 7.2 ± 1.2 days, $N = 19$; second and third male, 5 ± 1 days, $N = 4$; Wilcoxon two-sample test, $Z = 0.2$, $P = 0.6$). We observed one pair of spiders mating in the field, entering the mating position described in other *Stegodyphus* species where the female raises her front legs and her abdomen and the male positions himself beneath her to insert his pedipalps (C. Tuni and R. Berger-Tal, pers. observ.). Two courtship attempts were also observed. Males courted females by repeatedly touching ('drumming') the female's cephalothorax with their front legs, perform-

ing small vibrations and trying to position their pedipalps towards the female's epigyne. The first egg sac appeared in the field on 15 March 2010. By the end of the field survey only one male was found visiting a female, suggesting that the mating season was at its end. We can therefore conclude that our observations covered the entire mating season, which in this population of *S. bicolor* in Namibia lasted between January and March.

FEMALE FITNESS

Among the females ($N = 14$) collected from site 1 at the end of the field survey, 42.8% ($N = 6$) had been visited by males and were considered to have mated. However, a higher number of the females collected ($N = 12$) produced an egg sac, indicating that a certain number of male visits may have been missed, as in other *Stegodyphus* species unmated females do not lay eggs (T. Bilde, pers. comm.; C. Tunj and R. Berger-Tal, pers. observ.). We can therefore state that a minimum of 25 females (51%) in the study population were visited by a male. This number should not be taken as the absolute number of visits of males to females, as male visits may also have been missed for the females that did not survive the mating season. Egg sacs of mated females were laid on average 40.3 ± 4.2 days (range 29–55 days) after the first visit from a male. Among all of the females that produced egg sacs only four (33%) hatched in the laboratory, at an average of 59.2 ± 8.4 days (range 36–73 days) after the eggs were laid. These hatched egg sacs were from a female that mated once, a female that mated twice, and two females for which matings were not scored in the field. The average size of the measured brood was 62 ± 41 (median 22.5) spiderlings. The low hatching success was most likely a result of laboratory conditions, and an insufficient sample size prevented us from testing the effect of mating rate on offspring production.

To acquire additional estimates of fitness we calculated the offspring production of females collected at site 2 by adding these to the sample of females collected from site 1. A total number of 64 females (85.5%) produced an egg sac, after an average of 37.1 ± 2.03 days (median 43 days, range 3–91 days) from collection. Females collected while already tending an egg sac ($N = 4$) were excluded from the latter analysis. Only 32.8% ($N = 21$) of the egg sacs hatched after an average of 81.8 ± 4.3 days from egg-laying (range 36–125 days). The average number of hatched spiderlings was 53.2 ± 10.1 , ranging from 3 to 187. Female body size did not correlate with the number of offspring produced (Spearman's rank correlation coefficient, $\rho = 0.18$, $P = 0.45$, $N = 19$).

DISCUSSION

We conducted a field study on the spatiotemporal distribution of individuals, the operational sex ratio, survival rate, and female encounter rate with males, with the aim of inferring the mating system of the spider *S. bicolor*. The mating season in the Namibian population of *S. bicolor* occurred between January and March. Adult males and females appeared on average at the same time of the season, and matured to adulthood over a period of approximately 1 month. As in most spider species and other solitary *Stegodyphus* species, adult males search actively for females, whereas females remain sedentary (Schneider, 1997; Ruch *et al.*, 2009; Foelix, 2010).

We could only record half of the females from the surveyed population as having been visited by males, and females received on average 1.2 visiting males. We documented a remarkably high mortality rate of individuals (87.2%). Assuming that the primary sex ratio is 1 : 1 this mortality rate is likely to be male-biased, as we found an operational sex ratio that was biased towards females throughout the mating season (Fig. 3). These data may explain the low encounter rates between males and females. Adverse weather conditions (rain and storms), predators such as birds and other spiders, and damage by grazing animals are all factors that may reduce the survival of spiders. Although additional investigations are needed to evaluate the differences in survivorship between the sexes, males are likely to suffer from substantially increased mortality during mate search than are females (Vollrath & Parker, 1992; Kotiaho *et al.*, 1998; Andrade, 2003; Fromhage, 2007; Kasumovic *et al.*, 2007).

The female-biased operational sex ratio, the aggregated distribution, with multiple individuals found in close proximity to each other, and a relatively low risk of sperm competition suggests that males should reduce their investment in strategies to protect paternity and instead search for additional mating opportunities (Ims, 1988; Kvarnemo & Ahnesjö, 1996; Berger-Tal & Lubin, 2011). The duration of cohabitation of males in the nests of females was not shorter when distances to the nearest nests were small, with potential partners in close proximity. However, cohabitation duration became significantly shorter as the season progressed, with a larger overall availability of adult females. This pattern suggests that with increasing chances of finding additional females in the field, males were more likely to resume their search for mates. One function of cohabitation in spiders is mate guarding, where cohabiting males respond agonistically to rival males that approach female's nests (Fahey & Elgar, 1997; Toft, 1998). However, intra-sexual interactions were not directly tested in this

study, preventing us from drawing conclusions on the function of mate guarding in male–male interactions in *S. bicolor*. In a congener, *S. lineatus*, males were found to mate repeatedly and to exploit the webs of females for foraging and shelter (Erez *et al.*, 2005), as adult males lose the ability to build their own capture web (Erez *et al.*, 2005). The majority of the males in our study (76.2%) were found to cohabit with females for approximately 4 days, which is similar to *S. lineatus*, which cohabits for 2–4 days (Schneider, 1997; Berger-Tal & Lubin, 2011). One possibility is that male cohabitation is an integrated component of the male mating strategy to ensure insemination success through repeated matings (Ridley, 1988; Berger-Tal & Lubin, 2011), spend time recharging their pedipalps (Foelix, 2010) before resuming mate search, or use the nests for foraging and shelter. The latter hypothesis may explain the presence of *S. bicolor* males in deserted nests.

As a result of the low encounter rates and female-biased sex ratio, male–male competition may be relatively relaxed in this system. *Stegodyphus bicolor* males did not mature protandrously, in contrast to the congener *S. lineatus* where protandrous males compete for access to virgin females (Schneider, 1997; Maklakov *et al.*, 2004). We found that males preferentially visit mature females; a similar pattern was documented in *S. lineatus* (Tuni & Berger-Tal, 2012), and may imply that males do not guard immature females before mating.

Of the females that experienced a male visit, most were visited by a single male. Moreover, the females that mated more than once experienced a very low re-mating frequency (1–3 males), suggesting that moderate polyandry is the prevailing mating system in this species. Limited re-mating together with lack of male transfer of resources (i.e. food or parental care) may suggest a lack of direct benefits to *S. bicolor* polyandrous females. Females may re-mate to ensure sperm reserves (Thornhill & Alcock, 1983; Ridley, 1988; Arnqvist & Nilsson, 2000), although eresid spiders are unlikely to be limited by sperm supply because of their semelparous life history and relatively small broods. Females may accept additional mating partners to overcome the risk of an unsuccessful copulation (i.e. mating with an infertile male) or simply as a mate choice strategy to overcome the risk of mating with males of inferior quality (Jennions & Petrie, 2000; Hosken & Stockley, 2003), they may re-mate to increase the genetic diversity of the offspring or to avoid the risk of inbreeding (Yasui, 1998; Tregenza & Wedell, 2002; Welke & Schneider, 2009), or alternatively, females may re-mate to avoid male-induced costs (i.e. harassment or predation risks; Arnqvist & Rowe, 2005). Finally, divergent evolutionary interests among the sexes over mating rate may

lead to suboptimal re-mating patterns for females (Arnqvist & Rowe, 2005; Maklakov, Bilde & Lubin, 2005). We were unable to test the effect of natural mating rates on female fitness; therefore, we cannot draw conclusions on the mechanisms underlying the polyandrous mating system. Additional studies are required to determine whether polyandry results from sexual conflict over mating, as suggested by Schneider & Lubin (1998).

Low encounter rates and moderate levels of polyandry, combined with the clustered spatial distribution of individuals, are features that result from limited dispersal, and suggest a history of some degree of inbreeding, which is typical of other subsocial *Stegodyphus* species (Bilde *et al.*, 2005). In the Mediterranean *S. lineatus* (Johannessen & Lubin, 1999, 2001) and the southern African *Stegodyphus tentoriicola* Purcell, 1904 (Ruch *et al.*, 2009), clusters of spiders consist of aggregations of family members, and short male movements during mate search increase inbreeding risks (Bilde *et al.*, 2005; Ruch *et al.*, 2009); these species also show relatively low levels of polyandry in the field (Schneider, 1997; Ruch *et al.*, 2009; Tuni *et al.*, 2012).

Our study suggests that ecological factors that affect the mating system of *S. bicolor* are shared by other solitary congeneric species (Bilde *et al.*, 2005; Ruch *et al.*, 2009). Similar selective forces such as high mortality, high costs of mate search, philopatry, and limited dispersal result in a moderately polyandrous mating system. These shared traits in combination with moderate inbreeding tolerance in subsocial *Stegodyphus* species (Bilde *et al.*, 2005; Ruch *et al.*, 2009) are likely to facilitate the transition to permanent sociality via the subsocial route (Bilde *et al.*, 2005; Lubin & Bilde, 2007).

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