

Research article

Sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae: Eresidae)

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Summary

Sexual competition is shown to occur in the social spider *Stegodyphus dumicola* (Eresidae). While the secondary sex ratio in *S. dumicola* was female-biased, the overall operational sex ratio (numbers of breeding males to breeding females over the season) showed no strong female bias. Males matured before females and had a shorter lifespan than the females. Mating took place in the natal colony. Males fought over access to the few mature females available early in the reproductive season, but females appeared to control the duration of mating. Later in the season, some adults of both sexes dispersed alone to breed elsewhere. We conclude that different rates of maturation between the sexes within a colony provide the opportunity for females that mature early in the season to be choosy in selecting a mate and this forces males to compete. Early reproduction may be beneficial for both females and males, because the offspring of females that reproduce early may have a competitive advantage over later (and smaller) offspring in the colony.

Introduction

Many non-territorial permanent-social spiders (hereafter referred to as social spiders) have restricted dispersal as adults. The adults of both sexes remain to reproduce in the parental colony. Thus, regular inbreeding occurs and, consequently, there is reduced genetic variation within colonies (Lubin and Crozier, 1985; Smith, 1986; Roeloffs and Riechert, 1988; Wickler and Seibt, 1993; Riechert and Roeloffs, 1993; Avilés, 1993a). Riechert and Roeloffs (1993) suggested that under such circumstances, one would not expect males to compete for mates as they are all genetically similar. By the same token, courtship should be absent or reduced and

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females should derive less benefit from being choosy than in outbreeding populations.

We question this interpretation as it conflicts with evidence that social spiders frequently engage in sexual competition. Courtship, fighting among males and female choice have been reported for several social spiders: the eresid *Stegodyphus sarasinorum* (Bradoo, 1975), the theredid *Achaearanea wau* (Lubin, 1986), the dictynids *Aebutina binotata* (Avilés, 1993b) and *Mallos gregalis* (Jackson, 1978), and the agelenid *Agelena consociata* (Krafft, 1969, in the laboratory; but not observed in the field, Riechert and Roeloffs, 1993).

To this we add our observations of the social spider *Stegodyphus dumicola* Pocock 1898 (Eresidae) in Namibia. Individuals of this species live for 12–15 months, but colonies can endure for several generations. The females care for the young until the onset of winter, when they are eaten by the young (“gerontophagy” – Seibt and Wickler, 1987). Dispersal is primarily by adult females which leave the parent colony to establish webs on their own. There is no evidence that *Stegodyphus* can balloon large distances (Henschel, Schneider and Lublin, 1995), contrary to previous impressions (Jacson and Joseph, 1973; Wickler and Seibt, 1986). Colonies of *S. dumicola* are inbred (Wickler and Seibt, 1993) with female-biased secondary sex ratios, as is typical of social spiders (Avilés, 1995). A high coefficient of relatedness (0.69) was reported for this species (Wickler and Seibt, 1993), comparable to that of *A. consociata* (0.52; Riechert and Roeloffs, 1993). Allozyme electrophoresis showed low within-colony heterogeneity in *S. sarasinorum* (Smith and Engel, 1994). Thus, the contagious population structure of the social *Stegodyphus* species is similar to that of some other social spiders (Lubin and Crozier, 1985; Smith, 1986; Roeloffs and Riechert, 1988).

We observed courtship, male rivalry and mating, and estimated the overall operational sex ratio (OSR) in colonies. The overall OSR was the number of sexually active males to breeding females in a colony over the entire breeding season (Thornhill and Alcock, 1983). OSR provides an indication of the likelihood of sexual competition: if the OSR is male-biased, males may be forced to compete for scarce females. All adult males in a colony were assumed to be sexually active, while the number of breeding females was determined from the egg clutches produced (each female is assumed to produce a single eggsac; Seibt and Wickler, 1988). The instantaneous OSR which assesses the ratio of active males to females at any time (e.g., Heller and von Helversen, 1991) could not be determined independently.

Methods

Observations of colonies were carried out over 40 days during the summers of 1991–1993 on the farm Christirina in Namibia (23° 25' S, 18° 00' E) during a study of predation risk on *S. dumicola* (Henschel, submitted). The study population comprised over 500 colonies. It was possible to count the number of females in small colonies by pressing them out of the nest. Group size in large colonies was estimated by mark-recapture techniques using the Lincoln index (Southwood, 1978) which is appropriate for a closed population such as a social spider colony.

The secondary sex ratio was determined in 24 colonies that were dissected during the early breeding season (February–March). We counted egg cocoons in 236 nests when females were cooling them outside the nests during the heat of the day (this is a physiological requirement to avoid overheating of the eggs, similar to that found in *S. lineatus* by Henschel, Ward and Lubin, 1992). In solitary *Stegodyphus* spiders, females produce only a single cocoon (Schneider, 1992), and this is also the case for solitary females (foundresses of new colonies) of *S. dumicola* (pers. obs.), although *S. sarasinorum* females may produce as many as four cocoons (Bradoo, 1975). Consequently, the number of cocoons produced in a *S. dumicola* colony provides a conservative estimate of the number of breeding females, which allowed us to calculate the overall OSR. There is no direct visual method that we know of, short of continuous monitoring (not always possible in the narrow tunnels), to tell which of the adult females have actually mated or produced eggs. Nor could we use changes in female size as an indirect method, because clutch mass is too small to enable differences in female size to be detected visually.

We determined body masses and coefficients of variation of mass (CV) of males and females of different ages, both from social colonies and solitary individuals. A mechanical precision balance (± 0.1 mg; Roller-Smith, Biolar Corporation, North Grafton, Massachusetts) was used. Solitary foundresses were compared to social females in their parent colonies.

Results

The reproductive season was between January and March. The timing of male maturation differed between years and between colonies, but all of the males in a colony matured within about a week of each other at an age of 9–10 months. It was difficult to confirm how many females were mature at the time, as the epigynum resides in a groove and is not visible externally (Kraus and Kraus, 1988). However, females continued to moult after all the males in the colony had already reached maturity. The longevity of adult males was 4–6 weeks compared to 4–6 months for adult females. Egg laying occurred during February and March within a month after male maturation, followed by care of young and the gradual death of colony females by gerontophagy during April to June.

The adult (secondary) sex ratio in colonies was strongly female-biased. In 24 colonies of 12–355 spiders (2–41 adult males) the median proportion of males was 0.120 (lower-upper quartile: 0.083–0.182). The adult sex ratio was not significantly correlated with colony size ($R_s = 0.25$; $N = 24$; $P > 0.05$). The overall OSR was considerably less female-biased, as not all females reproduced. Using the number of cocoons to estimate the number of reproductively active females (409 cocoons from 1301 females in 236 nests), the overall operational sex ratio over the mating season was 0.421. The instantaneous OSR was probably male-biased, as females appeared to mature more gradually than males.

Adult males were antagonistic towards each other during the mating period. Aggression was most intense just after maturation. Between mating bouts, many males typically spaced themselves out below the nest in the region of the entrance, avoiding contact with one another, and became restless upon the approach of a

Table 1. Body mass of juveniles (unknown sex), 10-month old (adult) males, and 10-month old (adult or sub-adult) females from groups and from nests containing single females

	Mass (mg)		CV	N	# nests
	mean (SD)	range			
Groups					
Juveniles	35 (13)	12–82	37	122	5
Males	34 (6)	23–48	18	45	9
Females	149 (60)	56–260	40	150	14
Solitary					
Females	152 (34)	103–213	22	19	19

N = number of individuals measured.

female. All 30 observed cases of courtship and copulations occurred in this area of the nest. In about half of the cases, 1–6 rival males pushed in from the sides and sometimes engaged each other in combat. Twice, males killed conspecific males in the same colony. When eight males from one colony were placed together in a glass vial for measuring purposes, they all fought, leaving five of them dead.

Successful copulations took > 15 min. When rival males approached, a copulating female protected the mating male by straddling him with her legs, thus forming a cage around him against the nest wall. One copulation which occurred without this protection was interrupted by another male. Mating was terminated by the female breaking away from her mate, such that it appears that females control the duration of mating.

Emigration of single individuals was observed five times for males and 191 times for females in areas containing 45 colonies with a total population of 172 males and 1301 females. Single emigrating males were observed walking along branches away from a web late in the mating season; unlike emigrating females, they did not construct new nests. Two males were followed until they entered nests of solitary females of *S. dumicola*. At least four solitary females were immature when they dispersed and moulted only after emigrating. One of these mated within two days after moulting.

Coefficients of variation of body mass ranged from 18 to 40% (Table 1). Females in colonies were more variable than were dispersing females that established solitary webs ($F_{\max} = 3.16$, $N = 19$ randomly chosen pairs of solitary and social females).

Discussion

Our observations contradict the hypothesis that sexual competition is reduced in inbred social spiders (Riechert and Roeloffs, 1993) and confirm previous reports of male-male competition in other social spider species. Males of *S. dumicola* fought actively, and observations of mating suggest that females exert some control over mate choice and mating duration. Thus, the mating success of males may be determined by female choice or by male-male competition, or both.

Riechert and Roeloffs (1993) expected inbred social spiders to have reduced sexual competition because of the presumed genetic similarity between males and

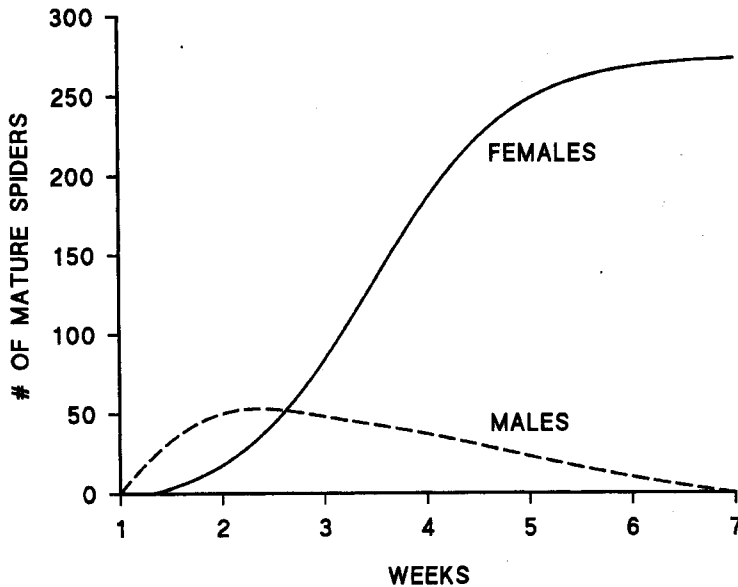


Figure 1. Schematic trajectory of male and female maturation in a colony containing 50 males and 300 females. Males mature within one week and have a life expectancy of up to 6 weeks. Female maturation extends over a longer period of time

the lack of any need for females to be selective. The female-biased primary sex ratios in social spider colonies appeared to support their idea that investment in males is redundant. However, even in inbred species, there may be enough variability among males for females to profit from being choosy. Additionally, traits such as body size, mating history or fighting history, which may be largely environmentally determined, will affect male mating success.

We suggest here that sexual competition in *S. dumicola* is associated with (1) early and synchronous maturation of males in a colony and (2) less synchronous rates of development and maturation of females. When females mature asynchronously, the number of receptive females will be low initially and will increase with time. Thus, in the beginning of the mating season, females are a scarce resource for males in spite of the overall female-biased sex ratio (Fig. 1). If *S. dumicola* females have conduit spermathecae like *S. sarasinorum* (Bradoo, 1975) – this may be a characteristic of eresids in general (Austad, 1984) – the first male to mate may have fertilization priority (Austad, 1984). This would reduce the value to a male of mating with an already mated female and would increase male competition over the first mating with a mature female. A consequence of first male sperm priority would be even more strongly male-biased instantaneous OSR than the overall OSR assessed by us.

In a social theridiid, *Achaeranea wau*, males matured several weeks before the females, and the instantaneous OSR at the beginning of the mating season was strongly male-biased (Lubin, 1986). Sexual competition among males is so pronounced in the latter species, that they fight over access to moulting females that are unable to defend themselves from the males (Lubin, 1986).

Our assessment of the OSR was based on the assumption that not all females reproduced in a colony. We suggest that owing to competition within the colony for access to prey, some females grow more slowly and mature only after the males have died. The large variance in adult female body size in *S. dumicola* groups lends support to this hypothesis. Late-maturing females can either remain as non-reproductive members of the colony, or disperse to establish new nests. If this hypothesis is correct, we predict that male-male competition will be greatest in colonies with large variance in female body size. This remains to be tested.

For males, early maturation is advantageous because it enables them to court and mate with females as they mature. For females, large body size and early maturation may be positively correlated. Females that mature and reproduce early will have offspring that benefit longer from maternal and step-maternal care, and have more opportunities for gerontophagy, than offspring of later females. Since the ability to compete for food is related to body size (see Rypstra, 1993), large spiders (early offspring) will maintain their competitive advantage over smaller (later) colony members. Thus, the offspring of early-reproducing females will grow faster and reach maturity and reproduce earlier. The large variation that has been observed in colonies in the size of adult females may reflect differences among them in the ability to compete for food (Ward and Enders, 1985; Vollrath, 1986; Rypstra, 1993; Willey and Jackson, 1993). In *S. dumicola* it is evident that there is considerable variation in the size of spiders at all stages (Table 1). We suggest that asynchronous breeding within colonies both contributes to this variation and is maintained by it.

Some late females may break out of this cycle by dispersing alone. The resulting increase in fitness, due to the absence of older competitors for their daughters, may explain why intermediate-sized females disperse alone (see Table 1), despite the high risk of predation (Henschel, submitted). Furthermore, dispersing females may escape gerontophagy by early offspring of other females (this appears to be an active process by the juveniles; Schneider, 1992).

As maturation is not synchronized between colonies in a population, males may increase their reproductive output by searching for unmated females away from the natal nest. However, because of the high risk of predation (Henschel, submitted), it will be advantageous to mate with females in the natal colony, and move only when these opportunities have been exhausted.

A migrating male might join another colony or a single female from a genetically different population. We consider this unlikely, because dispersal distances are small and most colonies and single females in an area are likely to be derived from the same original colony. Nonetheless, given that foreign individuals of either sex are accepted by members of a nest when experimentally introduced (Seibt and Wickler, 1988; pers. observation), male migration may be a means of increasing genotypic diversity within colonies.

Male rivalry and female choice may be even greater in social spiders compared to their less social relatives. *Stegodyphus dumicola* differs from its subsocial congeners, *S. lineatus* and *S. bicolor*, that temporarily cohabit as adult pairs in unbranched silk tubes (Schneider, 1992; Ward and Lubin, 1993; pers. obs.). Schneider (1992) noted that adults of both sexes of *S. lineatus* allowed visiting adult males to cohabit in their nests (64 times with a female, 20 times with a male, 68 times with

juveniles or unknown sex), and reported no evictions, which would have indicated male rivalry or female choice. Data are needed on courtship and mating in non-social or sub-social relatives of social species.

We conclude that the mating system of *S. dumicola* is shaped by group-living which creates unequal reproductive opportunities for females, leading to a relatively higher quality of early females. Males will benefit from mating with early-maturing females. The intensity of competition between males for early females is a consequence of synchronized, early male maturation. Males will also benefit more from mating in the natal colony, rather than searching for solitary females or joining another group. The latter options involve risky moves. This tendency would further promote inbreeding, as the female offspring of later outbred pairs (if they exist) would be at a competitive (size) disadvantage compared to the older, inbred colony members. These suggestions would be supported by demonstrating that early offspring have a better life-time competitive ability (and fitness) than late offspring.

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