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SHORT COMMUNICATION

Facultative iteroparity in a semelparous social spider, *Stegodyphus dumicola* (Araneae: Eresidae)

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Abstract. Organisms can optimize their reproductive success by differential resource allocation. When adult survival is low, investment of all resources into a single reproductive event can be beneficial, favouring a semelparous strategy. In the spider genus *Stegodyphus* Simon, 1873 (Eresidae), all species are considered semelparous, based on observations of ancestral subsocial species. However, derived social species show task differentiation and helping by non-reproducing females. This could facilitate a facultative iteroparous strategy by providing sufficient resources to meet the threshold for repeated reproduction. We investigated the reproductive behaviour of groups with single breeding females in the cooperative breeding *Stegodyphus dumicola* Pocock, 1898. We found that mothers can depart from a strictly semelparous lifestyle by producing more than one clutch. The facultative iteroparity in *S. dumicola* may enhance colony growth and survival, and act as a mechanism to maintain sociality.

Keywords: Mating, reproduction, matriphagy, sociality, life history

Natural selection acts on maximizing the reproductive success of organisms (Young 2010), leading to trade-offs between present and future reproduction (Williams 1966). In this context, two alternative reproductive strategies have evolved, namely iteroparity and semelparity. Iteroparous individuals invest only part of their resources in each reproductive event, while the remaining energy budget is directed to survival and future reproduction, allowing for multiple reproductive events. Iteroparity is pursued by most animals (Cole 1954; Fritz et al. 1982; Singer 2016) and is favoured when environmental conditions are variable and when juvenile mortality may be high (Murphy 1968). In contrast, semelparous species reproduce only once and allocate all available energy into the single reproductive event, with death as a by-product (Cole 1954; Fritz et al. 1982; Stearns 1992; Alonso-Alvarez & Velando 2012). Semelparity is exceedingly rare in vertebrates (Braithwaite & Lee 1979; Smith & Charnov 2001; Crespi & Teo 2002) but more commonly observed in invertebrates (Fritz et al. 1982; Trumbo 2013).

While most spiders are iteroparous, spiders of the genus *Stegodyphus* Simon, 1873 have a semelparous lifestyle (Schneider 1996; Schneider & Lubin 1997). Semelparity was shown to be obligatory in solitary, subsocial *Stegodyphus* species (Kullman et al. 1972; Schneider et al. 2003). In the subsocial species, juveniles cohabit with their mother and are fed by her through regurgitation for some weeks. Before the juveniles disperse, they consume their mother's body in a process called matriphagy. Females of the subsocial *Stegodyphus lineatus* (Latreille, 1817) produce a second egg sac if the first brood fails to hatch and develop (Schneider et al. 2003; Lubin & Bilde 2007; Salomon et al. 2008) and retain the ability to produce a replacement clutch until the last day before matriphagy occurs (Schneider 2002). Obligatory semelparity has been assumed to be a fixed trait for all *Stegodyphus* species, including the three social species, since they are derived from subsocial ancestors (Seibt & Wickler 1988; Bowden 1991; Avilés 1997; Whitehouse & Lubin 2005; Agnarsson et al. 2006; Settepani et al. 2016). In the social *Stegodyphus* species, females share a communal nest, breed cooperatively, and their offspring remain within the colony (Seibt & Wickler 1988; Bilde et al. 2007; Salomon et al. 2008; Ruch et al. 2009). Interestingly, only a fraction of the females in a colony reproduces (Salomon et al. 2008), but all females—be they reproductive females (mothers) or non-reproductive females (helpers or allomothers)—cooperate in brood care and other tasks such as hunting and nest building (Lubin & Bilde 2007; Junghanns et al. 2017,

2019). Due to this cooperation, resource availability for mothers might differ in social compared to subsocial species, potentially leading to changes in reproductive allocation (Junghanns et al. 2019).

We investigated the reproductive strategy of the social spider *Stegodyphus dumicola* Pocock, 1898, by monitoring the reproductive output of experimental female groups that contained only a single mated female. This allowed us to assign reproductive success to the single female and to assess the effects of helping by non-reproductive females on the reproductive strategy of this social species. We hypothesised that resource expenditure on reproduction is lower in social groups than in solitarily breeding females, which could allow for repeated oviposition by reproducing females. Consequently, the observation of more than one successful brood in the experimental groups would demonstrate a transition from a strictly semelparous to an iteroparous reproductive strategy in this social spider species.

We studied 51 reproducing *Stegodyphus dumicola* females in 2014/2015. Spiders originated from seven colonies collected in South Africa in November 2014 (Shingwedzi: 22°58'48.0"S, 31°18'00.0"E and Skukuza: 24°55'48.0"S, 31°41'24.0"E). Each female had matured in the lab and—as *S. dumicola* colonies are normally inbred (Settepani et al. 2014)—was kept with a male from the same colony for one to several days. A first indication that mating had taken place seemed to be a whitish amorphous material at the female genital opening that was not visible in virgin females. Whether mating had occurred was reliably determined in retrospect: Each of these females was kept in a group with three non-reproductive females (helpers) from the same colony. The helpers had matured in the laboratory and remained unmated. In 51 groups, an egg sac was produced from which spiderlings hatched. We report the reproductive performance of these 51 groups, which contained a reproductive female (mother) and three non-reproductive females (helpers). This group structure approximately reflects the reproductive skew in natural colonies, in which about 60 to 80 percent of females act as helpers (Salomon et al. 2008) and we assume that this ratio allowed typical helping behaviours. The 51 groups were kept in transparent plastic containers (122 x 82 x 52 mm) in a climate chamber with a 12:12 light:dark cycle and a temperature ramp of 27°C (5h): 30°C (2h): 27°C (5h): 19°C (12h). The groups were fed twice a week with two flies (*Calliphora*) each. Water was provided every morning via two spray pumps from a water bottle directed at the web.

Figure 1.—Results of observations on 51 groups of *Stegodyphus dumicola* in 2014/2015, each group consisting of one mated female and 3 non-reproductive helpers (setup). Latency between mating and first oviposition event, number of egg sacs at the end of the observation period, latency between first oviposition event and first hatching event and the reproductive outcomes recorded are given. Reproductive outcomes were: spiderlings emerged from egg sacs; egg sacs containing spiderlings hatched from eggs but dead; egg sacs containing eggs that could not be assigned to the mated female with certainty since they contained eggs only (they could be non-developing eggs laid by helpers). Stars: groups with evidence for iteroparity of the single reproductive female, based on hatching of spiderlings from eggs in more than one egg sac.

We recorded the occurrence and date of the first oviposition event and the emergence of spiderlings from egg sacs. Whenever possible, the date of further egg sac production was recorded. However, due to the increasingly dense web structure, and also in order not to disturb the groups, the date of egg laying of subsequent egg sacs could not always be determined. The observation period ended when the offspring started feeding on the mother (matriphagy) and/or on helpers (matriphagy/allophagy), which was two to three months after the spiderlings emerged from the first egg sac. For groups with multiple egg sacs, we ended the observation period two months after the production of the last egg sac. At this time, we examined the nest for the total number of egg sacs. Closed egg sacs were opened to determine if they contained undeveloped eggs or spiderlings (live or dead). As helpers occasionally produce egg sacs containing unfertilized eggs (Junghanns 2018), we chose this conservative classification: egg sacs containing eggs only were attributed to the helpers and egg sacs containing spiderlings were attributed to the mother.

In Fig. 1, the setup of the groups, the latencies to egg sac production and the reproductive outcomes of the groups are illustrated. In 2014/2015, 23 of the 51 groups (45%) contained more than one egg sac at the end of the brood care period. Our data show that social *S. dumicola* mothers produced more than one egg sac containing spiderlings in six groups (11.75%)(star symbol in Fig. 1). In three of these cases, the spiderlings did not emerge from the egg sac. Since we do not know if these spiderlings would have emerged under field conditions, a more conservative estimate for iteroparity is 5.88%, which includes only the three cases in which spiderlings emerged from the second egg sac. Females did not produce additional egg sacs in these three groups. The latency from first egg sac production to emergence of the offspring is given for all groups in Fig. 1. For the three groups with two successful reproductive events, emergence latency of offspring from the first egg sac was 36, 37 and 38 days. For the second egg sac emergence latency was 38 and 33 days (one case could not be observed). Since the production of the first and the second egg sac was only four and 20 days apart (in one case it could not be determined but the spiderlings were of two size categories), spiderlings from both egg sacs were cared for simultaneously in these three groups.

At the end of the observation period, 44 of the 51 groups had live offspring (86.3%). Those groups with a single emergence event contained an average of 31.48 ± 24.95 spiderlings (min = 0, max = 80; $N = 28$). For the three groups from which offspring emerged from two egg sacs, the total number of offspring was 26, 84 and 102 respectively.

In 2015/2016, we tested if the results from 2014/2015 were repeatable using the same set-up with 35 groups from eight colonies collected in South Africa in November 2015 (northern KwaZulu-Natal: 26°55'48.0"S, 32°49'12.0"E). We did not monitor the total number of egg sacs in this round. Spiderlings emerged from a second egg sac in two of 35 cases (5.71%). In both cases, the first brood was still being cared for. These observations confirmed the occurrence of iteroparity and that it occurred with a probability similar to that seen in the first set of experiments.

Demographic models suggest that semelparity is favoured under restrictive ecological conditions, in which adult mortality is high (Murphy 1968; Tallamy & Denno 1981), and when fitness can be increased by investing maximally in a single clutch (Stearns 1992; Roff 2002). However, cooperative brood care with non-reproductive female helpers increases the chance that at least one caring individual survives to the full extent of the care period (Queller 1994). Especially when mothers can feed during the brood care period, they might be able to gather sufficient resources for multiple reproductive events (Tallamy et al. 2004). This spread of parenting costs between multiple individuals and the higher probability of maternal survival might select for a strategy that enables mothers to produce more than one clutch (Trumbo 2013). We suggest that a shift from strict semelparity to facultative iteroparity in social *Stegodyphus* evolved as a consequence of cooperative brood care. By distributing the workload of brood care and other tasks amongst related females (Settepani et al. 2012; Junghanns et al. 2017, 2019) individual females can economize on their own resources (Junghanns et al. 2019). Cooperative maintenance of the capture web and continued foraging during brood care facilitates a prolonged provisioning period that might improve the chances of both female and offspring survival (Salomon & Lubin 2007) unlike subsocial *Stegodyphus* females, which cease to capture prey during brood care (Schneider et al. 2003). In addition to increased reproductive success in cooperatively breeding females, low chances of successful solitary reproduction (Henschel et al. 1995; Bilde et al. 2007) favours and maintains cooperative breeding in *S. dumicola*.

The reproductive strategy of *S. dumicola* might represent a facultative case of within-nest iteroparity as postulated by Trumbo (2013), in which

an extended foraging period and allomaternal care reduce the costs of extreme brood care for the mother, so that the threshold for a reproductive event can be met a second time under favourable conditions. The factors that determine if a female reproduces more than once and how often it occurs in nature remain to be investigated.

In conclusion, our observations show, that *S. dumicola* mothers can depart from a strictly semelparous lifestyle and that offspring from multiple egg sacs can be cared for simultaneously. We hypothesize that the transition to sociality and cooperative breeding might have relaxed selection for semelparity in favour of facultative iteroparity. Facultative iteroparity in *S. dumicola* both increases breeding success of the reproducing females, and boosts inclusive fitness effects for non-reproductive helpers, thus adding to the benefits of group living.

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