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Extreme allomaternal care and unequal task participation by unmated females in a cooperatively breeding spider

Anja Junghanns [a, *, 1], Christina Holm [b, 1], Mads Fristrup Schou [b], Anna Boje Sørensen [b], Gabriele Uhl [a, 2], Trine Bilde [b, 2]

[a] Department of General and Systematic Zoology, Zoological Institute and Museum, Ernst Moritz Arndt University, Greifswald, Germany
[b] Section for Genetics, Ecology and Evolution, Department of Bioscience, Aarhus University, Aarhus, Denmark

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Division of reproductive behaviour and alloparental care are key aspects of many animal societies. In cooperatively breeding species, variation in helping effort and unequal task participation are frequently observed. However, the extent to which the reproductive state of an individual affects the tasks performed during offspring care remains poorly understood. In the social spider *Stegodyphus dumicola*, approximately 40% of females reproduce, and mothers show extended maternal care including eggsac tending, regurgitation feeding and matriphagy, in which they are consumed by the offspring. We asked whether and to what extent virgin females participate in extreme maternal care and whether they differ from reproducing females in foraging activity. We show that virgin females contributed to all aspects of extended brood care, including regurgitation feeding and matriphagy. This suggests a physiological adaptation in virgin females to cooperative breeding, since in the subsocial *Stegodyphus lineatus* only mated females provide extended maternal care. Although virgin females and mothers are behaviourally totipotent, we found evidence for task differentiation as virgins engaged less in brood care and more in prey attack than mothers. High relatedness among nestmates and low probability of future reproduction in virgin helpers suggest alignment of reproductive interests between mothers and allomothers. Therefore, extreme allomaternal care by virgin helpers can be considered an adaptation to cooperative breeding in social spiders.

Group living in animals varies from anonymous collectives to highly specialized communities in which individuals cooperate in nest maintenance, predator defence, foraging and breeding (Clutton-Brock, 2002; Cockburn, 2006; Keller & Reeve, 1994; Lubin & Bilde, 2007). Cooperative breeding involves alloparental care, in which adult individuals in addition to the genetic parents participate in rearing the offspring. There are two types of cooperative breeding: in one type there is some degree of shared parentage of offspring and, more intriguingly, in the other adult nonbreeders help raise the young. The latter indicates the common occurrence of division of reproductive behaviour in cooperatively breeding societies, with one or a few individuals exclusively reproducing, while others act as helpers at the nest (e.g. in insects: Wilson, 1971; birds: Cockburn, 2006; mammals: Lukas & Clutton-Brock, 2012; fish: Taborsky, 2009; arachnids: Avilés, 1997; Lubin & Bilde, 2007). The evolutionary causes underlying decisions to forgo one's own reproduction and take on the helping role is often ascribed to kin selection (Boomsma, 2009; Hamilton, 1964a, 1964b; Ratnieks, Foster, & Wenseleers, 2006), which favours helping behaviour by inclusive fitness benefits. The degree of helping is shaped by relatedness between helper and recipient, the fitness costs of helping and the benefit of helping to the recipient. Variation in these terms between individuals may explain the frequently observed differences between group members in helping effort (Cant & Field, 2001; English, Browning, & Raihani, 2015; Huchard et al., 2014). Furthermore, individuals in cooperatively breeding societies often show differential task participation, leading to task differentiation or even to specialized castes as in eusocial insects (Jeanson & Weidenmüller, 2014; Oster & Wilson, 1978; Trumbo, 2012). In addition to kinship (Boomsma, 2009), behavioural variation and task differentiation may be influenced by proximate factors such as body size, age, place in the dominance hierarchy or

* Correspondence: A. Junghanns, Allgemeine und Systematische Zoologie, Anklamer Straße 20, D-17489 Greifswald, Germany.
E-mail address: anja.junghanns@arcor.de (A. Junghanns).
[1] Shared first authors.
[2] Shared senior authors.

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behavioural type (Carter, English, & Clutton-Brock, 2014; Clutton-Brock, 2002; Emlen & Wrege, 1991; Monnin & Peeters, 1999; Pruitt, Oufiero, Avilés, & Riechert, 2012; Radnieks & Anderson, 1999). One aspect that is not well understood is whether and/or how the reproductive state of individuals shapes their propensity to provide different types of help, that is, whether being mated or virgin influences their absolute and relative engagement in (1) alloparental care and (2) other helping tasks within cooperatively breeding societies.

Social spiders are cooperative breeders that share a communal nest and collaborate in prey capture, nest defence and brood care (Avilés, 1997; Lubin & Bilde, 2007). Sociality has evolved independently at least 20 times in seven spider families, and phylogenetic patterns suggest that it is derived from a subsocial state (Agnarsson, Avilés, Coddington, & Maddison, 2006; Settepani, Bechsgaard, & Bilde, 2016), by elimination of premating dispersal and the formation of family groups. Mating and reproduction take place in the nest among related group members, which results in extreme inbreeding and high genetic relatedness (Agnarsson, Avilés, & Maddison, 2013; Settepani, Bechsgaard, & Bilde, 2014; Settepani et al., 2017). Social spider species show a strong female-biased sex ratio; however, only a small proportion of females reproduce (Avilés, 1997; Lubin & Bilde, 2007; Salomon, Mayntz, & Lubin, 2008). As females mature asynchronously and males mature and die early, many females in a nest remain unmated (Grinsted, Breuker, & Bilde, 2014; Salomon & Lubin, 2007). These females are assumed to take on the role of helpers in brood care and other tasks in the nest (Lubin & Bilde, 2007; Salomon & Lubin, 2007). Previous studies showed that females of uncertain reproductive state direct care to offspring of other group members (Christenson, 1984; Kraus, 1988; Kullmann, Sittertz & Zimmermann, 1971; Samuk & Avilés, 2013). Notably, in the context of cooperative breeding and alloparental care, the role of mating status has not been investigated, and we currently do not know whether virgin females actually provide allomaternal care. We aimed to fill this gap by assessing the role of virgin females in cooperative breeding, and to investigate whether mating state shapes patterns of allomaternal care.

In the genus *Stegodyphus*, which contains three permanently social species, females show extreme and suicidal maternal care that includes eggsac construction, tending and guarding of eggsacs, regurgitation feeding of the hatched spiderlings and matriphagy where females are consumed by the offspring (Schneider, 2002; Seibt & Wickler, 1987, 1988). In the social *Stegodyphus dumicola*, brood size and offspring growth rate increase in the presence of mated but nonreproducing females, suggesting that helpers acquire indirect benefits and promote group productivity (Salomon & Lubin, 2007). However, since about 60% of females in a nest of *S. dumicola* remain unmated (Salomon et al., 2008), it is essential to investigate the contribution of these females to the various tasks to understand group organization. To this aim, we asked whether virgin females perform allomaternal care to the offspring of reproducing females, and whether the brood care provided includes all activities from eggsac care and regurgitation feeding to matriphagy. Interestingly, in the subsocial solitarily breeding congener *Stegodyphus lineatus*, only mated females that have produced an eggsac provide maternal care, suggesting that brood care and regurgitation feeding are triggered by a preceding reproductive event (Schneider, 2002). Maternal care behaviours in virgin *S. dumicola* females would therefore indicate an adaptation to cooperative breeding in social species (Jones, Riechert, Dalrymple, & Parker, 2007; Schneider, 2002).

Accumulating evidence for behavioural specialization in prey capture, web construction and defence behaviour, as well as brood care, shows that despite the lack of morphological differentiation, social or facultative social spiders exhibit some degree of task differentiation (Pruitt & Riechert, 2011; Settepani, Grinsted, Granfeldt, Jensen, & Bilde, 2013; Wright, Holbrook, & Pruitt, 2014; but see Ainsworth, Slowtow, Crouch & Lubin, 2002; ; Settepani, Bilde, & Grinsted, 2015). Although there is some evidence for unequal task participation among subordinate and (presumably) nonreproducing helpers in various animal groups (Cant, 2003; Emlen & Wrege, 1991; Monnin & Peeters, 1999; Mooney, Filice, Douglas, & Holmes, 2015), in general we have little knowledge about how the reproductive state of individuals shapes behavioural specialization. Therefore, we asked whether the relative investment in reproductive and nonreproductive tasks differs between virgin females and mothers. If there is differential task participation between virgins and mothers, we expected virgin females to specialize on prey capture, which is assumed to be a risky task that exposes individuals to injury, parasitism or predation (Bradoo, 1980; Griswold & Meikle, 1990; Henschel, 1998; A. Junghanns & C. Holm, personal observation 2013; V. Settepani, personal communication 13 March 2017), whereas mothers are predominantly occupied with brood care.

METHODS

Study Species

The genus *Stegodyphus* contains at least 18 subsocial species (Kraus & Kraus, 1988) in which offspring share a nest with the mother for an extended period of brood care. The mother provides the spiderlings with a nourishing fluid through regurgitation feeding for a period of several weeks and eventually is eaten by her offspring (matriphagy; Kullmann, Nawabi, & Zimmermann, 1971). After matriphagy, the spiderlings of the subsocial species disperse and live solitarily. In three species in this genus, including *S. dumicola,* spiderlings do not disperse but live socially throughout their lives (Kraus & Kraus, 1988). *Stegodyphus dumicola* can be found in dry and warm habitats of southern Africa (Kraus & Kraus, 1988). The spiders inhabit a dense retreat of silk and plant material with one or more two-dimensional capture webs attached. New nests are founded by local budding or fission of nests or by propagule dispersal by a single mated female (Bilde et al., 2007). Nests grow over several generations to a size of a few tens up to more than a thousand individuals. Males mature early and mate with the first females that become adult within their natal nest (Henschel, Lubin, & Schneider, 1995). Male dispersal is limited to interconnected nearby nests (Lubin, Birkhofer, Berger-Tal, & Bilde, 2009), which are usually closely related (Johannesen, Hennig, Dommermuth, & Schneider, 2002) and at a similar developmental stage (A. Junghanns & C. Holm, personal observation 2013; Salomon et al., 2008). This highly inbred mating system results in a high relatedness between members of a nest (Agnarsson et al., 2013). Males die within a few weeks after maturation while females mature over a period of several months (Henschel et al., 1995). This can result in a situation with about 60% of all females of a nest remaining unmated (Salomon et al., 2008).

Point-sampling Trials

Groups of *S. dumicola* were composed as specified below. They were checked daily for eggsac care behaviour and during feeding bouts prey attack behaviour was recorded. Since the recording rule resulted in sample points over the course of the observation phase, we refer to these trials as point-sampling trials.

Collection site, spider maintenance and group composition

Twenty-four nests (called source nests hereafter) of *S. dumicola* were collected in South Africa in November 2013 from Shingwedzi