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High male mate search costs and a female-biased sex ratio shape the male mating strategy in a desert spider

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Theory predicts that males that provide little or no parental investment can increase their reproductive success by fertilizing as many females as possible. By contrast, low male mating rate is often related to a large investment in a single mating. This view is challenged, however, by the occurrence of species in which males achieve only one or a few matings, yet invest little in mate guarding or paternity assurance. An explanation of this requires knowledge of the ecological factors affecting the mating system. When there is a female-biased sex ratio and a low probability of a female mating with additional males, the benefits of paternity protection are reduced. Under these conditions males are expected to search actively for females and invest little in each mating to maximize their mating rate. We investigated the influence of the sex ratio and male mortality on the male mate search strategy of the desert spider *Stegodyphus lineatus* (Eresidae), by following marked males in their natural habitat over the entire mating season. Males searching for mates suffered high mortality but encountered multiple females. During the mating season the sex ratio was highly female biased and females mated on average with a single male in their lifetime. We conclude that high costs of male mate search together with a female-biased sex ratio reduce the likelihood of multiple mating per female and the chances of male–male competition. Under these conditions males should invest in searching for more females and increasing their encounter rate.

In sexually reproducing organisms, finding a mate usually requires movement of at least one of the sexes. Mate search behaviour improves the rate of encountering potential mates and usually includes active search or attraction to specific signals (Gwynne 1987; Acharya 1995; Bonduriansky 2001; DeRivera et al. 2003; Kasumovic et al. 2007). According to theory, males are expected to search while females remain sedentary. This is usually the outcome of the relative amount of resources each sex puts into caring for and rearing the young (Trivers 1972; Framenau 2005; Kokko & Wong 2007). There is a trade-off between the time and energy invested in raising offspring and the time available to search for more mates (Clutton-Brock & Parker 1992; Kokko & Wong 2007), and in the absence of high investment in a single mating, males are expected to mate with as many females as they can to maximize the number of eggs they fertilize (Clutton-Brock & Parker 1992). Mate search, however, is a costly behaviour and there are constraints on encounter rate that may reduce mating opportunities for searching individuals. Such constraints may include risk of predation (Gwynne 1987; Grafe 1997; Kasumovic et al. 2007) and lower energy intake during searching (Vollrath & Parker 1992; Foelix 1996; Byers et al. 2006; Kasumovic et al. 2007). Moreover, the spatial and temporal distribution of receptive females can change the availability of females for a male, and accordingly the opportunities a male has to reach several mates in its lifetime (Emlen & Oring 1977).

The cost of mate search has been explored in various organisms (e.g. Sakaluk & Belwood 1984; Gwynne 1987; Byers et al. 2006), including spiders, in which high costs are sometimes associated with male monogamy (Andrade 2003; Segoli et al. 2006; Kasumovic et al. 2007). Nevertheless, the influence of costly mate search on mating systems lacking male monogamy has not been fully explored. The cost of mate search for males can have a twofold effect, reducing not only the number of males within the population, but also the likelihood of encountering competition from rivals (Fromhage et al. 2005). Thus, one needs to know the sex ratio (the number of females to males) in the population to evaluate and quantify the selection pressures on male mate search strategy and mating behaviour.

The operational sex ratio (OSR) is defined as the average ratio of sexually active males to fertilizable females (Emlen & Oring 1977).

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A bias in the OSR can explain the variance in reproductive success of the limiting sex and thus which sex will compete for access to mates (Kvarnemo & Ahnesjo 1996, 2002). The OSR may change over the mating season as females and males become unavailable to mate. Fromhage et al. (2005) suggested, however, that the sex ratio in adults that achieve mating (i.e. the effective sex ratio, ESR) is the main factor that determines the male mating strategy. In a system with high costs of mate search, the ESR can predict two alternative strategies. On the one hand, in a mating system with a male-biased ESR, the risk of polyandry should increase the benefit of paternity protection and investment in a single mating for the male (male monogamy; Segoli et al. 2006; Fromhage et al. 2007; Kasumovic et al. 2007). On the other hand, when there is a female-biased ESR, the chances that a female will encounter a second male are low. Under these conditions it is easier for males to achieve full paternity and intrasexual competition among males is reduced (Fromhage et al. 2007). Consequently, males should seek more mating opportunities rather than stay and invest mainly in a single mating.

Factors such as the distribution of receptive females in time and space will influence the male's ability to monopolize females, and ensure their paternity (Emlen & Oring 1977). When there is a female-biased sex ratio, but females are scattered or mature synchronously, the potential to monopolize several females is low and males should roam widely to increase their encounter rate with females (Ims 1988). When females are clustered, the local OSR and the ability of the male to ensure paternity by mate guarding will determine the male mating strategy (Eberle & Kappeler 2002). Thus, mate search behaviour may also be influenced by ecological factors such as the time in the season and distance between available females. It is important, therefore, to investigate male mate-searching strategies and mate encounter rate under natural conditions to understand the relationships between the cost of mate search, demographic traits and male mating strategy (e.g. Say et al. 2001).

In this study we examined the mating system of the desert web-building spider *Stegodyphus lineatus* (Eresidae) and assessed how the sex ratio and the male's survival prospects during mate search over the mating season influence its search strategy. A low mating rate was previously found in *S. lineatus*: 80% of females received only one or two male visitors during the course of the mating season (Schneider 1997). Multiple mating is costly for females and they are reluctant to remate (Maklakov et al. 2005); males that encounter already mated females must overcome female resistance in aggressive encounters (Schneider & Lubin 1997). The distribution of males and females is clumped because of juvenile philopatry, and clusters of spiders occupying single host plants may be widely spaced in the desert environment (Johannesen & Lubin 1999). Searching males were found to visit females within a cluster and only subsequently to move between clusters (Bilde et al. 2005). The low mating rate per female suggests that in spite of the clumped distribution of spiders, searching may be energetically costly and risky. Males may cohabit with a female for up to 18 days, with most males remaining 2–3 days with one female (Schneider 1997). Duration of cohabitation, whether to obtain resources from the female's web (Erez et al. 2005) or as a mate-guarding strategy (Maklakov & Lubin 2004), clearly comes at the expense of searching for additional females. From the available data, however, it is still unclear whether males adopt a polygynous or monogynous strategy, and to what extent the costs of searching and availability of females influence the male's searching behaviour. Detailed field observations of male search in relation to the distribution of females are necessary to answer this question.

We investigated male searching strategy as a function of search costs and the sex ratio (Fromhage et al. 2007). We hypothesized that a male's searching strategy will depend on its future mating prospects and that will depend on the time in the season, the sex ratio and the distribution of females. To test this hypothesis we measured cohabitation duration with females as an indication of male strategy (guarding versus mate searching), distance between female nests and movement distances of males. The cost of mate search was determined by estimating male survival rate between successive visits. We predicted high male mortality rates owing to movement of males between clusters of females in nature. We further predicted that movement distance and the time a male remains with a female will decrease as the number of available adult females increases. Similarly, when females are locally more abundant, that is the distance to females' nests is short, males should stay for shorter periods with a female. This should result in males adopting a polygynous strategy.

METHODS

Study Species

Stegodyphus lineatus is found in arid and semiarid areas around the Mediterranean basin and east to central Asia (Kraus & Kraus 1988). The spiders inhabit a permanent silk nest with a sticky capture web that surrounds it. The nests are built on bushes, usually at the tips of branches (personal observation). During March to June, the spiders moult to adulthood and become sexually active (Schneider 1997). Females have a slightly but significantly wider prosoma than males (females: 3.47 ± 0.49 mm, $N = 48$; males: 3.04 ± 0.48 mm, $N = 72$; t test: $t = -4.72$, $P < 0.0001$). Prosoma width is a standard measure of body size in spiders, since the exoskeleton is hard and therefore does not change with body condition (Maklakov et al. 2004). Males begin to moult to adulthood 2 weeks before the females, but continue to moult into the mating season with the females (Schneider 1997; Maklakov et al. 2004). Females remain sedentary in their nests during the mating season, while the males leave their nests in search of females. The adult males do not construct a capture web and steal food (kleptoparasitism) from the female's web during cohabitation (Schneider 1997; Erez et al. 2005). There is no specific evidence of sperm precedence: first and second males sired on average an equal proportion of offspring, but a bimodal distribution of paternity indicates that sperm precedence patterns are more complicated and possibly subject to cryptic manipulation (Schneider & Lubin 1996).

Once mated, a female produces a single eggsac and cares for it for about 3 weeks, and then opens it to release the young. The female reproduces only once in its lifetime, as it gives suicidal maternal care to the young (Kullmann et al. 1971). Nevertheless, the female can make a replacement eggsac if the first one is damaged or removed by a predator or by an infanticidal male (Schneider & Lubin 1996, 1997). Unlike many entelegyne spiders, unmated *S. lineatus* females do not lay unfertilized eggsacs (based on our extensive experience raising spiders in the laboratory).

Field Survey

The study area was in Wadi Zipporim in the Negev highlands (latitude: 30′82″; longitude: 34′72″), 12 km south of Midreshet Ben-Gurion, Israel. The vegetation consists of scattered perennial shrubs such as *Thymelaea hirsuta*, *Hammada scoparia* and *Retama raetam*. The shrubs occur mainly in the wadi (a seasonally dry stream bed) and are more widely scattered on the adjacent slopes. *Stegodyphus lineatus* nests were found on the shrubs or on dry annual plants in the wadi.

We marked all the *S. lineatus* nests in an area of 2000 m^2 along the wadi. The population sampled was delimited by slopes without vegetation and separated by 50 m from adjacent patches of