Social foraging and exploitative behaviour in group-living crab spiders

DISSERTATION

for the degree of Doctor of Natural Sciences

at the Faculty of Mathematics, Informatics and Natural Science
Department of Biology
of Universität Hamburg

&

at the Faculty of Science and Engineering
Department of Biological Sciences
of Macquarie University

submitted by

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Hamburg, 2017

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Date of oral defense:	14.05.2018
(Datum der Disputation)	

ACKNOWLEDGEMENTS

Foremost, I would like to express my great appreciation to my doctoral supervisors Jutta M. Schneider and Marie E. Herberstein for their tremendous support throughout my joint-PhD candidature. They enthusiastically embraced the project, believed in my skills, contributed greatly with creative ideas and valuable advice, and overall provided excellent guidance in my professional development as a scientist. I am particularly grateful for the warm welcome my supervisors extended to me every time I arrived back in Hamburg or travelled to Sydney.

I deeply appreciate the financial support given by Macquarie University in Australia and by the Konrad-Adenauer-Foundation in Germany, without which this thesis could not have been realised.

My appreciation extends to Angelika Taebel-Hellwig and Tomma Dirks for maintaining 'my' crab spiders in Hamburg while I was abroad, to Jay Stafstrom and Ina Geedicke for helping greatly with fieldwork, and to Tanja Rüthemann for contributing to my project with her conscientious social network study. Moreover, I am indebted to Darrell Kemp, who ensured that I had access to the necessary lab equipment at Macquarie University. I owe special thanks to Leigh Simmons and his group for welcoming me as a visiting researcher at the University of Western Australia, and for ensuring that I received everything I needed to conduct my experimental research. I would also like to acknowledge Nerida Wilson and Nikolai Tartanic for their kind hospitality in Perth. I further wish to thank my colleagues at University Hamburg and Macquarie University, who enriched my social life, and I greatly appreciate the support given by the administration staff at the Faculty of Science and Engineering at Macquarie University.

My sincere thanks go to Jasmin Ruch for introducing me into the field of social crab spiders and for sharing her professional and practical expertise. I further wish to extend my sincere thanks to Pauline Scholzgart, who supported me as a field assistant, but even more importantly as a great friend and flat mate during my stay in Australia in 2017. Last, but by no means least, I would like to pay special thankfulness to Giselle Muschett for our enlightening scientific and non-scientific conversations over countless Chai Latte's, and for the precious friendship.

Finally, I express my deep gratitude to my family and to my friends for the immeasurable amount of unfailing support and unconditional encouragement they provided throughout this journey. My heartfelt thanks go to my parents Marianne and Ingolf Dumke, my siblings Ines and Jens Dumke, and to Vincent Stangenberg.

CONTENTS

SUMMARY

When animals live and forage in groups, the food discoveries made by a few are usually shared among many individuals. Food sharing can improve the per-capita foraging success of group members, but competition over food resources may adversely reduce the payoff return. Moreover, in the absence of mechanisms that reinforce the cooperative nature of group foraging, some group members (scroungers) may exploit the efforts of food-procuring individuals (producers), leading to unequal reward distributions on the individual level. By investigating the cooperative and exploitative ways in which individuals interact when foraging in groups, studies on social foraging assess the interplay between advantages and disadvantages to group foraging - but the existing research mostly concerns non-predatory species. However, the costs that predators avoid by scrounging from the prey laboriously subdued by others, and thus the payoffs reaped from this defective tactic, should be particularly substantial. In consequence, the evolution and maintenance of group foraging - and more generally of group living - in social predators will be severely challenged by the rise of exploitative foraging behaviour.

In this thesis, I study social foraging and exploitative behaviour using Australia's group-living, subsocial crab spiders as a predatory model system, in particular the species *Australomisidia ergandros* and furthermore *Australomisidia socialis* and *Xysticus bimaculatus*. Since these crab spiders do not build capture webs, but nonetheless attack and feed communally in offspring groups, insights gained from this study system may be projected on many other social carnivorous species. I conducted an array of laboratory foraging experiments to investigate the common pros and cons of foraging as a group at the level of species, the effects of group size and group composition on exploitative foraging behaviour at the level of groups within species, and the existence and determinants of individual specialisation in social foraging tactic at the level of individuals within groups.

On the level of species, my results indicate that group formation and group retention in subsocial crab spiders are driven by competition-reducing advantages associated with maternal provisioning beyond the nutritional independence of young - and later, in offspring groups, by enhanced predatory success in groups as compared to solitary individuals. I thus disprove the presumption that non-webbuilding spiders which live in groups do not enjoy foraging benefits of grouping owing to the absence of a large communal capture web. Further, this suggests that group foraging in crab spiders is based on the same principles that promote social living as cooperatively hunting vertebrates.

On group level, I provide novel empirical support for a relevant prediction of social foraging models: in *A. ergandros*, I demonstrate that the extent of scrounging increases with group size, mediated via shifts in the ratio of tactic-specialised producers to scroungers. Given tactic specialisation, negative frequency dependent selection is thought to limit the spread of the scrounger type, because that tactic only promises high rewards as long as producers are common. Accordingly, I show that *A. ergandros* scroungers adhere to their defective strategy by not sharing food in groups of their own, consequently suffering negative fitness payoffs. The tactic of producers, on the other hand, seems to be remarkably adaptive to group composition. In this respect, inherent producers are here shown to receive food shares from other producers. On individual level, I finally reveal that the evidently cooperative tendency to procure and share food is sex-dependent in *A. ergandros*, with males acting as providers. Based on my findings, I suggest an explanatory framework for the evolution and maintenance of group living and cooperative group foraging in social predators despite the temptation to exploit.

ZUSAMMENFASSUNG

Gehen Mitglieder sozialer Tierverbände gemeinschaftlich auf Nahrungssuche, kommen die Beschaffungen weniger Individuen häufig vielen weiteren zugute. Hieraus erschließt sich ein entscheidender Vorteil des Gruppenlebens: Die Steigerung des Fresserfolgs pro Individuum. Diesem Vorteil stehen jedoch inhärente Kosten des Nahrungserwerbs in der Gruppe gegenüber - beispielsweise konkurrieren Gruppenmitglieder um begrenzte Nahrungsressourcen. Des Weiteren begünstigt der gemeinschaftliche Nahrungserwerb, dass Individuen („Scrounger") die kostspieligen Leistungen ihrer nahrungsbeschaffenden Gefährten ausbeuten. Studien, die sich dem Aspekt des „social foraging" widmen - gemeint sind die kooperativen und kompetitiven Interaktionen zwischen Individuen auf Nahrungssuche - untersuchen die Auswirkungen von Nahrungskonkurrenz und Ausbeute auf die Kosten-Nutzen Bilanz des Gruppenlebens. Soziale Prädatoren werden in experimentellen Studien des „social foraging" bisher allerdings kaum berücksichtigt. Hier umgehen Scrounger jedoch außergewöhnlich hohe energetische Kosten, nämlich die des Beutefangs. Demzufolge sind soziale Prädatoren dem Aufkommen ausbeuterischen Fressverhaltens in besonderer Weise ausgesetzt.

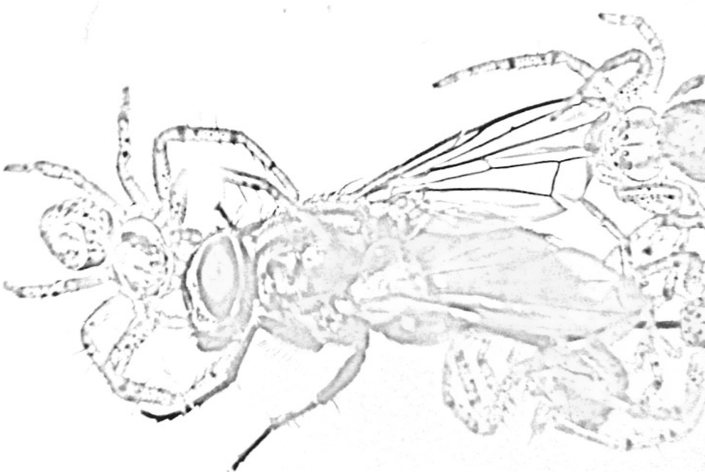
In der vorliegenden Arbeit erforsche ich die Auswirkungen von ausbeuterischem Fressverhalten in Prädatoren am Beispiel subsozialer australischer Krabbenspinnen. Ich untersuche drei Arten: *Australomisidia ergandros*, *Australomisidia socialis* and *Xysticus bimaculatus*. Gruppenlebende Krabbenspinnen bauen kein Fangnetz, attackieren und fressen aber dennoch gemeinschaftlich und liefern daher Einblicke, die auch auf viele weitere soziale Prädatoren zutreffen könnten. In einer Reihe von Laborexperimenten untersuche ich systematisch die Vorteile und Nachteile der Nahrungssuche in der Gruppe, die Zusammenhänge zwischen Gruppengröße beziehungsweise Gruppenkomposition und Ausbeuterverhalten, sowie die Existenz und die phänotypischen Bestimmungsfaktoren von individueller Fresstaktik-Spezialisierung.

Auf der Ebene der Arten weisen meine Befunde darauf hin, dass Krabbenspinnen-Gruppen im Vergleich zu einzeln jagenden Individuen, erhöhten Prädationserfolg erzielen, selbst wenn Attacken nicht von mehreren Individuen gleichzeitig durchgeführt werden. Dieser Effekt sollte die Nahrungskonkurrenz zwischen den Mitgliedern einer Gruppe reduzieren - und kann somit die Evolution und den Erhalt des Gruppenlebens bei subsozialen Krabbenspinnen mitbegründen. Weiterhin widerlegt dieses Ergebnis die bisherige Vermutung, dass lediglich netzbauende soziale Spinnen Nahrungsvorteile des Gruppenlebens genießen. In Bezug auf die Nahrungsbeschaffung scheint das Gruppenleben bei Krabbenspinnen dementsprechend auf den gleichen evolutiven Prinzipien aufzubauen wie bei gruppenlebenden Vertebraten.

Darüber hinaus liefert die vorliegende Arbeit empirische Belege für Vorhersagen, die mittels theoretischer Modellierungen des „social foraging" getroffen wurden. Insbesondere zeige ich für *A. ergandros*, dass das Ausmaß ausbeuterischen Fressverhaltens mit steigender Gruppengröße zunimmt. Dieser Effekt operiert auf Individuenebene, durch Veränderungen im Verhältnis von spezialisierten Nahrungsbeschaffern („Producer") zu spezialisierten Ausbeutern („Scrounger"). Ein Anstieg der Scrounger-Anzahl innerhalb der Gruppe sollte jedoch schlussendlich durch negative frequenz-abhängige Selektion limitiert sein, da die Scrounger-Taktik nur dann besondere Vorteile verspricht, wenn genügend Producer genug Nahrungsressourcen erschließen. Diesbezüglich weisen die Befunde dieser Arbeit darauf hin, dass Scrounger ihre charakteristische Strategie in homogenen Scrounger-Gruppen beibehalten, mit negativen Folgen für die Fitness pro Individuum. Die Producer-Taktik erweist sich hingegen als adaptiv: Producer teilen ihre Beute wahrscheinlich bereitschaftlich, so dass tatsächlichen Producern oftmals Scrounger-ähnliche Vorteile zugutekommen. Schließlich belege ich mittels sozialer Netzwerkanalyse, dass männliche Tiere eine gesteigerte Tendenz zur Nahrungsbeschaffung und –Teilung aufweisen. Insgesamt präsentiere ich ein erklärendes Rahmenwerk für die Evolution und den Erhalt von Gruppenleben und kooperativer Nahrungsbeschaffung in sozialen Prädatoren.

CHAPTER 1

General introduction
into social foraging and exploitative behaviour in group-living crab spiders



General introduction

Advantages of group living

The transition from solitary to group living is an evolutionary phenomenon pervading almost all taxonomic entities (Wilson 1971; Alexander 1974; Koenig & Dickinson 2004; Lubin & Bilde 2007; Silk 2007; Thiel 2007; Clutton-Brock 2009; Rubenstein & Abbot 2017). Correspondingly, there is a wealth of scientific literature providing concepts on how this transition has occurred, and in synthesis of this literature, fundamental keys for understanding the evolution of group living become apparent (reviewed in Krause & Ruxton 2002).

Anti-predator advantages

Thus, group formation is thought to be a common evolutionary response to predation pressure (Lima 1995; Krause & Ruxton 2002). This is partly because grouping can improve attack abatement (Turner & Pitcher 1986; Wrona & Dixon 1991): a group of individuals, clumped in space, may be less likely to be encountered than the identical number of solitary individuals that are scattered over the hunting range of a predator (encounter avoidance effect; Inman & Krebs 1987). Moreover, if the predator has encountered the group nonetheless, the probability for one group member to be chosen as prey will still be lower than that for a solitary individual (dilution effect, Foster & Treherne 1981). In combination, these and other anti-predator effects of grouping (for further examples see Elgar 1989; Krause & Ruxton 2002) will diminish the risk of falling victim to a predator for group members as compared to solitary living individuals.

Foraging-related advantages

Furthermore, living in groups is presumed to be advantageous as it improves the foraging success of individuals, according to the principle that the food discoveries of a few lead to the feeding of many (Clark & Mangel 1986; Giraldeau & Caraco 2000). For instance, group members may actively pass on information about the location and quality of food patches. Consequently, the searching time per individual (i.e. ‘per capita’) declines while the food intake per capita increases (Clark & Mangel 1986; Valone 1989). The waggle dance of eusocial honey bees, which indicates both the direction and distance to food or water resources, is the prime example of active, beneficial foraging information transfer among group members (Wenner et al. 1969; Ratnieks & Shackleton 2015).

Alternatively (or concurrently), individuals in groups may enjoy enhanced foraging success due to the passive transfer of foraging information: group members may increase their feeding rates by observing and following successful individuals to feeding sites (Ward & Zahavi 1973; Greene 1987), or by using coincidentally created trails and acoustic cues (Galef & Giraldeau 2001). A specific case of foraging advantages to grouping is prevalent in social predators, where group members benefit from capturing more and larger prey in cooperative hunts (Packer & Ruttan 1988; Creel & Creel 1995; Yip et al. 2008).

Payoffs to social foraging

The above advantages of foraging in groups appear straightforward, but to comprehensively understand the significance that foraging carries in promoting the evolution and maintenance of group living, one needs to consider that grouping also bears foraging-related costs. These costs innately arise from the aggregation of individuals in space and time and counteract the beneficial rewards that individuals receive from foraging and, more generally, from living in groups (reviewed in Krause & Ruxton 2002). The perhaps most prevalent foraging-related detriment of grouping is that members of groups should be exposed to greater competition over food resources than solitary living individuals (Rubenstein 1978; Ranta et al. 1993; Grand & Dill 1999; Giraldeau & Dubois 2008). Whether and to what extent competition among group members diminishes the payoffs of group foraging depends on the abundance and distribution of food resources - but also, at the social level, on group size as well as on the existence of cooperative mechanisms and behaviours that mitigate the costs of food competition (Ranta et al. 1993). In this respect, studies of social foraging seek to unravel the complex cost-benefit relationships that finally determine if individuals reap positive or, conversely, negative payoffs of group foraging (e.g. Ranta et al. 1993; Giraldeau & Caraco 2000; Shen et al. 2013).

Explicitly, social foraging studies address the cooperative and competitive ways in which individuals interact when foraging as a group. Thereby, these studies account for the social predicament that an individual's payoffs depend on the decisions of its group members (Marshall et al. 2012). In a simple example of this interplay, one may regard two food items that differ in nutritional value. An individual that forages solitary will achieve the highest payoff by choosing the item of higher nutritional value (Pyke et al. 1977), but for a group member it may be more profitable to select the less nutritious food item in order to avoid potential food competition over the other (Packer & Ruttan 1988; Giraldeau & Caraco 2000).

Effects of group size

The degree to which group members incur costly food competition is strongly influenced by the size of the foraging group (Janson 1988; Grand & Dill 1999): the larger the group the higher the competition, especially if groups forage in environments where food resources are scarce or patchily distributed (Giraldeau & Caraco 2000; Krause & Ruxton 2002). Yet, larger groups may discover greater numbers of food patches, leading to higher consumption rates and reduced variance in per capita foraging success (Pitcher et al. 1982; Valone 1989). To investigate whether the concurrence of such group size effects results in negative payoffs (competition overrides the beneficial increase in consumption rates) or positive payoffs (the increase in consumption rates overrides the costs of competition) per capita is a central purpose of social foraging studies on group level (Creel & Creel 1995; Coolen 2002; Shen et al. 2013).

Effects of exploitation

Yet, even if foraging in a group is advantageous on average, individual group members may still achieve asymmetric foraging payoffs, especially when they apply different social foraging tactics (Barnard & Sibly 1981; Packer & Ruttan 1988). In particular, whenever the food procurements of a few result in the feeding of many, exploitative foraging strategies are promoted: provided that cooperative (i.e. food acquiring) group members are present, individuals may achieve the highest direct payoff by avoiding own efforts and instead feeding from the food acquired by others (Barnard & Sibly 1981; Doebeli & Hauert 2005). The factors that govern an individual's decision to cooperate or exploit, and the impact that exploitation exerts on the payoffs of living and foraging in groups are other essential areas of interest in social foraging studies (Barnard & Sibly 1981; Vickery et al. 1991; Ranta 1996; Giraldeau & Beauchamp 1999; Coolen et al. 2001). The overall objective, hereby, is to identify mechanisms that constrain the detrimental extent of exploitation in favour of group living.

Exploitative foraging behaviour

In behavioural ecology, the act to take advantage of the communal resources provided by others is referred to as freeloading', 'joining' defecting' or 'scrounging' (Barnard & Sibly 1981; Giraldeau & Beauchamp 1999; Avilés 2002; Imhof et al. 2005). The latter term is typically used in social foraging contexts, where model analyses of scrounging behaviour have taken two converse approaches.

Information-sharing models

On the positive side, information sharing models predict that the option to scrounge invokes the previously described advantages of group foraging (e.g. the increase in feeding rates; Giraldeau & Dubois 2008). Information-sharing models assume compatibility of social foraging tactics, picturing a scenario in which all group members primarily search for food - hence contributing to the groups' corporate effort - and concurrently monitor their companions to eventually converge on discoveries (Clark & Mangel 1984; Beauchamp & Giraldeau 1996). In this case, group members are predicted to scrounge with similar frequencies, such that the rewards of group foraging are evenly distributed.

Producer-scrounger models

Labelling the use of food resources acquired by others as 'exploitative behaviour' becomes more applicable if foraging tactics are incompatible, i.e. if individuals refrain from the attempt to acquire food (to 'produce') in order to seize the chance to scrounge (Barnard & Sibly 1981). Incompatibility of producing and scrounging entails that individuals who look for scrounging opportunities no longer contribute to the corporate effort to produce food, making the payoffs of producing and scrounging strongly frequency-dependent (Barnard & Sibly 1981): scrounging promises the highest payoffs as long as sufficient food resources to scrounge from are produced (i.e. when scrounging is rare), but these payoffs decrease when the production of food resources declines (i.e. when scrounging is frequent; Giraldeau & Beauchamp 1999). This negative frequency-dependence is simulated in the so-termed producer-scrounger models of social foraging (Barnard & Sibly 1981; Vickery et al. 1991; Giraldeau & Beauchamp 1999).

Producer-scrounger systems

Non-predators

Flocks of ground-feeding finches likely conform to the assumption of tactic incompatibility and consequent frequency-dependence made in producer-scrounger models (Coolen et al. 2001; David & Giraldeau 2011). Finches apply the producer tactic by searching for grains with their head pointing down, or the scrounger tactic by searching for scrounging opportunities with their head pointing up (Ranta et al. 1996) Alternate but not concurrent use of these tactics is possible, and if an increasing proportion of individuals searches for scrounging options, the number of food finding events decreases (Coolen 2002).

To evade negative payoffs, flock members in the spice finch *Lonchura punctulata* adjust their scrounging rate according to the effectiveness of that tactic. As a result, spice finches maintain a profitable equilibrium frequency of scrounging and producing (Coolen et al. 2001). Importantly, the respective behaviours associated with producing and scrounging in spice finches (looking down or looking up) can be assumed to entail rather similar costs, such that the two alternative foraging tactics are readily interchangeable (Giraldeau & Dubois 2008; Morand-Ferron et al. 2011). This should be different for group-living predators that engage in producer-scrounger games (Packer & Ruttan 1988; Giraldeau & Caraco 2000).

Predators

In African wild dogs (*Lycaon pictus*), spotted hyenas (*Crocuta crocuta*) and pride lions (*Panthera leo*), as well as in predatory birds, insects or spiders, group members who do not participate in hunting still receive shares of the prey subdued by others (Kruuk 1972; Scheel & Packer 1991; Creel & Creel 1995). The hunting costs avoided by these scrounging group members, but payed by the producing individuals, are substantial (Packer & Ruttan 1988). This asymmetry in costs has been suggested to evoke individual specialisation in foraging tactic (Packer & Ruttan 1988; Bergmüller & Taborsky 2010; Giraldeau & Caraco 2000).

In a competitive scenario, tactic specialisation may be driven by dominance: physically superior group members need to invest less effort to claim their share of the prey - and thus may adopt the scrounger role, whereas inferior individuals are forced to produce (Barta & Giraldeau 1998). Conversely, in a cooperative scenario, the producer role may be occupied by group members with greater hunting abilities, as these face lower-than-average costs of producing (Beauchamp 2006).

Either way, the higher payoffs of scrounging compared to producing should select for the emergence and spread of scrounging behaviour in social predators (Doebeli & Hauert 2005; Imhof et al. 2005; Giraldeau & Dubois 2008). Therefore, social predators present a particularly relevant system for studies that examine the significance of social foraging and exploitative scrounging behaviour in the transition from solitary to group living. So far, however, questions revolving around individual specialisation in foraging tactic, group size effects on scrounging behaviour, or frequency- dependent effects on scrounger payoffs have received little scientific attention in predatory species that form groups.

In my thesis, I explore the above social foraging questions in group-living crab spiders (Araneae: Thomisidae). Although spiders are usually solitary and known for their cannibalistic habits, group living and group foraging occurs in several lineages. The following paragraphs provide insight into the various group-living systems in spiders.

Group-living spiders

Colonial and cooperative spiders

Group-living spiders are typically subdivided into being colonial or cooperative (Kullmann 1972; Uetz 1989; Whitehouse & Lubin 2005; Bilde & Lubin 2011). Colonial spiders constitute foraging societies: individuals aggregate at prey-rich or otherwise favourable sites and benefit from increased foraging success owing to the proximity of their webs (Lubin 1974; Ventura et al. 2017). Despite forming aggregations, colonial spiders are territorial and rarely feed communally (Whitehouse & Lubin 2005). Cooperative or simply 'social' spiders, on the other hand, occupy a communal web and engage in cooperative activities, such as web maintenance and group feeding (Kullmann 1972; Avilés 1997; Lubin & Bilde 2007; Bilde & Lubin 2011).

The communal capture web is believed to be a preadaptation that facilitates such social activities (Avilés 1997; Avilés & Guevara 2017). For instance, silk vibrations caused by prey may alert numerous group members - and several may be needed to subdue and transport large insects to the centre of the web (Pasquet & Krafft 1992).

To date, 19 species in eight genera spanning over five different families form permanent family alliances and are therefore considered being social. Furthermore, about 70 species in 16 families exhibit 'subsociality' (Avilés & Guevara 2017). In subsocial spiders, offspring remain in their natal groups after a period of maternal care, but normally disperse when reaching reproductive maturity (Yip & Rayor 2014; Avilés & Guevara 2017). Subsocial spiders are considered to present an evolutionary link between solitary and social spider species, as permanent sociality in spiders is thought to have evolved via a 'subsocial route' (Figure 1).

The subsocial route to sociality

Permanently social spiders probably evolved from subsocial ancestors, which themselves probably evolved from ancestors that exhibited extended maternal care. Thus, sociality in spiders appears to

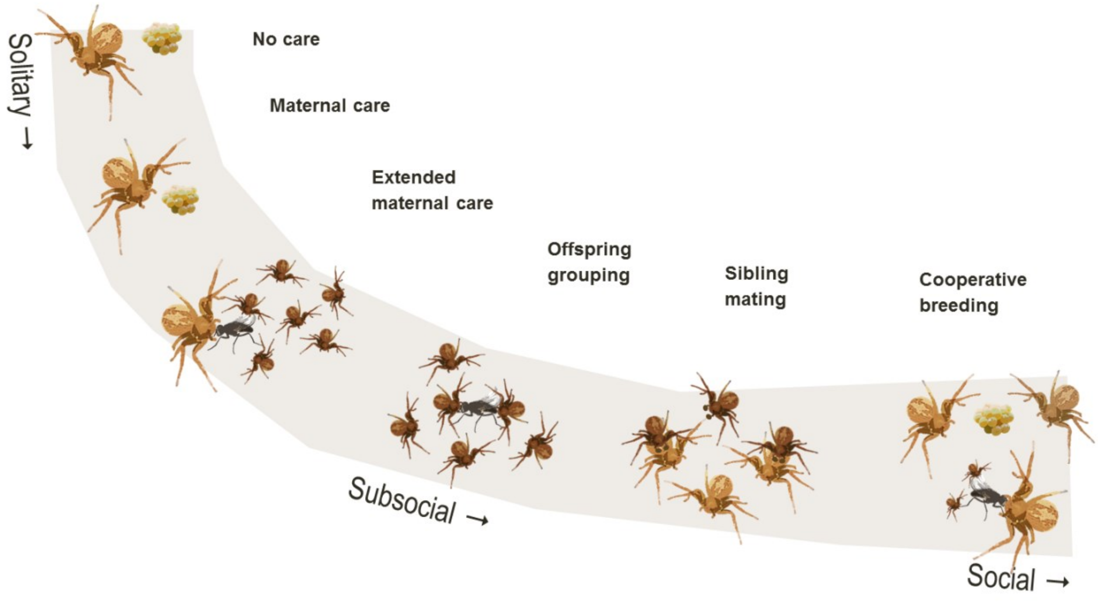


Figure 1 | The subsocial route to sociality as presumed for cooperative spiders. The subsocial route describes the evolution of social group-living via extended maternal care, which in spiders includes the depicted transitions from no care to cooperative (or communal) breeding. In general, these transitions are characterised by the postponement of dispersal from offspring groups, up to the entire elimination of dispersal in favour of permanent sociality accompanied by inbreeding.

be the result of a series of major evolutionary transitions prolonging the grouping of offspring within their natal retreat (Figure 1; Tallamy 1984; Lubin & Bilde 2007; Yip & Rayor 2014).

The presumed series of evolutionary transitions starts with a switch in maternal care behaviour: from showing no brood care to protecting eggs and from protecting only eggs to protecting and/or provisioning hatched offspring. The next transition leads to the persistence of offspring grouping past maternal care, accompanied by cooperation among juveniles and by pre-mating dispersal. This temporal form of group living defines the majority of subsocial spider species (Yip & Rayor 2014). In the subsequent transition to permanent group-living, dispersal is ultimately eliminated (Avilés & Bukowski 2006; Ruch et al. 2009). At this social stage, siblings mate within their natal retreat, and adult females may even cooperate in caring for their broods (Salomon & Lubin 2007). As a consequence of inbreeding, subsocial and social spiders show female-biased sex ratios (Frank 1987; Avilés 1986; Bilde et al. 2005).

Recent extensive reviews by Bilde & Lubin (2011), Yip and Rayor (2014) or Avilés & Guevara (2017) describe the factors that may have selected for the extension of maternal care and the prolongation of offspring group living at each transitional step. In this context, Yip & Rayor (2014) call for investigations into social foraging and exploitative behaviour in offspring groups. The sharing of prey among group members has been reported in many subsocial species, and Yip &Rayor (2014) point to a lack of insight into the mechanisms that regulate potential scrounging behaviour to a level at which spider societies can persist.

Study system: subsocial crab spiders

The family of crab spiders (Thomisidae) contains over 2100 described species in 172 genera (Benjamin et al. 2008; Szymkowiak 2014). Crab spiders do not build capture webs; typically, they are solitary sit-and-wait predators that ambush prey insects by using their colouration patterns for camouflage (Théry & Casas 2002; Wignall et al. 2006). Despite the lack of a capture web, which - as mentioned earlier – has been suggested to facilitate cooperation and therewith the evolution of social group living in spiders, four Australian crab spider species are subsocial. Instead of building communal webs, these species construct communal nests from tree leaves (Main 1988; Evans 1995; Ruch et al. 2014a).

Taxonomy and distribution

Three of the four subsocial crab spider species belong to the genus *Australomisidia*, but were formerly allocated to the genus *Diaea* (reallocation by Szymkowiak 2014). Two of these species, *Australomisidia ergandros* (see Figure 2A) and *Australomisidia inornata*, occur in eucalyptus-dominated forests and farmland at varying altitude across South-Eastern Australia. Their distribution ranges from Tasmania to Queensland, potentially according to a tolerance of maximal temperatures no higher than ~33° Celsius (Evans 1997). The third subsocial *Australomisidia* species, *Australomisidia socialis* (Figure 2B) has a rather limited distribution that is restricted to the coastal eucalyptus forests of Western Australia (Evans 1997). The distribution ranges from Albany in the South to Margaret River in the South-West and thus appears to follow a similar climatic pattern as in the other subsocial *Australomisidia* species (Rowell and Main 1992; Evans 1997).

Furthermore, the genus *Xysticus* contains one species that was recently identified as subsocial by J. Ruch (Figure 2C; Ruch et al. 2014a). The communal nests of *Xysticus bimaculatus* can be found on *Acacia* and *Alphitonia* trees in bushland and forests of coastal Queensland.

Nest groups

The communal leafnests that subsocial thomisid spiders construct in their host trees have a distinct structure (e.g. Figure 2D). For nest construction, the tree leaves remain attached to the twig but are bound together with silk threads, resulting in an oval-shaped nest with a labyrinthine interior. Nests are continuously expanded with fresh leaves that are attached to the surface (detailed description in Main 1988). Silk-reinforced entrances on the surface of the nest serve as foraging 'portholes' (Main 1988; Evans 1995; Ruch et al. 2014a).

Figure 2 | The vertical black lines are scale bars, each representing 10mm. **A:** An adult female and caring mother of the subsocial thomisid species *Australomisidia ergandros.* The mother is sitting on the surface of the nest that she inhabits with her young offspring. **B:** A juvenile in late instar, judged from the body size presumably a female, of the subsocial thomisid species *Australomisidia socialis*. **C:** An adult female and caring mother of the subsocial thomisid species *Xysticus bimaculatus*. The mother is maintaining the nest by weaving additional silk threads. **D:** A communal nest constructed from eucalyptus tree leaves and inhabited by an offspring group of the subsocial crab spider *Australomisidia ergandros.* The leaves are bound together by repeatedly and multi-directionally woven silk threads. The portholes serve as nest entrances and foraging areas suitable to ambush prey, for example ants and sometimes wasps.

A suitable tree may host several spider nests. Each nest is initiated by another mated female that lays her eggs inside. Accordingly, each nest is later inhabited by a group consisting of the mother and her young offspring. After the caring mother has died, the offspring continue to live together for several months, either until or beyond reproductive maturity (details on the respective life cycles are given in Main 1988; Evans 1995; Ruch et al. 2014a). The size of these offspring groups varies between nests. Documented mean group sizes per nest are 24.9 ± 1.9 individuals for *A. ergandros (N* = 52 nests; Evans 1997*)*, 26.9 ± 2.1 individuals for *A. socialis* (*N* = 42 nests; unpublished data) and 10.5 ± 0.3 individuals (*N* = 120 Nests; Ruch et al. 2014a) for *X. bimaculatus*.

Social behaviours

It is assumed that offspring-group members gain benefits from cooperating in nest building and foraging-related activities (Main 1988; Evans 1998; Evans 2000; Ruch et al. 2014b; Yip & Rayor 2014). For *A. ergandros* and *A. socialis*, it has been reported that offspring-group members engage in communal attacks and share prey with group members that have not participated in the capture (Evans 1993; Ruch et al. 2014c; Ruch et al. 2015a).

Furthermore, the crab spider *A. ergandros* has been studied intensively to test hypotheses addressing the foraging interactions among related group members and unrelated 'immigrants' (Ruch et al. 2014b; Ruch et al. 2014c). I contributed to a study in which the foraging interactions among members of sibling groups or non-sibling groups were analysed as social networks (Appendix 1; Ruch et al. 2015a). The presence of unrelated individuals was shown to detrimentally affect the extent of communal feeding. Therefore, and because immigration into offspring groups is presumably low in nature (Evans & Goodisman 2002), studies using *A. ergandros* to explore more general social foraging questions (e.g. group size effects) may best be conducted on kin groups. The mentioned study further provides a pilot example of how social foraging questions on individual level can be addressed with social network analysis. This thesis was influenced by these methodological findings.

Study aims

Owing to the absence of a capture web as a means to ease foraging cooperation, subsocial crab spiders may offer insights into social foraging and exploitative behaviour that are also applicable to group-living predators outside the Araneae. Accordingly, I treat group-living crab spiders as a model system to experimentally address several social foraging questions revolving around the payoffs that group members achieve through foraging communally. I combine investigations on the level of species, on the level of groups within species and on the level of individuals within groups. The overall objective of this multi-level approach is to identify probable mechanisms that contribute to the evolution and maintenance of group foraging in particular and of group living in general. I specifically focus on the potential mechanisms that regulate exploitative foraging behaviour.

Common social behaviours

A phylogenetic study suggests that subsociality in *Xysticus bimaculatus* evolved independently from the subsocial *Australomisidia* species (Ruch et al. 2015b). Species-comparative studies could therefore reveal common mechanisms driving the evolution and maintenance of social group living in crab spiders, but such comparative studies require detailed knowledge about the life history patterns of all included species. However, *X. bimaculatus* was only recently discovered to periodically live in groups, and the knowledge on its subsocial lifestyle is still very limited.

In the first data chapter of this thesis (**Chapter 2**), I explore whether *X. bimaculatus* shows social behaviours similar to those reported for the two well-studied subsocial congeners in the *Australomisidia* genus: *Australomisidia ergandros* and *Australomisidia socialis*. To answer whether *X. bimaculatus* exhibits extended maternal care, I examine the nest group characteristics and experimentally test whether offspring benefit from maternal food provisioning. Regarding the possible social foraging interactions between offspring, I further evaluate whether *X. bimaculatus* exhibits communal attacking and prey sharing.

Common advantages of group foraging

With the insights into the subsocial lifestyle of *X. bimaculatus* from **Chapter 2**, three subsocial thomisids are studied to an extent that enables species-comparative investigations into the advantages of group foraging as drivers of social group living. I follow this purpose in **Chapter 3**, where I experimentally investigate potential benefits of foraging in a group compared to foraging solitary across *A. ergandros*, *A. socialis* and *X. bimaculatus*. To account for the various foraging tactics that individuals can use in groups, I include an examination of the respective immediate payoffs of producing, scrounging and feeding alone.

On the downside of group foraging, individuals may experience increased competition over food resources (e.g. Grand & Dill 1999), and group-living animals are likely to have evolved behavioural adaptations to reduce food competition. The social spider *Anelosimus eximius* compensates for food competition by capturing larger prey (Yip et al 2008). To evaluate this possibility for subsocial crab spiders, I extended my study to investigating the effect of grouping on prey size preference across the three mentioned species.

Emergence of scrounging

The occurrence of scrounging has already been reported in previous studies on *A. ergandros* and seems to be more pronounced than in the other subsocial crab spider species (Main 1988; **Chapter 2**). In the subsequent Chapters, I use *A. ergandros* to explore the impact of scrounging behaviour.

In **Chapter 4**, I test two producer-scrounger model predictions that have not been previously tested in social predators. The first prediction concerns the level of groups and states that the extent of scrounging increases with increasing group size (Packer & Ruttan 1988; Vickery et al. 1991). The second prediction concerns the level of individuals and states that members of predatory foraging groups specialise in foraging tactic (see before). I simultaneously test both predictions in a foraging experiment, in which I manipulate group sizes and track the foraging behaviour of all group members over time. Thus, I merge group level and individual level analyses to account for the possibility that the group-level effects of group size (e.g. increased scrounging) may reflect shifts in the frequency of specialised feeding types (e.g. more scroungers). This eventuality has not been considered in earlier studies on group size effects.

Frequency dependence of scrounging

If individuals specialise in producing or scrounging, the spread of the scrounger type, which especially in predators should initially reap higher payoffs (Packer & Ruttan 1988; Carbone et al. 2007), may be limited by frequency-dependent selection: individuals that tend to apply the scrounger tactic achieve negative fitness payoffs at high scrounger frequencies (Giraldeau & Beauchamp 1999). This requires tactic consistency irrespective of group composition: scroungers must continue to refrain from producing even when being (mostly) among other scroungers, such that they suffer minimal food intake. To answer whether group foraging could be maintained via frequency-dependent selection, I examine whether foraging tactic use is consistent across group composition in **Chapter 5**.

Furthermore, if prey sharing is an intentionally cooperative behaviour and not the result of lost competition, the payoffs to producers should be positively frequency-dependent (Giraldeau & Beauchamp 1999). **In Chapter 5**, I test the hypothesis that producers have a higher cooperative tendency (instead of a lower competitive ability) compared to scroungers. Finally, I develop a verbal model that delineates the per-capita foraging payoffs to cooperative producers and defective scroungers dependent on the frequency of scroungers within the foraging group. The model allows for predictions with regard to the stable maintenance of profitable group foraging, and may be relevant to social predators in general.

Phenotypic determinants of foraging tactics

Throughout the thesis, I elaborate on the possible phenotypic determinants of foraging tactic specialisation. In **Chapter 4**, I ask whether an individual's hunting abilities explain its tactic specialisation. In **Chapter 5,** I apply a social network approach to determine whether the tendency to produce or scrounge is dependent of an individual's sex.

NOTE

The use of American or British English varies between the data chapters as it conforms to the respective requirements of the journals where the chapters have been published, or to which they have been submitted as manuscripts.

REFERENCES

Alexander RD (1974). The evolution of social behavior. Annual Review of Ecology and Systematics 5: 325-383.

Avilés L (1986). Sex-ratio bias and possible group selection in the social spider *Anelosimus eximius*. The American Naturalist 128: 1-12.

Avilés L (1997). Causes and consequences of cooperation and permanent-sociality in spiders. In: Choe JC, Crespi BJ (eds) *The evolution of social behavior in insects and arachnids*. Cambridge University Press: Cambridge, pp. 476-498.

Avilés L (2002). Solving the freeloaders paradox: genetic associations and frequency-dependent selection in the evolution of cooperation among nonrelatives. PNAS 99: 14268-14273.

Avilés L, Bukowski TC (2006). Group living and inbreeding depression in a subsocial spider. Proceedings of the Royal Society of London B 273: 157-163.

Avilés L, Guevara J (2017). Sociality in spiders. In: Rubenstein DR, Abbott P (eds) *Comparative social evolution*. Cambridge University Press: Cambridge, pp. 188-223.

Barnard CJ, Sibly RM (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29: 543-550.

Barta Z, Giraldeau L-A (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. Behavioral Ecology and Sociobiology 42: 217-223.

Benjamin SP, Dimitrov D, Gillespie RG, Hormiga G (2008). Family ties: molecular phylogeny of crab spiders (Araneae: Thomisidae). Cladistics 24: 708-722.

Bergmüller R, Taborsky M (2010). Animal personality due to social niche specialisation. Trends in Ecology & Evolution 25: 504-511.

Beauchamp G, Giraldeau L-A (1996). Group foraging revisited: Information sharing or producer-scrounger game? The American Naturalist 148: 738-743.

Beauchamp G (2006). Phenotypic correlates of scrounging behavior in zebra finches: role of foraging efficiency and dominance. Ethology 112: 873-878.

Bilde T, Lubin Y, Smith D, Schneider JM, Maklakov AA (2005). The transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. Evolution 59: 160-174.

Bilde T, Lubin Y (2011). Group living in spiders: cooperative breeding and coloniality. In: Herberstein ME (ed) *Spider behaviour: flexibility and versatility*. Cambridge University Press: Cambridge, pp. 275-306.

Carbone C, Teacher A, Rowcliffe JM (2007). The costs of carnivory. PLoS biology 5: e22.

Clark CW, Mangel M (1984). Foraging and flocking strategies: information in an uncertain environment. The American Naturalist 123: 626-641.

Clark CW, Mangel M (1986). The evolutionary advantages of group foraging. Theoretical Population Biology 30:45-75.

Clutton-Brock T (2009). Cooperation between non-kin in animal societies. Nature 462: 51-57.

Coolen I, Giraldeau LA, Lavoie M (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Animal Behaviour 61: 895-903.

Coolen I (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in Nutmeg Mannikins (*Lonchura punctulata*). Behavioral Ecology and Sociobiology 52: 232-238.

Creel S, Creel NM (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour 50: 1325-1339.

David M, Giraldeau L-A (2011). Zebra finches in poor condition produce more and consume more food in a producer–scrounger game. Behavioral Ecology 23: 174-180.

Doebeli M, Hauert C (2005). Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. Ecology Letters 8: 748-766.

Elgar MA (1989). Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. Biological Reviews 64: 13-33.

Evans TA, Main, BY (1993). Attraction between social crab spiders: silk pheromones in *Diaea socialis*. Behavioral Ecology 4: 99-105.

Evans TA (1995). Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. Records of the Western Australian Museum 52: 151–158.

Evans TA (1997). Distribution of social crab spiders in eucalypt forests. Australian Ecology 22: 107-111.

Evans TA (1998). Factors influencing the evolution of social behaviour in Australian crab spiders (Araneae: Thomisidae). Biological Journal of the Linnean Society 63: 205-219.

Evans TA (2000). Male work and sex ratio in social crab spiders. Insectes Sociaux 47: 285-288.

Evans TA, Goodisman MA (2002). Nestmate relatedness and population genetic structure of the Australian social crab spider *Diaea ergandros* (Araneae: Thomisidae). Molecular Ecology 11: 2307-2316.

Foster W, Treherne J (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293: 466-467.

Frank SA (1987). Demography and sex ratio in social spiders. Evolution 41: 1267-1281.

Galef BG, Giraldeau L-A (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Animal Behaviour 61: 3-15.

Giraldeau L, Beauchamp G (1999). Food exploitation: searching for the optimal joining policy. Trends in Ecology & Evolution 14: 102-106.

Giraldeau L-A, Caraco T (2000). *Social foraging theory*. Princeton University Press: Princeton.

Giraldeau L- A, Dubois F (2008). Social foraging and the study of exploitative behavior. Advances in the Study of Behavior 38: 59-104.

Grand TC, Dill LM (1999). The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? Animal Behaviour 58: 443-451.

Greene E (1987). Individuals in an osprey colony discriminate between high and low quality information. Nature 329: 239-241.

Imhof LA, Fudenberg D, Nowak MA (2005). Evolutionary cycles of cooperation and defection. PNAS 102: 10797-10800.

Inman A.J, Krebs J (1987). Predation and group living. Trends in Ecology & Evolution 2: 31-32.

Janson CH (1988). Food competition in brown Capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. Behaviour 105: 53-76.

Koenig WD, Dickinson JL (2004). *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press: Cambridge.

Krause J, Ruxton GD (2002). *Living in groups*. Oxford University Press: Oxford.

Kruuk H (1972). *The spotted hyena: a study of predation and social behavior*. University of Chicago Press: Chicago.

Kullmann, E.J. (1972). Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). The American Zoologist 12: 419-426.

Lamprecht J (1978). The relationship between food competition and foraging group size in some larger carnivores. Ethology 46: 337-343.

Lima SL (1995). Back to the basics of anti-predatory vigilance: the group-size effect. Animal Behaviour 49: 11-20.

Lubin Y (1974). Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zoological Journal of the Linnean Society 54: 321-339.

Lubin Y, Bilde T (2007). The evolution of sociality in spiders. Advances in the Study of Behavior 37: 83-145.

MacNulty DR, Tallian A, Stahler DR, Smith DW (2014). Influence of group size on the success of wolves hunting bison. Plos One 9: e112884.

Main BY (1988). The biology of a social thomisid spider. In: Austin AD, Heather NW (eds) *Australian Arachnology* Australian Entomological Society: Brisbane, pp 55–73.

Marshall HH, Carter AJ, Rowcliffe JM, Cowlishaw G (2012). Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. Animal Behaviour 84: 1295-1305.

Morand-Ferron J, Wu G-M, Giraldeau L-A (2011). Persistent individual differences in tactic use in a producer-scrounger game are group dependent. Animal Behaviour 82: 811-816.

Packer C, Ruttan L (1988). The evolution of cooperative hunting. The American Naturalist 132: 159-198.

Pasquet A, Krafft B (1992). Cooperation and prey capture efficiency in a social spider, *Anelosimus eximius* (Araneae, Theridiidae). Ethology 90: 121-133

Pitcher T, Magurran A, Winfield I (1982). Fish in larger shoals find food faster. Behavioral Ecology and Sociobiology 10: 149-151.

Pyke GH, Pulliam, HR, Charnov EL (1977). Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology 52: 137-154.

Ranta E, Rita H, Lindstrom K (1993). Competition versus cooperation: success of individuals foraging alone and in groups. The American Naturalist 142: 42-58.

Ranta E, Peuhkuri N, Laurila A, Rita H, Metcalfe NB (1996). Producers, scroungers and foraging group structure. Animal Behaviour 51: 171-175.

Ratnieks FL, Shackleton K (2015). Does the waggle dance help honey bees to forage at greater distances than expected for their body size? Frontiers in Ecology and Evolution 3: 31.

Rowell DM, Main BY (1992). Sex ratio in the social spider *Diaea socialis* (Araneae: Thomisidae). Journal of Arachnology 20: 200-206.

Rubenstein DR (1978). On predation, competition, and the advantages of group living. In: Bateson PPG, Klopfer PH (eds) *Social Behavior*. *Perspectives in Ethology*, vol 3. Springer: Boston, pp 205-231.

Rubenstein DR, Abbot P (2017). *Comparative social evolution*. Cambridge University Press: Cambridge.

Ruch J, Heinrich L, Bilde T, Schneider JM (2009). The evolution of social inbreeding mating systems in spiders: limited male mating dispersal and lack of pre-copulatory inbreeding avoidance in a subsocial predecessor. Biological Journal of the Linnean Society 98: 851-859.

Ruch J, Riehl T, Michalik P (2014a). Re-description of *Xysticus bimaculatus* L. Koch, 1867 (Araneae, Thomisidae) and characterization of its subsocial lifestyle. ZooKeys 427: 1–19.

Ruch J, Herberstein ME, Schneider JM (2014b). Offspring dynamics affect food provisioning, growth and mortality in a brood-caring spider. Proceedings of the Royal Society of London B 281: 20132180.

Ruch J, Herberstein, ME, Schneider JM (2014c). Families hunt more successfully: effect of group composition on hunting and communal feeding. Animal Behaviour 91: 171–178.

Ruch J, Dumke M, Schneider JM (2015a). Social network structure in group-feeding spiders. Behavioral Ecology and Sociobiology 69: 1429-1436.

Ruch J, Riehl T, May-Collado LJ, Agnarsson I (2015b). Multiple origins of subsociality in crab spiders (Thomisidae). Molecular Phylogenetics and Evolution 82: 330-340.

Salomon M, Lubin Y (2007). Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). Behavioral Ecology and Sociobiology 61: 1743-1750.

Scheel D, Packer C (1991). Group hunting behaviour of lions: a search for cooperation. Animal Behaviour 41: 697-709.

Shen S-F, Akçay E, Rubenstein DR (2013). Group size and social conflict in complex societies. The American Naturalist 183: 301-310.

Silk JB (2007). Social components of fitness in primate groups. Science 317: 1347-1351.

Szymkowiak P (2014). Revision of Australian species of the genus *Diaea* (Araneae: Thomisidae) with redefinition of their taxonomic status. Annales Zoologici 64: 333-477.

Tallamy DW (1984). Insect parental care. BioScience 34: 20-24.

Théry M, Casas J (2002) Visual systems: predator and prey views of spider camouflage. Nature 415: 133-133.

Thiel M (2007). *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford University Press: Oxford.

Turner GF, Pitcher TJ (1986). Attack abatement: a model for group protection by combined avoidance and dilution. The American Naturalist 128: 228-240.

Uetz GW (1989). The “ricochet effect” and prey capture in colonial spiders. Oecologia 81: 154-159.

Valone TJ (1989). Group foraging, public information, and patch estimation. Oikos 56: 357-363.

Ventura L, Smith DR, Lubin Y (2017). Crowding leads to fitness benefits and reduced dispersal in a colonial spider. Behavioral Ecology 28: 1384-1392.

Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA (1991). Producers, scroungers, and group foraging. The American Naturalist 137: 847-863.

Ward P, Zahavi A (1973). The importance of certain assemblages of birds as “information-centres” for food-finding. Ibis 115: 517-534.

Wenner AM, Wells PH, Johnson DL (1969). Honey bee recruitment to food sources: olfaction or language? Science 164: 84-86.

Whitehouse ME & Lubin Y (2005). The functions of societies and the evolution of group living: spider societies as a test case. Biological Reviews 80: 347-361.

Wignall AE, Heiling AM, Cheng K, Herberstein ME (2006). Flower symmetry preferences in honeybees and their crab spider predators. Ethology 112: 510-518.

Wilson EO (1971). *The insect societies*. Harvard University Press: Harvard.

Wrona FJ, Dixon RJ (1991). Group size and predation risk: a field analysis of encounter and dilution effects. The American Naturalist 137: 186-201.

Yip EC, Powers KS, Aviles L (2008). Cooperative capture of large prey solves scaling challenge faced by spider societies. PNAS 105: 11818-11822.

Yip EC, Rayor LS (2014). Maternal care and subsocial behaviour in spiders. Biological Reviews 89: 427-449.

CHAPTER 2

Extended maternal care and offspring interactions in the subsocial Australian crab spider *Xysticus bimaculatus*

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Published in *Australian Journal of Zoology* 64:344-352, doi: 10.1071/ZO16070
February 2017

Abstract

Extended maternal care is considered a prerequisite for the evolution of permanent family grouping and eusociality in invertebrates. In spiders, the essential evolutionary transitions to permanent sociality along this ‘subsocial route’ include the extension of care beyond hatching, the persistence of offspring groups to maturation and the elimination of premating dispersal. Subsocial Australian crab spiders (Thomisidae) present a suitable system to identify the selective agents prolonging group cohesion. Particularly, the recent discovery of independently evolved subsociality in the thomisid *Xysticus bimaculatus* provides new potential for comparative studies to expand the limited understanding of group cohesion beyond the offspring’s potential independence and despite socially exploitative behaviour. Providing fundamental knowledge, the present study investigated maternal care and offspring interactions in *Xysticus bimaculatus* for the first time. Nest dissections revealed that mothers produce exceptionally small clutches, potentially reflecting a limit in the number of juveniles they can successfully care for. A laboratory experiment demonstrated crucial benefits for offspring in receiving maternal care beyond nutritional independence, mediated by extensive maternal food provisioning. However, prey-sharing also occurred between juveniles irrespective of maternal presence, which marks this species’ predisposition for exploitative feeding behaviour. I therefore suggest *Xysticus bimaculatus* as a suitable model for investigating the regulation of communal feeding in group-living spiders.

Introduction

Extended maternal care, defined as any post-hatching maternal behaviour that enhances the fitness of the mother's offspring (Clutton-Brock 1991; Klug et al. 2012), appears to be a pre-requisite for the evolution of stable family groups and eusocial societies in invertebrates (Tallamy 1984; Lubin & Bilde 2007; Thiel 2007). In most invertebrate species, however, maternal care is limited to egg attendance (Royle et al. 2012; Trumbo 2012). Prolonged forms of maternal care, such as food provisioning or defence of young against predators, have evolved exceptionally often in the Hymenoptera (Wilson 1971), but also in various other arthropods, including crustaceans (Thiel 1999), beetles (Brandmayr 1992) and spiders (Yip & Rayor 2014).

In spiders, the evolutionary pathway from extended maternal care to permanent sociality has been intensively studied. Generally, there is evidence for at least 18 independent origins of permanent cooperative sociality in spiders, a style of sociality that is characterised by stable family-group living in communal nests, foraging cooperation and inbreeding (Agnarsson et al. 2006; Bilde & Lubin 2011; Walter & Bilde 2015). Specifically, it is widely accepted that this permanent cooperative sociality evolved through the 'subsocial route', where family-group living arose from multiple evolutionary transitions in which the gregarious phase of offspring was prolonged and cooperation among siblings became more pronounced (Avilés 1997; Lubin & Bilde 2007). These transitions particularly include the evolution of extended maternal care resulting in the initial formation of motheroffspring groups, as well as the subsequent cohesion of sibling groups that cooperate in certain tasks beyond the mother's death, and ultimately the elimination of premating dispersal in favour of inbred social systems (Whitehouse & Lubin 2005; Avilés & Bukowski 2006; Schneider & Bilde 2008; Walter and Bilde 2015).

Yet, when examining each of these transitional steps, researchers have stressed limitations in our understanding of the benefits in maintaining group cohesion. In this context, Yip & Rayor (2014) point to a lack of insight into the benefits of the extension of maternal care beyond the period when the offspring are nutritionally dependent on their mother. Further, there is a demand for investigating the regulation of exploitative behaviour in resource-sharing offspring groups, as costly 'food-scrounging' should counteract group cohesion (Yip & Rayor 2014; Dumke et al. 2016). Finally, the shift to inbreeding might, in the long run, result in elevated extinction due to inbreeding depression, and thus becomes an evolutionary dead end in the transition to permanent sociality (Agnarsson et al. 2006).

Group-living Australian crab spiders (Thomisidae) present a promising study system to comparatively investigate how group cohesion is maintained despite the costs of maternal care extension, exploitative behaviour and inbreeding. Within the *Australomisidia* genus, three species - *A. ergandros*, *A. inornata* and *A. socialis* - live in groups and have similar ecology and life-history strategies. In particular, they all practise extended maternal care, and family groups of potentially independent offspring persist for several months (Main 1988; Evans & Main 1993; Evans 1998a). For *A. ergandros* and *A. socialis*, it has been documented that prey is shared among juveniles (spiderlings) beyond maternal presence (i.e. beyond dispersal or death of the mother; Main 1988; Ruch et al. 2014a). The occurrence of potentially exploitative feeding behaviour in offspring groups has been demonstrated in the well-studied species *A. ergandros* (Dumke et al. 2016). Finally, a shift to inbreeding is evident in *A. socialis*, where mating takes place among siblings within the natal nest (Main 1988).

Moreover, Ruch et al. (2014c) have recently discovered subsociality outside *Australomisidia* in the thomisid *Xysticus bimaculatus*. This discovery opens new potential for comparative studies to identify common selective agents that promote group cohesion in crab spiders, because group living in *X. bimaculatus* has likely evolved independently from the *Australomisidia* species (Ruch et al. 2015). To date, however, the fundamental knowledge on the subsocial lifestyle of *X. bimaculatus* is extremely limited.

This study is the first to document maternal care and offspring interactions in *X. bimaculatus*. Descriptive and experimental methods were combined to investigate the mode and extent of maternal care and its effect on offspring fitness. Another objective was to investigate the occurrence and nature of interactions among siblings during the period of maternal care. For these purposes, I examined the nest characteristics of *X bimaculatus* in early-instar groups, as early instars are most likely to benefit from maternal care (Ruch et al. 2014c). With a special focus on the effect of maternal provisioning, I experimentally compared predation success and communal feeding behaviour, as well as weight change and mortality of spiderlings, between early-instar groups with and without a mother.

Methods

Study species

The crab spider *Xysticus bimaculatus* L. Koch, 1867 (Thomisidae) builds and inhabits nests on *Acacia* and *Alphitonia* trees in sclerophyll woodlands throughout Queensland, Australia. The nests are constructed from tree leaves, which are firmly attached with silk threads and form a labyrinthine structure inside. Ruch et al. (2014c) characterised *X. bimaculatus* as subsocial because they discovered nests inhabited by several spiderlings and found evidence for dispersal only just before maturation. The results of Ruch et al. (2014c) further suggest that *X. bimaculatus* exhibits extended maternal care, as adult females were present in most nests, which then contained higher numbers of spiderlings.

X. bimaculatus has an annual life cycle in which the late Australian summer and early autumn (March-May) seem to constitute the critical period of maternal care for early-instar offspring. In this respect, Ruch et al. (2014c) found that the likelihood of maternal presence declines with increasing spiderling size and time of year (56.57% in April vs. 26.79% in November). In further support, subadult and adult males were exclusively found late in the year. *X. bimaculatus* is remarkably similar in its ecology and subsocial lifestyle to *Australomisidia ergandros*, another leafnest building thomisid with extended maternal care (Evans 1995). *A. ergandros* juveniles feed communally even in the absence of an adult female (Evans 1998b; Unglaub et al. 2013) - an aspect that has not yet been addressed for *X. bimaculatus*.

Nest characteristics

To describe the nest characteristics of *X. bimaculatus* for early-instar groups, 82 nests were collected in late March of 2015 ($N_{\text{nests}} = 33$) and 2016 ($N_{\text{nests}} = 49$) at Toohey State Forest (27°32’44.5’’S, 153°2’47.3’’E) and at Mount Coo-Tha Forest (27°27’41.4’’S, 152°57’38.2’’E) in Brisbane, QL. The nests were transferred to the laboratory at Macquarie University in Sydney, where they were dissected to determine the number of leaves composing each nest, the number as well as the size class of the spiderlings within and the presence of an adult female (following Ruch et al. 2014c). Nests containing subadult spiderlings were excluded from data descriptions, as they logically do not qualify as early-instar groups.

Maternal care

In a comparative feeding experiment conducted in April 2015, I investigated the effect of maternal presence on predation success and communal feeding behaviour of early-instar offspring. In addition, I examined how maternal presence affected weight change and mortality of spiderlings. Nests were selected for this purpose if they met the following three criteria: (1) the nest contained a living mother, (2) the nest contained an even number of at least eight spiderlings and (3) the spiderlings within the nest had, according to visual judgement, similar body sizes. Each of the selected nest groups was then split up into two equally sized groups of siblings, which were transferred into separate Petri dishes (50 mm diameter) with *Acacia* leaves for shelter. One of these two sibling groups was randomly chosen to also contain the mother, thus being allocated to the 'mother present' treatment, while the other group was assigned to the 'mother absent' treatment ($N_{\text{groups}} = 10$ per treatment). This matched-pairs design reduced variation between treatments in else uncontrolled factors (e.g. pre-experimental experience; Heath 2002). Overall, the number of spiderlings per sibling group ranged between four and eight.

After a three-day acclimation phase, all experimental groups were tested in eight consecutive feeding trials. The trials took place every fourth day, which ensured that groups were sufficiently hungry to attack. Thus, the total duration of the experiment amounted to 28 days. In each trial, the groups were presented with one living, large fruit fly (*Drosophila hydeii*). I recorded whether the fly was attacked (yes or no), the time in minutes until the attack and, for the 'mother present' treatment, the identity of the attacker (mother or spiderling). If the fly was not attacked within 60 minutes, it was removed. Unsuccessful attacks, defined as 'attacking the prey without subduing it', did not occur, possibly due to the small size of the fly. Groups that had attacked were continuously observed for an additional 60 minutes after the attack to record the number of spiderlings that joined the attackers in feeding on the prey - a behaviour termed scrounging. On the basis of these data, a set of parameters describing predation success and communal feeding behaviour was calculated (Table 1).

To investigate differences between treatments in the weight change of spiderlings, four randomly chosen spiderlings of each group were weighed jointly three days before the start as well as three days after the end of the feeding experiment with an electronic balance (Mettler Toledo NewClassic MS, accuracy: 0.0001 g). Spiderling weight had to be an average since most spiderlings were too small to be weighed individually with that balance. For each group, the relative *spiderling weight change*, a measure factoring in the weight of spiderlings before the experiment, was calculated using the following formula (Crawley 2007):

$$\textit{spiderling weight change} = \log\left(\frac{\text{final weight}}{\text{initial weight}}\right)$$

Similarly, I determined *maternal weight change* to gain insight into the sacrificial extent of maternal food provisioning. I used the same methodology as above, but weighed each mother separately.

To assess *spiderling mortality*, experimental groups were checked for dead spiderlings before every trial and again when measuring final weight. Dead bodies were carefully removed to reduce the risk of weight gain via cannibalistic scavenging. However, spiderlings likely died for reasons other than cannibalism (e.g. low body condition or infection) as dead bodies did not show severe damage, which would be a typical indicator (personal observation). Mortality was calculated for each group as the final ratio of dead spiderlings to living spiderlings by the end of the experiment. The change in group sizes over the course of the experiment, resulting from the death of spider-

Table 1 | Parameters describing predation success and communal feeding behaviour of *Xysticus bimaculatus* in the laboratory feeding experiment to investigate the effect of mother presence

Parameter	Definition
Number of attacks	Sum of attacks over the eight trials (per group)
Number of spiderling attacks	Sum of attacks being performed by one or more spiderlings over the eight trials (per group)
Attack latency	Time in minutes until an attack (per group and trial)
Attack latency of spiderlings	Time in minutes until an attack being performed by one or more spiderlings (per group and trial in which spiderlings attacked)
Scrounger percentage	Maximal number of simultaneously scrounging spiderlings in relation to the theoretically possible maximum number (per group and attack)
Scrounger percentage for spiderling attacks	Maximal number of simultaneously scrounging spiderlings in relation to the theoretically possible max. number for attacks being performed by spiderlings (per group and attack)

lings, was taken into account in the calculation of the feeding parameters *scrounger percentage* and *scrounger percentage for spiderling attacks* (see Table 1).

Statistical analyses

Descriptive statistics are given as mean ± SE. All data analyses were performed in R 3.2.2 (R Core Team 2015). Pairs of treatment groups (‘mother present’ group and the related ‘mother absent’ group) were excluded from statistical analyses of the maternal care experiment if the mother died before the end of the trials ($N_{\text{pairs}} = 3$). Thus, final sample size comprised seven groups per treatment. The data on *spiderling weight change* were tested for normal distribution as well as for equal variance. As the data fulfilled these criteria, I applied a paired *t*-test to analyse differences between treatments. Count and proportional data summarizing the behaviour of groups over the eight trials (*number of attacks* (Table 1) and *spiderling mortality*) were analysed using Poisson and binomial GLMMs (generalized linear mixed models). Treatment and startweight were included as explanatory variables, as the matched-pairs design did not fully control for this trait. Group origin (nest ID) was included as a random factor to account for relatedness between paired treatment groups. To assess the statistical significance of treatment effects, I compared the full models with nested models (without each explanatory variable) using ANOVAs, and dropped non-significant terms until the minimal adequate model with the lowest AIC was determined.

Responses that were recorded for each trial rather than over the entire experiment (*attack latency* and *scrounger percentage*; Table 1) were analysed using gamma and binomial GEEs (generalised estimation equations). This modelling approach allows controlling for repeated measurements from the same subjects over time (Zuur et al. 2009). Consequently, I specified group ID as the grouping variable and included the temporal correlation structure AR-1 into the GEE models. To assess the statistical significance of treatment effects, maximal models with treatment, startweight and nest ID as explanatory variables were simplified by stepwise elimination of the least significant term and comparing the nested models with Wald statistics until the minimal adequate model was found.

Results

Nest characteristics

Xysticus bimaculatus spiderlings were found in 64 of the 82 collected nests (78.05% early-instar nests). Four further nests contained an egg sac and an adult female. The remaining 14 nests were either no longer inhabited ($N_{\text{nests}} = 7$) or contained only subadult spiders ($N_{\text{nests}} = 7$). The early-instar nests were constructed from 5.98 ± 0.28 leaves (range = 2 - 14 leaves, $N_{\text{nests}} = 61$), with a ratio of 3.67 ± 0.26 older brown leaves to 2.31 ± 0.25 newer green leaves. In contrast, the seven nests that contained subadult spiders comprised mostly brown leaves, with a brown-to-green leaf ratio of approximately seven to one. Thus, they might have been constructed in the previous year, inhabited by individuals from the mother’s generation that did not reach maturation. Group size in the early-instar nests ranged from two to a maximum of 33, resulting in a mean of 11.27 ± 0.72 spiderlings per nest ($N_{\text{nests}} = 64$).

All spiderlings within a nest had a relatively similar body size, but body size differed slightly between nest groups. Three size classes, defined by body length, were found (size class 1 with <1.5 mm: $N_{\text{nests}} = 19$, size class 2 with 1.5 - 2.5 mm: $N_{\text{nests}} = 25$, size class 3, with 2.5 - 3.5 mm: $N_{\text{nests}} = 19$), with the exception of one nest group assigned to size class 4 (3.5 - 4.5 mm). An adult female, presumably the mother, was present in most of these nests (85.94% of $N_{\text{nests}} = 64$).

I tested whether the likelihood of an adult female present differed for the three common size classes and detected no significant difference (Pearson: $\chi^2 = 2.03$, $P = 0.36$, $N_{\text{nests}} = 63$). However, there was a slight decrease in the percentage of nests containing a mother with increasing spiderling size class (size class 1 with 94.74%, size class 2 with 84.00%, size class 3 with 78.95%). There was no significant difference between size classes in the number of spiderlings per nest (Kruskal-Wallis: $\chi^2 = 0.68$, $P = 0.71$, $N_{\text{nests}} = 63$).

Maternal care

Predation success

I recorded 42 attacks in the 'mother present' treatment and 28 attacks in the 'mother absent' treatment. There was a significant difference between treatments in the *number of attacks* per group (Table 2), which was notably higher for groups with a mother present (Figure 1A). The comparison of attacks by spiderlings between the two treatments (excluding attacks by mothers) had the opposite pattern: the *number of spiderling attacks* per group was considerably lower in the 'mother present' treatment than in the 'mother absent' treatment (Table 2; Figure 1A). This indicates that the mothers' predation success accounted for the higher attack numbers in the 'mother present' treatment, where indeed 71.43% of the 42 observed attacks were performed by the adult females. Mothers always attacked alone and group attacks performed by multiple spiderlings were the exception ('mother present': 16.67% of $N_{\text{attacks}} = 12$; 'mother absent': 10.71% of $N_{\text{attacks}} = 28$). The distinction in predation success between treatments was not reflected in *attack latency*, which was statistically similar across groups (Table 2; Figure 1B). There was, however, a tendency for earlier attacks in groups with a mother present (Table 2). The mean attack latency was 22.17 ± 3.11 min ($N_{\text{attacks}} = 42$) for groups with a mother compared with 25.77 ± 4.80 min ($N_{\text{attacks}} = 28$) for groups without a mother.

Communal feeding behaviour

Communal feeding on prey captured by mothers or by one or two spiderlings was generally common, occurring in 72.86% of all 70 attacks. Treatment had a significant effect on the overall *scrounger percentage*, indicating that the number of simultaneously scrounging spiderlings per prey item was higher for groups with a mother present (Table 2; Figure 1C). The *scrounger percentage for spiderling attacks*, however, did not differ between treatments (Table 2; Figure 1C). These results suggest a higher tolerance by mothers in comparison to spiderlings towards scroungers. Nonetheless, mothers were also observed to feed alone in five of the 30 attacks by mothers (16.66%). This feeding-alone proportion was the same for attacks by spiderlings in groups with a mother present (16.66% of $N_{\text{attacks}} = 12$). Interestingly, spiderlings in groups without a mother were more likely to feed alone (57.14% of $N_{\text{attacks}} = 28$; Fisher's exact test: $P = 0.0354$). This result contradicts the finding that the *scrounger percentage for spiderling attacks* (calculation of which included events where

Table 2 | Model analyses of the effect of maternal presence on predation success and communal feeding behaviour as well as on spiderling fitness measures for the subsocial crab spider *Xysticus bimaculatus*

Parameter	Analysis	Test statistics	*P*-value
Number of attacks	GLMM (binomial)	$\chi^2 = 11.94$	**$P = 0.0005$**
Number of spiderling attacks	GLMM (poisson)	$\chi^2 = 6.83$	**$P = 0.0090$**
Attack latency	GEE (gamma family)	$\chi^2 = 3.70$	*$P = 0.0545$*
Attack latency of spiderlings	GEE (gamma family)	$\chi^2 = 1.84$	$P = 0.17$
Scrounger percentage	GEE (binomial family)	$\chi^2 = 11.40$	**$P = 0.0007$**
Scrounger percentage for spiderling attacks	GEE (binomial family)	$\chi^2 = 0.69$	$P = 0.41$
Spiderling weight change	paired *t*-test	$t = 2.56$	**$P = 0.0426$**
Spiderling mortality	GLMM (binomial)	$\chi^2 = 0.70$	$P = 0.40$

The significance of treatment differences in experimentally determined parameters (Table 1), the two treatments being offspring groups with their mother present and offspring groups with their mother absent, was assessed. Significant *P*-values are indicated in bold, trends in italic.

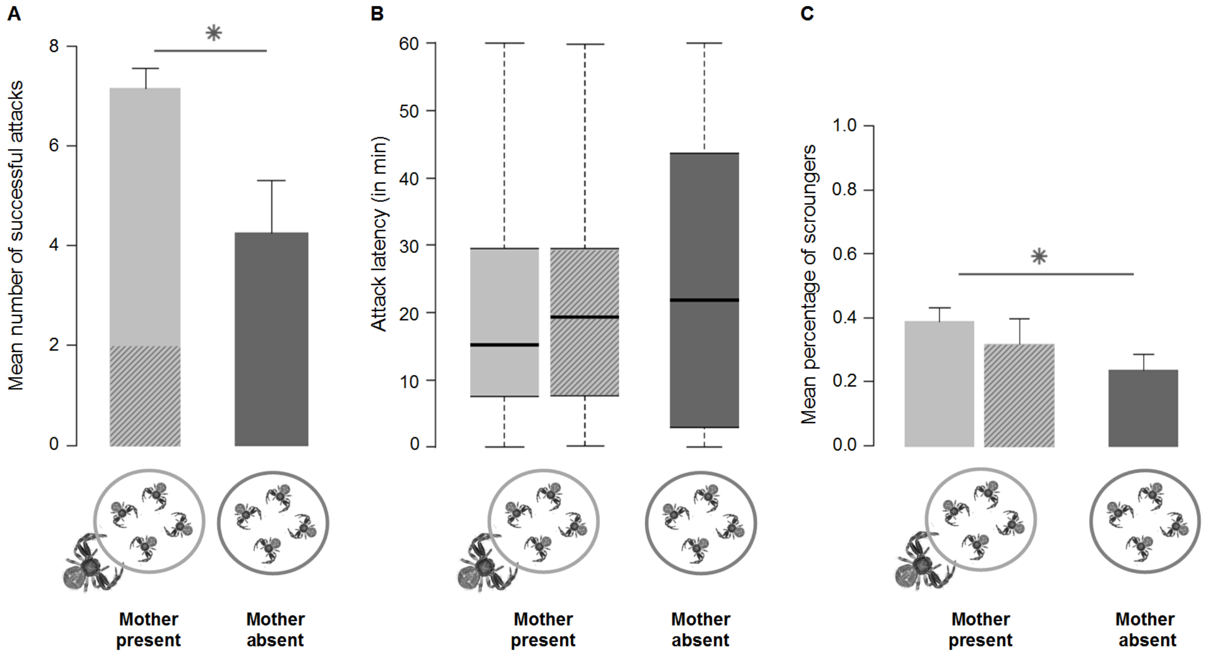

Figure 1 | A: Mean number of attacks per group depending on treatment. The hatched area within the 'mother present' bar represents the mean number of attacks performed by spiderlings within the total number of attacks. The asterisk marks a significant treatment difference. **B:** Attack latency displayed separately for all attacks in the 'mother present' treatment (light grey), attacks performed by spiderlings in this treatment (hatched light grey) and all attacks in the 'mother absent' treatment (dark grey), with no significant difference. **C:** Mean scrounger percentage of groups with a mother (light grey; $N_{\text{attacks}} = 42$) and of groups without a mother (dark grey; $N_{\text{attacks}} = 28$). The hatched bar represents the mean scrounger percentage for attacks performed by spiderlings in the 'mother present' treatment ($N_{\text{attacks}} = 12$). The asterisk marks a significant treatment difference.

spiderlings fed alone) did not differ between the treatments. A re-analysis excluding feeding-alone events revealed that, when spiderlings in the 'mother absent' treatment did share, they shared with significantly more siblings than those spiderlings that shared in the 'mother present' treatment (GEE: $\chi^2 = 9.68$, $P = 0.0019$).

Weight change and mortality

Spiderling mortality did not differ significantly between the treatments (Table 2), with ten dead spiderlings in the 'mother present' treatment and 13 dead spiderlings in the 'mother absent' treatment by the end of trials. The distribution of death events over time was similar among the pairs of treatment groups (graphical inspection), overall indicating that spiderlings in one treatment did not die earlier than spiderlings in the other. Although there was no difference between treatments in *spiderling mortality* over the duration of the experiment, there was a significant difference in *spiderling weight change* that could eventually lead to higher death rates in the 'mother absent' treatment (Table 2; Figure 2): while spiderlings in groups with a mother gained weight, spiderlings in groups without a mother lost weight (absolute *spiderling weight change*: 'mother present': 0.17 ± 0.05 mg; 'mother absent': –0.06 ± 0.04 mg).

The *maternal weight change* values showed that all mothers (exception one) lost weight over the course of the experiment, even though they had attacked the prey in most cases (Figure 1A). Specifically, maternal weight at the end of the trials was lowered by 6.45 ± 3.28% compared with the initial weight, which translated into an absolute *maternal weight change* of –0.72 ± 0.38 mg. These findings indicate that the mothers restricted their own food intake. I examined whether the tendency to lose weight was significant compared with the expectation that weight gain and weight loss were equally likely and found a marginally significant trend for maternal weight loss (one-sided sign test (paired): s=1, $P = 0.0625$, $N_{\text{mothers}} = 7$).

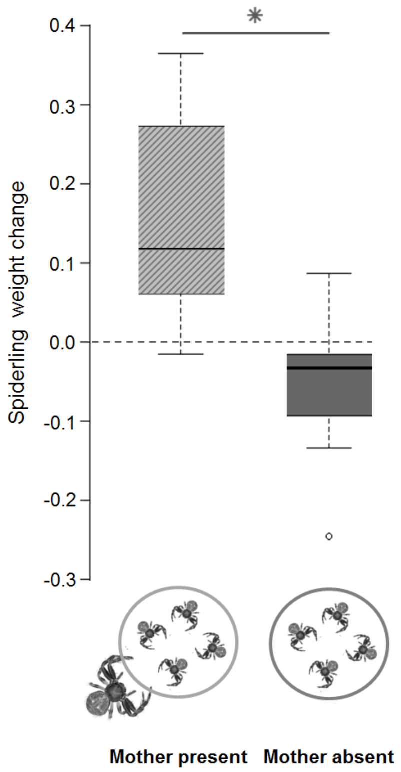

Figure 2 | Weight change of spiderlings depending on treatment, calculated as log(final weight/initial weight). The dashed zero line represents the gain-and-loss threshold; the asterisk marks a significant treatment difference.

Discussion

This study investigated nest characteristics as well as maternal food provisioning and prey-sharing among juveniles in early-instar groups of the Australian crab spider *Xysticus bimaculatus*. The subsocial lifestyle of *X. bimaculatus* was only recently discovered by Ruch et al. (2014c), and the present study is the first to document the mode and extent of maternal care in this species.

Spiderlings within early-instar nests were found to be of similar small size, and size class variation between the nests was low. Moreover, the likelihood of maternal presence did not decrease with increasing spiderling size. With regards to the temporal extent of maternal care in *X. bimaculatus*, these results indicate that mothers typically lay a single egg sac early in the year and, after egg hatching, stay with their offspring for several instars. Since the nests examined here were exclusively collected in late March, it cannot be excluded that *X. bimaculatus* mothers produce subsequent clutches later in year - as is the case in some other subsocial spider species (e.g. *Delena cancerides*: Rowell & Avilés 1995; *Menemerus bracteatus*: Rienks 2000). In support of this, Ruch et al. (2014c) found four *X. bimaculatus* nests each with two distinct broods as well as one adult female inside.

Furthermore, I documented a group-size mean of 11 spiderlings within a range of 2 - 33 spiderlings per nest. This result accords with the findings of Ruch et al. (2014c), who report a similar average within a range of 1 - 38 juveniles per nest. Such consistency suggests an upper offspring limit of ~35 spiderlings for *X. bimaculatus*. That limit is likely set by the adult female body size of this species (Marshall & Gittleman 1994; Simpson 1995), but could additionally be determined by the number of offspring a mother can successfully rear through the most demanding period (limit hypothesis: Burley 1980). In indirect support of the limit hypothesis, most other subsocial spiders - some smaller than *X. bimaculatus* - produce much higher numbers of offspring, with mean clutch sizes lying between 20 and 80 eggs (data from 35 species; Yip & Rayor 2014). Juvenile groups of the crab spider *Australomisidia ergandros*, which is similar in body size and subsocial lifestyle to *X. bimaculatus* (Ruch et al. 2014c), comprise, on average, 30 spiderlings (Dumke et al. 2016).

In light of the limit hypothesis, this variation in clutch size between species may correlate with different strategies of maternal food provisioning (Simpson 1995). In subsocial spiders, mothers provision their offspring through prey-sharing (e.g. Rowell & Avilés 1995), regurgitation (e.g. Salomon et al. 2005) and/or trophic eggs (e.g. Kim & Roland 2000). In extremes, maternal food provisioning also occurs in the form of obligate or facultative matriphagy, where the mother herself is eaten by her offspring (e.g. Kim & Horel 1998). The different modes of maternal provisioning could yield different efficiency in terms of the successfully provisioned number of offspring, thus selecting for (or being selected by) clutch size (after Burley 1980). *A. ergandros* spiderlings have been shown to be matriphagous (Evans et al. 1995), while no case of matriphagy was observed for *X. bimaculatus* in the experimental groups of this study or in any other nests kept in the laboratory (personal observation). It would therefore be interesting to investigate correlations between clutch size and maternal care strategies in a broader sample of subsocial spider species.

All different forms of maternal care have one substantial thing in common: for them to evolve, the entailed costs - such as reduced maternal condition and survival - must be outweighed by the fitness benefits to the caring mother (Clutton-Brock 1991; Royle et al. 2012). Maternal care is beneficial if it increases offspring survival, growth and/or quality, ultimately leading to enhanced reproductive success of offspring (Royle et al. 2012). In this regard, numerous experimental studies have shown a positive effect of maternal presence on offspring survival and growth for group-living spiders (Ruttan 1991; Evans 1998a; Kim & Roland 2000). Similarly, this study experimentally demonstrates that maternal presence enhances spiderling fitness in *X. bimaculatus*. Spiderlings in groups with a mother present gained weight, while orphaned spiderlings lost weight after a one-month period of regular availability of prey. Higher mortality rates in orphaned groups, as documented for other subsocial species (e.g. *Coelotes terrestris*: Gundermann et al. 1991; *Amaurobius ferox*: Kim & Roland 2000), were not found in the present study - but this disparity must be put in context given that the above-mentioned authors investigated the effect of maternal care in the form of regurgitation and matriphagy under prey-deprived conditions. In such cases of obligate dependence of offspring on maternal food provisioning, where the young cannot capture prey themselves and consequently starve without their mother (as demonstrated by Brach 1977), the beneficial effect of maternal presence on offspring fitness is rather obvious. However, the most common, and supposedly ancestral, form of maternal provisioning is prey-sharing - and there the benefit of maternal provisioning is not as transparent when the juveniles can also capture and share prey on their own (Yip & Rayor 2014).

My results demonstrate that *X. bimaculatus* exhibits such a two-fold provisioning system: in the maternal-care experiment, prey-sharing occurred between mothers and offspring, but also between offspring alone, irrespective of maternal presence. Therefore, spiderlings did survive in the absence of a caring mother, a fact that reflects their potential nutritional independence (Clutton-Brock 1991). Nonetheless, there was a benefit of maternal presence in terms of offspring growth, mediated by greater predation success and higher feeding rates for spiderlings as a result of the mothers' extensive predation and prey-sharing activity. The consequent lower predation activity by spiderlings in groups with a mother present mirrored a lesser energy expenditure for offspring receiving maternal care. These findings contribute to explaining the persistence of care beyond the offspring's nutritional independence - a phenomenon that has not yet received much attention (Clutton-Brock 1991; Royle et al. 2012). One studied example is the burying beetle *Nicrophorus vespilloides*, in which self-feeding and begging are coexisting foraging strategies of larvae that would also survive in the absence of care (Smiseth et al. 2003). In spiders, concurrence of maternal provisioning and offspring prey capture has, for example, been described in subsocial *Anelosimus* (Marques et al. 1998) and was observed in *A. ergandros* (Evans 1998b).

As a further positive influence on offspring growth and survival, maternal presence might facilitate cooperation among juveniles (Trumbo 2012). With regard to the food-provisioning system in *X. bimaculatus*, one could therefore propose that the mother's prey-supplying activity reduces food competition and ensures developmental homogeneity, thus indirectly promoting prey-sharing between spiderlings (Kim et al. 2005). The finding that spiderlings with their mother present shared their prey more frequently than orphaned spiderlings supports this hypothesis. On the other hand, orphaned spiderlings were found to feed in larger numbers than spiderlings with their mother present in the cases where prey-sharing between spiderlings did occur. This finding, however, is not necessarily contradictive. Orphaned spiderlings tended to exhibit extremes - either feeding alone or feeding communally with many - and the latter might be the result of higher numbers of hungry spiderlings in orphaned groups, combined with an inability of the specific attackers to defend the resource (Giraldeau & Caraco 2000). Thus, the extensive communal feeding in orphaned offspring groups may be interpreted as an indicator of competition among spiderlings over food resources, arising in the absence of maternal care.

When mothers had performed the attack, the number of scrounging juveniles per fly was overall notably higher than in the case of spiderling attacks. This result suggests that mothers, after having attacked, signal the presence of food to 'uninformed' offspring, possibly through vibratory or chemical cues (Yip & Rayor 2014). Maternal signaling of food presence does occur in other subsocial spiders: Nørgaard (1956) described a 'sweeping movement' by female *Theridion saxatile* causing young to approach captured prey. Prey recognition by *Anelosimus crassipes* spiderlings correlates with a certain walking behaviour of the mother (Ito & Shinkai 1993) and in the funnel web *Ischnothele caudate* the mother appears to attract her young to the prey by plucking and beating the web (Jantschke & Nentwig 2001). It remains to be studied whether maternal signaling of food presence to offspring occurs in subsocial spiders of the crab spider family.

In possible reflection of a cost of care, *X. bimaculatus* mothers tended to lose weight over the experimental period in which they provisioned their weight-gaining young. I therefore propose that caring mothers in this species dedicate the largest share of their prey to their offspring. Sacrificial food provisioning also occurs in *A. ergandros*: in a nine-week feeding experiment, Ruch et al. (2014b) observed *A. ergandros* mothers to commonly share their prey with offspring. While the provisioned young gained weight, the mothers lost weight (~5 - 10% of their initial weight). Yet in both species, *X. bimaculatus* and *A. ergandros*, the amount of maternal weight loss during care seems rather low, supporting the hypothesis that mothers maintain the body condition necessary for efficient and persistent prey provisioning.

Finally, I demonstrated the occurrence of prey-sharing between spiderlings even in the absence of the mother - and thus the predisposition of *X. bimaculatus* for the emergence of exploitative foraging behaviour: as only one or rarely two juveniles captured prey on which multiple juveniles fed, *X. bimaculatus* spiderlings may be prone to developing a 'scrounger' feeding tactic. When scrounging, individuals repeatedly leave the costs associated with attacking - such as energy and venom loss and the risk of injury (Kim et al. 2005) - to their 'producer'-siblings, while gaining the benefits of feeding (Barnard & Sibly 1981). Although group persistence and prey-sharing beyond the death of the mother are typical traits of many subsocial spiders (Evans 1998a; Kim et al. 2005; Yap & Li 2009), producer-scrounger dynamics have been investigated only in the subsocial crab spider *A. ergandros*. Experimental evidence indicated that *A. ergandros* spiderlings specialize in this feeding tactic as a function of group size, with higher scrounger-type frequencies in larger groups (Dumke et al. 2016). Whether *X. bimaculatus* exhibits similar dynamics in feeding tactic specialization is a compelling question for future studies specifically designed to examine group size effects.

Given its ecological and ethological similarity to *A. ergandros* (Ruch et al. 2014c; this study), *X. bimaculatus* is a particularly eligible model species to include into much-needed comparative investigations on the group-size-dependent emergence and regulation of scrounging behaviour, and its impact on group cohesion in communally feeding spiders (Yip and Rayor 2014). Providing fundamental quantifications of maternal care, the benefits of maternal provisioning beyond nutritional independence and the mode of prey-sharing among offspring in *X. bimaculatus*, this present study paves the way for such a research purpose.

ACKNOWLEDGEMENTS

I thank my fieldwork assistants, who helped greatly to collect the spider nests in Brisbane (J. A. Stafstrom in 2015 and V. Stangenberg in 2016), as well as J. Ruch for sharing her formidable expertise on both *X. bimaculatus* and *A. ergandros*. Moreover, I am grateful for the constructive comments on the manuscript made by J. M. Schneider and

M. E. Herberstein, as well as for the thoughtful suggestions made by two anonymous reviewers. I was cofounded by the doctoral scholarship 'Promotionsförderung' of the Konrad-Adenauer Foundation (Germany) and by the International Macquarie Research Excellence Scholarship (Macquarie University, Australia).

REFERENCES

Agnarsson I, Avilés L, Coddington JA, Maddison W P (2006). Sociality in theridiid spiders: repeated origins of an evolutionary dead end. Evolution 60: 2342–2351.

Avilés L (1997). Causes and consequences of cooperation and permanent sociality in spiders. In: Choe JC, Crespi BJ (eds) *The evolution of social behavior in insects and arachnids*. Cambridge University Press: Cambridge, pp. 476–498.

Avilés L, Bukowski TC (2006). Group living and inbreeding depression in a subsocial spider. Proceedings of the Royal Society of London B 273: 157–163.

Barnard CJ, Sibly RM (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29: 543–550.

Bilde T, Lubin Y (2011). Group living in spiders: cooperative breeding and coloniality. In: Herberstein ME (ed) *Spider behaviour: flexibility and versatility*. Cambridge University Press: Cambridge, pp. 275-306.

Brach V (1977). *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution 31: 154–161.

Brandmayr P (1992). Short review of the presocial evolution in Coleoptera. Ethology, Ecology and Evolution 4: 7–16.

Burley N (1980). Clutch overlap and clutch size: alternative and complementary reproductive tactics. The American Naturalist 115: 223–246.

Clutton-Brock TH (1991). *The evolution of parental care*. Princeton University Press: Princeton.

Crawley MJ (2007). Proportion data. In: Crawley MJ (ed*) The R book*. Wiley & Sons: West Sussex, pp. 569–591.

Dumke M, Herberstein ME, Schneider, JM (2016). Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. Proceedings of the Royal Society of London B 283: 20160114.

Evans TA (1995).Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. Records of the Western Australian Museum 52: 151–158.

Evans TA (1998a). Factors influencing the evolution of social behaviour in Australian crab spiders (Araneae: Thomisidae). Biological Journal of the Linnean Society 63: 205–219.

Evans TA (1998b). Offspring recognition by mother crab spiders with extreme maternal care. Proceedings of the Royal Society of London B 265: 129–134.

Evans TA, Main BY (1993). Attraction between social crab spiders: silk pheromones in *Diaea socialis*. Behavioral Ecology 4: 99–105.

Evans TA, Wallis EJ, Elgar MA (1995). Making a meal of mother. Nature 376: 299.

Giraldeau L-A, Caraco T (2000). *Social foraging theory*. Princeton University Press: Princeton.

Gundermann J-L, Horel A, Roland C (1991). Mother-offspring food transfer in *Coelotes terrestris* (Araneae, Agelenidae). The Journal of Arachnology 19: 97–101.

Heath D (2002). Tests for two related samples. In: Heath D (ed) *An introduction to experimental design and statistics for biology*. CRC Press: New York, pp. 253–257.

Ito C, Shinkai A (1993). Mother-young interactions during the broodcare period in *Anelosimus crassipes* (Araneae: Theridiidae). Acta Arachnologica 42: 73–81.

Jantschke B, Nentwig W (2001). Sub-social behaviour in the diplurid *Ischnothele caudata (*Araneae, Dipluridae). Bulletin of the British Arachnological Society 12: 12–16.

Kim KW, Horel A (1998). Matriphagy in the spider *Amaurobius ferox* (Araneidae, Amaurobiidae): an example of mother–offspring interactions. Ethology 104: 1021–1037.

Kim KW, Roland C (2000). Trophic egg laying in the spider, *Amaurobius ferox*: mother-offspring interactions and functional value. Behavioural Processes 50:31–42.

Kim KW, Krafft B, Choe JC (2005). Cooperative prey capture by young subsocial spiders. Behavioral Ecology and Sociobiology 59: 92–100.

Klug H, Alonzo SH, Bonsall MB (2012). Theoretical foundations of parental care. In: Royle NJ, Smiseth PT, Kölliker M (eds) *The evolution of parental care*. Oxford University Press: Oxford, pp. 21–38.

Lubin Y, Bilde T (2007). The evolution of sociality in spiders. Advances in the Study of Behavior 37: 83-145.

Main BY (1988). The biology of a social thomisid spider. In: Austin AD, Heather NW (eds) *Australian arachnology* Australian Entomological Society: Brisbane, pp 55–73.

Marques ES, Vasconcelos-Netto J, de Mello MB (1998). Life history and social behavior of *Anelosimus jabaquara* and *Anelosimus dubiosus* (Araneae, Theridiidae). The Journal of Arachnology 26: 227–237.

Marshall SD, Gittleman JL (1994). Clutch size in spiders: is more better? Functional Ecology 8: 118–124.

Nørgaard E (1956). Environment and behaviour of *Theridion saxatile*. Oikos 7: 159–192.

R Core Team (2015). *R: A Language and environment for statistical computing*. R Foundation for Statistical Computing: Vienna.

Rienks JH (2000). Extended nest residence and cannibalism in a jumping spider (Araneae, Salticidae). The Journal of Arachnology 28: 123–127.

Rowell D, Avilés L (1995). Sociality in a bark-dwelling huntsman spider from Australia, *Delena cancerides* Walckenaer (Araneae: Sparassidae). Insectes Sociaux 42: 287–302.

Royle NJ, Smiseth PT, Kölliker M (2012). *The evolution of parental care*. Oxford University Press: Oxford.

Ruch J, Herberstein, ME, Schneider JM (2014a). Families hunt more successfully: effect of group composition on hunting and communal feeding. Animal Behaviour 91: 171–178.

Ruch J, Herberstein ME, Schneider JM (2014b). Offspring dynamics affect food provisioning, growth and mortality in a brood-caring spider. Proceedings of the Royal Society of London B 281: 20132180.

Ruch J, Riehl T, Michalik P (2014c). Re-description of *Xysticus bimaculatus* L. Koch, 1867 (Araneae, Thomisidae) and characterization of its subsocial lifestyle. ZooKeys 427: 1–19.

Ruch J, Riehl T, May-Collado LJ, Agnarsson I (2015b). Multiple origins of subsociality in crab spiders (Thomisidae). Molecular Phylogenetics and Evolution 82: 330-340.

Ruttan LM (1991). Effects of maternal presence on the growth and survival of subsocial spiderlings (Araneae: Theridiidae). Journal of Insect Behavior 4: 251–256.

Salomon M, Schneider J, Lubin Y (2005). Maternal investment in a spider with suicidal maternal care, *Stegodyphus lineatus* (Araneae, Eresidae). Oikos 109: 614–622.

Schneider J M, Bilde T (2008). Benefits of cooperation with genetic kin in a subsocial spider. PNAS 105: 10843–10846.

Simpson MR (1995). Covariation of spider egg and clutch size: the influence of foraging and parental care. Ecology 76: 795–800.

Smiseth PT, Darwell CT, Moore AJ (2003). Partial begging: an empirical model for the early evolution of offspring signalling. Proceedings of the Royal Society of London B 270: 1773–1777.

Tallamy DW (1984). Insect parental care. Bioscience 34: 20-24.

Thiel M (1999). Extended parental care in marine amphipods: II. Maternal protection of juveniles from predation. Journal of Experimental Marine Biology and Ecology 234: 235–253.

Thiel M (2007). Social behaviour of parent–offspring groups in crustaceans. In: Thiel M (ed) *Evolutionary ecology of social and sexual systems: crustaceans as model organisms.* Oxford University Press: Oxford, pp. 294–318.

Trumbo ST (2012). Patterns of parental care in invertebrates. In: Royle NJ, Smiseth PT, Kölliker M (eds) *The evolution of parental care.* Oxford University Press: Oxford, pp. 81-100.

Unglaub B, Ruch J, Herberstein ME, Schneider JM (2013). Hunted hunters? Effect of group size on predation risk and growth in the Australian subsocial crab spider *Diaea ergandros*. Behavioral Ecology and Sociobiology 67: 785-794.

Walter A, Bilde T (2015). Social recognition in the Arachnida. In: Aquiloni L, Tricarico E (eds) *Social recognition in invertebrates*. *The knowns and the unknowns.* Springer: New York, pp. 101–124.

Whitehouse ME & Lubin Y (2005). The functions of societies and the evolution of group living: spider societies as a test case. Biological Reviews 80: 347-361.

Wilson EO (1971). *The insect societies*. Harvard University Press: Harvard.

Yap LM, Li D (2009). Social behaviour of spitting spiders (Araneae: Scytodidae) from Singapore. Journal of Zoology 278: 74–81.

Yip EC, Rayor LS (2014). Maternal care and subsocial behaviour in spiders. Biological Reviews 89: 427-449.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009). Generalised estimation equations. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) *Mixed effects models and extensions in ecology with R*. Springer: New York, pp. 295–342.

CHAPTER 3

Advantages of social foraging in crab spiders: groups capture more and larger prey despite the absence of a web

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Submitted

Abstract

Among group-living spiders, subsocial representatives in the family of crab spiders (Thomisidae) are a special case, as they build protective communal leaf nests instead of extensive communal capture webs. It could thus be inferred that anti-predator benefits (e.g. enhanced protection in larger nests) rather than foraging-related advantages (e.g. capture of more and larger prey) promote sociality in this family. Nonetheless, subsocial crab spiders do share prey, and if this behavior does not reflect mere food scramble but has a cooperative character, crab spiders may offer insights into the evolution of social foraging applicable to many other cooperative predators that hunt without webs. Here, we performed a cross-species experiment including three of four subsocial species - *Australomisidia ergandros*, *Australomisidia socialis* and *Xysticus bimaculatus* - to determine if crab spiders derive advantages from foraging in groups. In a nuanced approach, we tested groups versus singles in predatory success and prey size preference. Across species, groups had higher predatory success and were more likely to attack large, sharable prey - dynamics leading to reduced food competition among group members in favour of living and foraging in groups. We further compared food extraction efficiency among the different social foraging tactics our crab spiders applied: producing, scrounging and feeding alone. In *A. ergandros*, individuals were exceptionally efficient when using the non-cooperative scrounger tactic. Thus, our multi-species comparison confirms foraging advantages in maintaining a cooperative life-style for crab spiders, but also demonstrates the relevance of research into exploitation of cooperative foraging in this family.

Introduction

Alongside the considerable advantages that group living provides in terms of predator avoidance, mate search or offspring care, the evolutionary success of group-living invertebrates is partially attributable to enhanced access to food resources (Krause & Ruxton 2002; Whitehouse & Lubin 2005; Trumbo 2012; Rubenstein & Abbot 2017). Accordingly, eusocial bees and some social wasps efficiently deplete food patches because they recruit additional foragers via information transfer (Overmyer & Jeanne 1998). Group-living shrimp communally defend their sponge habitat that also serves to be a life-long food supply (Duffy 1996; Hultgren et al. 2014), and worker ants join forces to retrieve large prey (reviewed in McCreery & Breed 2014).

The effect of grouping on foraging payoffs appears to be of special significance in the evolution of group living in spiders (Kim et al. 2005; Whitehouse & Lubin 2005; Yip et al. 2008; Ventura et al. 2017). It is widely accepted that foraging advantages have selected for spider coloniality, where territorial individuals aggregate to exploit prey-rich sites inaccessible to single individuals (Lubin 1974) or to profit from trapping insects that bounce off a neighboring web (Uetz 1989). The so-termed subsocial and social spiders, on the other hand, are non-territorial and live in either temporal or permanent family alliances, respectively (Kullmann 1972; Avilés 1997). Their form of sociality is thought to have arisen from the prolonged grouping of offspring beyond maternal care, but possibly owing to reproductive and protective benefits (Kullmann 1972; Avilés 1997; Lubin & Bilde 2007) and only secondary to foraging advantages (Avilés & Guevara 2017).

In this respect, several studies on social spiders revealed negative effects of grouping on the foraging payoff per individual (i.e. the per-capita foraging payoff) (Ward & Enders 1985; Schneider 1995; Yip et al. 2008). For instance, group members suffered reduced per-capita food intake with increasing group size. These findings indicate that food competition among group members counteracts the benefits of social group living in spiders (Rubenstein 1978; Ranta et al. 1993; Avilés & Guevara 2017), which potentially explains why subsocial and social spider species are truly rare (Agnarsson et al. 2006; Yip & Rayor 2011, 2014). Spiders that do form social groups, however, likely exhibit compensatory mechanisms and behavioral adaptations that reduce food competition and thus diminish the detrimental decrease in the per-capita foraging payoffs to group members (Nentwig 1985; Packer & Ruttan 1988; Yip et al. 2008). Thus, studies establishing such grouping-derived mechanism and adaptations contribute substantially to understanding the stable maintenance of social group living in spiders – even if the initial evolution of spider group-living was primarily driven by reproductive and anti-predator advantages.

A prevalent behavioral adaptation reducing food competition among group members is the communal capture of large prey items that a single attacker would not subdue, either because of inability or because of overly high costs (Packer & Ruttan 1988). Communal capture of large prey occurs in many social predators including spiders; it expands the prey spectrum and increases the feeding rates of group hunters (Creel & Creel 1995; Kim et al. 2005; Yip et al. 2008; Majer et al. 2015). Food competition among group members is further reduced when only one to a few individuals are needed to seize prey that feeds many (Packer & Ruttan 1988; Vickery et al. 1991). In rare cases specific to spiders, the costs of food competition may be compensated in yet another way. To extract nutrients, spiders inject digestive enzymes into the prey, and a recent study on *Stegodyphus dumicola* suggests that the cumulative effect of enzymes injected by multiple individuals increases the extraction efficiency: group-feeding individuals extracted more nutrients per unit time than singles (Vanthournout et al. 2016).

The capture web that (sub-) social spiders typically share is thought to have promoted the above adaptations (Avilés 1997). It withstands the struggle of large prey, prey vibrations transmitted through the web recruit cooperators, and the web may even facilitate communication by which members of groups can coordinate hunting and feeding activities (Nentwig 1985; Krafft & Pasquet 1991; Whitehouse & Lubin 2005). Obviously, spiders that do not construct webs cannot take advantage of this multifunctionality. It follows that non-webbuilding species presumably had to overcome greater constraints in evolving advantageous group foraging and thus in maintaining social group living (Yip & Rayor 2011). Such a 'handicap' could explain why most subsocial and social spiders are web builders (Avilés 1997; Agnarsson et al. 2006; Avilés & Guevara 2017).

Nevertheless, the non-webbuilding family of crab spiders (Thomisidae) contains four Australian species that exhibit subsociality: offspring-group members hunt and feed communally on the surface of leafnests, which they jointly construct and inhabit beyond the mother's death, until dispersal at reproductive maturity (Main 1988; Ruch et al. 2014a; Ruch et al. 2015; Dumke 2017). The occurrence of subsociality and in particular of social foraging suggests that these crab spiders have evolved similar adaptations to group foraging as their web-building equivalents. Moreover, group-living crab spiders may offer insights applicable to group-living animals outside the arachnid class, which also do not rely on a communal web.

In this study, we aim to identify common advantages and adaptations to group foraging that reduce food competition among group members and thus may contribute to the maintenance of group living in Australia's subsocial crab spiders. Therefore, we comparatively investigated the pros and cons of group foraging versus solitary foraging in three of the four subsocial species: *Australomisidia ergandros*, *Australomisidia socialis* and *Xysticus bimaculatus* (the classification of these species as subsocial follows Yip & Rayor 2014). Because detailed observations of individual foraging behavior in the field are obstructed by the labyrinthine structure of nests, we designed a comprehensive laboratory experiment, where individuals were kept either solitary or in conspecific kin groups. All singles and groups had to pass a one-time feeding trial in which they received either a small or a large prey item, or both simultaneously. The experiment served to test three specific hypotheses.

The first hypothesis stated that grouping increases the gross prey capture success (not to be confused with the per-capita prey capture success), which we tested by comparing capture rates and attack latencies between singles and groups within each species. The second hypothesis stated that the ratio of captured small to captured large prey would shift from singles to groups towards higher amounts of captured large prey - reflecting a behavioral response that reduces food competition and potentially an expansion in the prey spectrum accessed by groups. We tested this hypothesis by examining whether singles and groups within species differed in their 'prey preference' for small versus large prey items. Third, we tested the hypothesis that group feeding enhances the prey extraction efficiency of the involved individuals as compared to feeding alone (following Vanthournout et al. 2016).

At last, it is important to recognize that even if groups capture more prey faster, furthermore capture larger prey and additionally extract more nutrients in group feeds, these effects may still be insufficient to offset a decline in the per-capita food intake resulting from food competition among group members (Jones & Parker 2000; Yip et al. 2008; Avilés & Guevara 2017). However, any gross positive effect of foraging in groups will mitigate the possibly negative per-capita effect, eventually maintaining the point where group living is in summary of all reproductive, protective and foraging-related payoffs more advantageous than a solitary life.

Methods

Study species

The here investigated thomisids *Australomisidia ergandros*, *Australomisidia socialis* and *Xysticus bimaculatus* do not occur sympatrically, yet are ecologically very similar (Main 1988; Evans 1995; Ruch et al. 2014b): they all build leafnests in either *Eucalyptus* (*A. ergandros* and *A. socialis*) or *Acacia* trees (*X. bimaculatus*), and they all inhabit these

Collection sites

Australomisidia ergandros *Australomisidia socialis* *Xysticus bimaculatus*

Figure 1 | Collection sites and nest habitus for the three crab spider species studied. These species do not occur sympatrically but all build nests by firmly bundling tree leafs using silk threads. GPS coordinates for collection sites of *A. ergandros*: S34°55'20.50" E149°6'15.53". GPS coordinates for *A. socialis*: S34°39'08.8" E117°52'18.8" & S35°04'06.5" E117°38'16.8". GPS coordinates for *X. bimaculatus*: S27°32'44.5" E153°02'47.3" & S27°27'41.4" E152°57'38.2". All nests were collected alongside roads within 250 m radius from these coordinates.

leafnests for several months in groups of roughly five up to 40 individuals. Nest groups usually comprise the offspring of one caring female that initiates the protective nest into which she deposits her egg sac, and that later provisions her young until her own death (Main 1988; Evans 1998; Dumke 2017). During and beyond maternal care up to adulthood, group members feed communally on large prey that was usually captured by one to a few individuals (Main 1988; Ruch et al. 2014a; Ruch et al. 2015; Dumke 2017).

Nest collection

For our comparative study of how grouping affects foraging in Australia's group-living crab spiders, we collected a total of 54 *A. ergandros* nests nearby Yass, NSW in February of 2015 (25 nests) and 2016 (29 nests), as well as 36 *A. socialis* nests nearby Albany, WA in March 2017 and 61 *X. bimaculatus* nests nearby Brisbane, QL in April 2017 (Figure 1). *A. socialis* were collected under the "Licence to take Fauna for Scientific Purposes" (Department of Parks and Wildlife, WA); special permits for the other species were not required. We cut the spider nests off their host trees with extendable pruners and separately stored them in zip bags. Within three days after collection, we took the nests of *A. ergandros* and *X. bimaculatus* to a laboratory at Macquarie University in Sydney and the nests of *A. socialis* to a laboratory at University of Western Australia in Perth, WA. The following descriptions of the experimental protocol applied to all of the three species, unless stated otherwise.

Experiment preparation

In the laboratories, we opened each nest to conduct a census and a size class estimation of the individuals inside (size class (sc) by body length, sc 1: < 1.5 mm, sc 2: < 2.5 mm, sc 3: < 3.5 mm, sc 4 < 4.5 mm, sc 5 < 5.5 mm). Usually, nest mates had a similar body size (Evans & Main 1993). Per suitable nest (more than 18 individuals) we randomly allocated a subset of individuals to one of two social treatments: the 'single' treatment, where individuals were kept alone, or the 'group' treatment, where individuals were kept in groups of five.

Specifically, we established at least three singles and three groups per nest (if possible four and four). We chose these numbers because the singles and the groups per nest were further split into three different prey treatments (Figure 2). We thus achieved balance across treatment combinations in terms of nest-origin and body size. To achieve balance across species, we further restricted our selection to nests with inhabitants of the size classes 2 to 4. Twenty *A. ergandros* nests, 10 *A. socialis* nests and 19 *X. bimaculatus* nests fulfilled our selection criteria, allowing us to initially establish $N = 80$ (20 times four) singles and groups of

A. ergandros, *N* = 40 (10 times four) singles and groups of *A. socialis* and *N* = 68 (11 times four and 8 times three) singles and groups of *X. bimaculatus*.

The three prey treatments that singles and groups were further allocated to were 'S': receiving a small prey item (<1 mg) weighing notably less than the tested spider (which weighed at minimum 1.5 mg), 'L': receiving a large prey item (3-4 mg) weighing at least half than the tested spiders (which weighted at maximum 6.0 mg), or 'SL': simultaneously receiving a small and a large prey item with the respective weight characteristics (Figure 2). In cases where four singles and groups had been established from a nest, we assigned two singles and two groups to the 'SL' prey treatment. This sample size elevation was favorable as two of the study objectives - prey preference and prey extraction efficiency - were investigated within the singles and groups receiving 'SL'.

To standardize the hunting space per spider, we transferred singles to petri dishes with a volume of 8.5 cm^3 and groups to petri dishes of 42.5 cm^3. Each petri dish contained a sheltering leaf (1 cm x 5 cm), cut to one fifth its standardized size for singles. We completed all experiment preparations within three days after the species had been taken to the laboratories. Subsequently, all singles and groups were allowed to acclimate without disturbance for at least four days.

Experiment procedure

The purpose of our experiment was to test the effects of grouping on (a) prey capture success, (b) prey preference and (c) prey extraction efficiency. For this purpose, we tested each single and each group in one feeding trial. At trial start, we introduced the assigned prey items alive into the petri dish and recorded whether the prey was captured within 120 min ('1' if yes and '0' if no) and where applicable the attack latency (in min; detailed definition in Dumke et al. 2016). *A. ergandros* and *X. bimaculatus* received *Drosophila melanogaster* as small and *Drosophila hydeii* as large prey. Due to an import restriction into Western Australia, we were unable to source adequate flies for *A. socialis* and instead used crickets (*Acheta domesticus*) matching the S and L sizes of the *Drosophila* used for the other species. For comparison, we tested another 13 *A. socialis* singles and groups with *D. melanogaster* available in-house. There was no statistical difference between the capture rates for

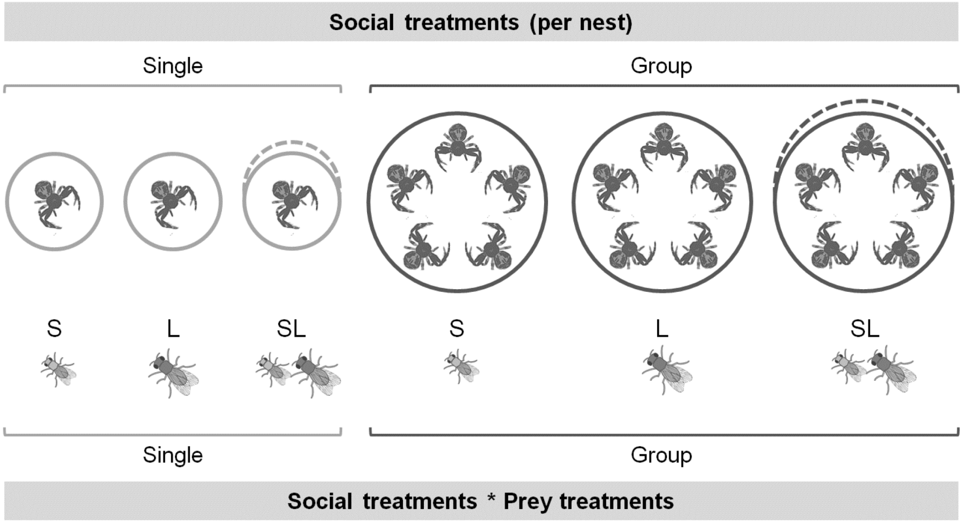

Figure 2 | The combinations of social treatment ('single' or 'group') and prey treatment (small prey 'S', large prey 'L', or small and large prey 'SL') established per nest. The dashed line added to the single and the group receiving the prey treatment 'SL' indicates that at times, two singles and two groups from the same nest were assigned to this prey treatment. The visual example here shows *Xysticus bimaculatus* with *Drosophila melanogaster* or *D. hydeii* as small or prey, respectively. However, *Australomisidia socialis* received mostly crickets (see Methods). Final sample sizes for each treatment combination (i.e. less any deaths) are given in Table 1.

small flies and small crickets (Fisher's exact test, $P = 0.114$), however crickets were captured more frequently. We tested singles and groups from the same nest simultaneously so as to maintain the balance between treatment combinations in terms of test day and time and therewith of hunger state and daytime-dependent activity. We completed all feeding trials per species within four days.

In addition to the above procedure, the singles and group members receiving a small and a large prey item simultaneously ('SL') were individually marked and weighted to the nearest 0.01 mg on a 'Mettler Toledo New Classic MS' fine balance right before trial start (see also Dumke et al. 2016). During trials, we noted which prey type was captured first and which second, with the respective attack latency. For groups, we also noted the IDs of the attackers and the feeding individuals in five-minute intervals. This allowed us to determine the feeding tactic (feeding alone or feeding as a group) and the feeding time (in min) of every individual in these groups. At trial end, we removed the prey and weighted each previously feeding individual to assess its weight gain in mg (by subtracting start weight from end weight).

Statistical analyses

We present all descriptive parameters except percentages as mean ± SE. Model analyses were performed in R 3.2.2 (R Core Team 2015). The statistical sample sizes are stated in Table 1.

Effect of grouping on prey capture success

To assess the effect of grouping on capture rates, the binary data indicating whether prey had been captured or not were pooled over the three prey treatments ('S', 'L' and 'SL'), separately for singles and groups within species. For *A. socialis*, we included the 13 data points obtained from the trials with *D. melanogaster*. Thus, final sample sizes was $N_{\text{singles/groups}} = 80$ for *A. ergandros*, $N_{\text{singles/groups}} = 51$ for *A. socialis* and $N_{\text{singles/groups}} = 68$ for *X. bimaculatus* (Table 1). We compared the capture rates of singles and groups (i.e. the proportion of singles and groups that had successfully captured prey) with separate Chi-squared tests per species. Similarly, we compared the attack latencies between singles and groups. The sample sizes for this comparison equaled the respective number of singles and groups that had captured prey (Table 1). Because normal distribution of data could not be achieved, we compared attack latencies between singles and groups using Mann-Whitney-Wilcoxon tests.

Effect of grouping on prey preference

We examined prey preference within species using the singles and groups that received both prey types at once ('SL'). This approach conformed to the recommended choice design to test 'true preference' (Roa 1992). Specifically, we wanted to know whether singles and groups differed in their tendency to capture one prey type over the other, which we measured as the difference between small and large prey in being captured first. Thus, we asked for 'a difference in a difference', a question to be addressed via interaction effects (Zuur et al. 2009). We applied mixed effects logistic regression to analyse the interaction effect between prey type and social treatment on a binary response variable coding for each prey item whether it was captured first or not (Roa 1992; Zuur et al. 2009). We included the IDs of singles and groups as random effects. The singles and groups that received either a small or a large prey item ('S' and 'L') served as control treatments to test whether our spiders were in principle able to seize both prey types. This was to not confuse inability with preference in the choice tests. We compared the capture rates between 'S' and 'L' singles and between 'S' and 'L' groups with Fisher's exact tests.

Effect of grouping on prey extraction efficiency

We examined prey extraction efficiency within the groups that simultaneously received both prey types ('SL' groups). Even in groups, some individuals feed together while others feed alone, such that we were able to compare the prey extraction efficiency between group-feeding and single-feeding group members ('loners'). This approach most closely mirrored the natural situation in which our crab spiders encounter prey. For group-feeding individuals, we distinguished ‘producers’, who had engaged in capturing the prey, and ‘scroungers’, who had joined to feed (Vickery et al. 1991; Dumke et al. 2016). We measured extraction efficiency as a rate describing the weight gain of individuals in mg per minute time it spent feeding. Statistical outliers were removed from the data. We then analysed differences among loners, producers and scroungers with GLS (generalized least squares) models. This allowed us to correct variance heterogeneity by employing the ‘varIdent’ variance function (Pekár & Brabec 2016). To control for measurements made on individuals from the same group, we defined an exchangeable correlation structure with group ID as a grouping factor (Pekár & Brabec 2016). Individual weight at trial start was included as a covariate to separate body size effects.

Results

Effect of grouping on prey capture success

Capture rates

In all three species, groups were more successful in capturing prey than singles (Figure 3A; Table 1). In *Australomisidia ergandros*, 58.75% of the singles captured prey, while this proportion increased to 90.00% for groups ($\chi^2 = 18.89$, $P < 0.0001$). In *A. socialis*, singles succeeded in 37.25% but groups in 78.43% of cases ($\chi^2 = 17.27$, $P < 0.0001$). In *Xysticus bimaculatus*, 57.35% of the singles and 79.41% of the groups were successful ($\chi^2 = 6.67$, $P = 0.0098$).

Attack latencies

Generally, groups were significantly faster in capturing prey than singles (Figure 3B). Comparing the average attack latencies, *A. socialis* singles captured prey ~24 minutes later than groups ($W = 238.5$, $P = 0.0212$), and *X. bimaculatus* singles required an additional ~11 minutes as compared to groups ($W = 801.5$, $P = 0.0486$). In *A. ergandros*, where singles took ~10 minutes longer to capture prey, we found a statistical tendency for faster captures in groups ($W = 428$, $P = 0.0825$).

Effect of grouping on prey preference

Control

The comparison of capture rates between the singles/groups receiving small prey (‘S’) and the singles/ groups receiving large prey (‘L’) served to evaluate the spiders’ ability to seize the two prey types. *A. ergandros* singles captured both types equally ($P = 0.751$) and *in A. ergandros* groups, the capture rate was marginally lower, yet remained high for large compared to small prey ($P = 0.092$; Figure 3A; Table 1). *X. bimaculatus* did not exhibit any differences (singles: $P = 1.00$, groups: $P = 1.00$; Figure 3A; Table 1). It can be inferred that *A. ergandros* and *X. bimaculatus* were generally able to seize both prey types. By contrast, *A. socialis*

Table 1 | Sample sizes for social treatments and prey treatments within social treatments, together with the respective capture rates that formed the sample size for analyses regarding captures only

Species	Social treatment over all prey tr.	Capture rates per social tr.	Prey treatment equal in social tr.	Capture rates singles per prey tr.	Capture rates groups per prey tr.
Australomisidia ergandros	$N_{\text{singles}} = 80$	$N_{\text{singles}} = 47$	$N_S = 20$	$N_S = 10$	$N_S = 19$
	$N_{\text{groups}} = 80$	$N_{\text{groups}} = 72$	$N_L = 20$	$N_L = 8$	$N_L = 14$
			$N_{SL} = 40$	$N_{SL} = 29$ (24S, 5L)	$N_{SL} = 39$ (21S, 18L)
Australomisidia socialis	$N_{\text{singles}} = 51$	$N_{\text{singles}} = 19$	$N_S = 9+13^{a}$	$N_S = 6+3^{a}$	$N_S = 8+10^{a}$
	$N_{\text{groups}} = 51$	$N_{\text{groups}} = 40$	$N_L = 9$	$N_L = 0$	$N_L = 5$
			$N_{SL} = 20$	$N_{SL} = 10$ (7S, 3L)	$N_{SL} = 17$ (8S, 9L)
Xysticus bimaculatus	$N_{\text{singles}} = 68$	$N_{\text{singles}} = 39$	$N_S = 19$	$N_S = 9$	$N_S = 13$
	$N_{\text{groups}} = 68$	$N_{\text{groups}} = 54$	$N_L = 19$	$N_L = 9$	$N_L = 14$
			$N_{SL} = 30$	$N_{SL} = 21$ (15S, 6L)	$N_{SL} = 27$ (13S, 14L)

[a] For *Australomisidia socialis*, a summation term describes the sample sizes and capture rates (respective N_S) in the prey treatment ‘S’. The summands refer to the respective numbers of baby crickets (first summand) and *Drosophila melanogaster* (second summand) that *A. socialis* received within this prey treatment (see Methods).

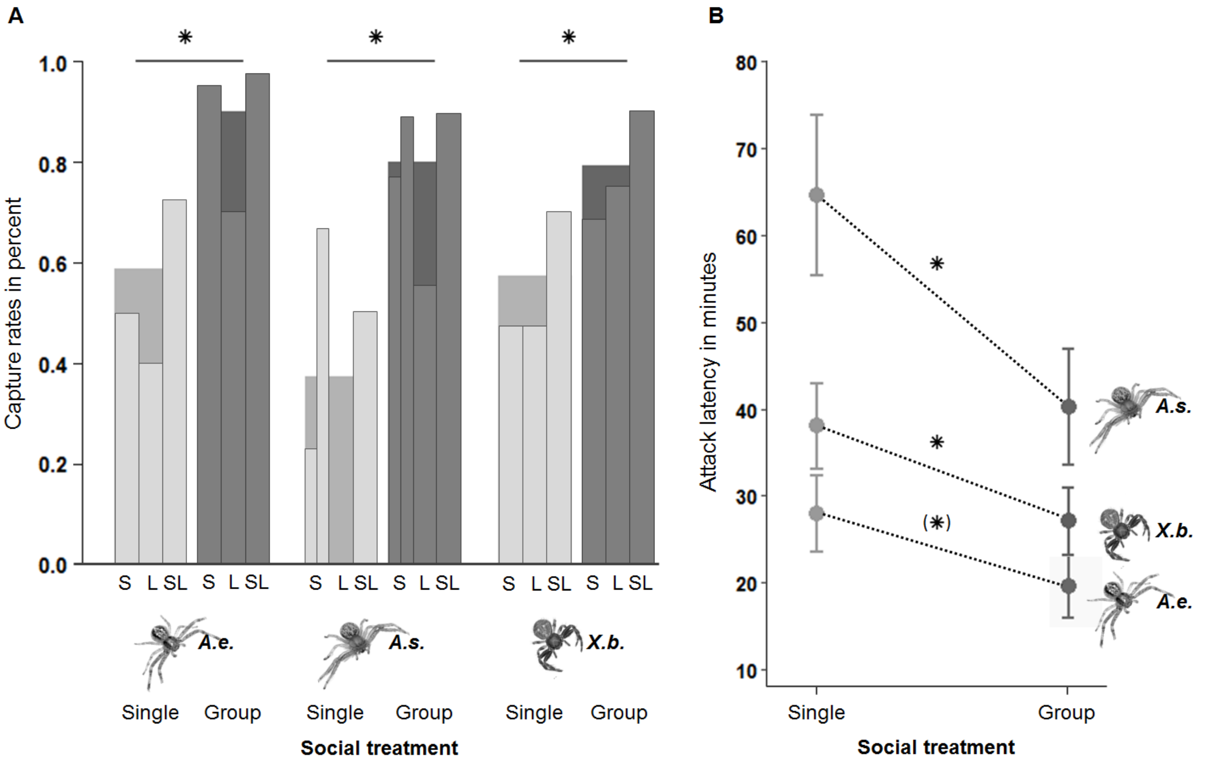

Figure 3 | Differences in prey capture success between spider singles and spider groups within the three tested crab spider species, described via capture rates and attack latencies. Each asterisk marks a significant (in brackets a marginally significant) difference between singles and groups. **A**: The capture rates of singles and groups given in percent. Because singles as well as groups received one of three prey treatments - small prey ('S'), large prey ('L'), or both prey types simultaneously ('SL') - the outlined bars show the success per prey treatment. The shaded areas behind these bars mark the overall capture rate of singles and groups, i.e. combined over prey treatments. Sample sizes for each bar are given in Table 1. **B**: The attack latency of singles and groups in minutes until the prey was seized. Dots and whiskers represent mean ± SE.

singles captured two thirds of the small but none of the large prey items (*P* = 0.0091). Groups captured most small but only few large prey, although there was no statistical difference (*P* = 0.2941). This suggest that *A. socialis* was not well able to capture the offered large prey (Figure 3A; Table 1).

Prey preference

The analysis of interaction effects revealed that singles and groups categorically differed in their choice of prey type when receiving small and large prey simultaneously ('SL'; Figure 4; Table 1): in *A. ergandros* and *X. bimaculatus*, the interaction effect of prey type and social treatment was significant (*A. ergandros*: *L*-Ratio = 13.05, *P* = 0.0003; *X. bimaculatus*: *L*-Ratio = 5.36, *P* = 0.0206), and a marginal significance was detected for *A. socialis* (*L*-Ratio = 2.74, *P* = 0.0978). To be specific, *A. ergandros* singles tended to capture small over large prey (first captures: 82.76% small vs. 17.24% large prey) while groups displayed no preference (first captures: 53.85% small vs. 46.15% large prey; Figure 4; Table 1). In *A. socialis* and *X. bimaculatus*, singles chose small over large flies in 70.00% and 71.42% of cases while again, groups displayed no preference (Figure 4; Table 1). Thus, the preference patterns were remarkably similar across all three species. Communal attacks on large prey were comparably rare (communally seized large prey: 24.24% in *A. ergandros*; 9.09% in *A. socialis*; 13.04% in X. *bimaculatus*).

Effect of grouping on prey extraction efficiency

Prevalence of group feeding

Within groups that received both prey types ('SL' groups), group-feeding occurred frequently on large prey items (shared large prey: 66.67% in *A.*

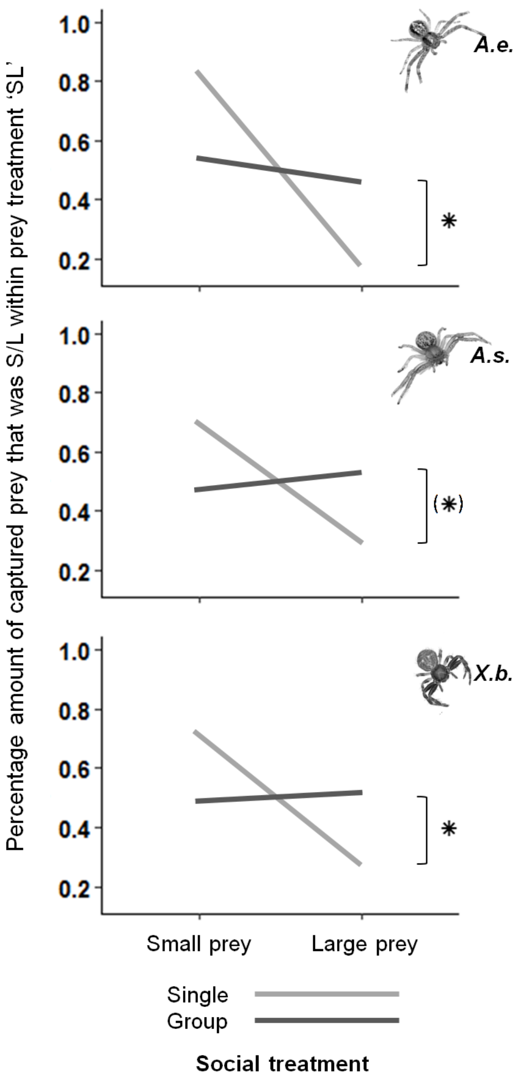

Figure 4 | The preference (in percent) of singles (light grey line) and groups (dark grey line) for small versus large prey. Preference patterns are shown separately for the three tested crab spider species. The slope of the lines indicates the respective preference, with a negative slope indicating a preference for small over large prey. The asterisks mark (marginally) significant differences between the preference patterns of singles and groups within the species.

ergandros, 45.45% in *A. socialis*, 69.57% in *X. bimaculatus*) but rarely on small prey (perc. shared small prey: 20.00% in *A. ergandros*, 10.00% in *A. socialis*, 25.00% in *X. bimaculatus*). This pattern remained stable when taking an individual perspective: the vast majority of *N* = 95 foragers in *A. ergandros* fed communally on large prey (48.42%) or alone on small prey (25.26%). Similar respective values were found in *A. socialis* (55.55% & 22.22%, *N* = 27 foragers) and *X. bimaculatus* (50.77% & 23.08%, *N* = 65 foragers). A Chi-squared test indicated an exceptional similarity among the three species in the percentage distribution of individuals over the four options (feeding alone or feeding together on small or large prey; $\chi^2 = 0.58$, *P* = 0.9966).

Prey extraction efficiency

With regards to the effect of group-feeding on the extraction efficiency of individuals, we obtained heterogeneous results for the different species (Figure 5). We only considered the three most prevalent individual feeding tactics, which were feeding alone on small, producing on large or scrounging on large prey (see above). In *A. ergandros*, loners (*N* = 24) and producers (*N* = 25) achieved a similar weight gain per minute time spent feeding (*t* = 0.45, *P* = 0.66). Scroungers (*N* = 21), however, had a higher prey extraction efficiency than loners (*t* = 2.36, *P* = 0.0215) and a marginally higher extraction efficiency than producers (*t* = 1.77, *P* = 0.0807). For *X. bimaculatus*, we found a reverse effect (Figure 5), where loners (*N* = 15) achieved significantly less weight gain per minute than producers (*N* = 16, *t* = 2.05, *P* = 0.0465). Scroungers (*N* = 19) had an 'in-between status', with an insignificantly higher efficiency than loners (*t* = 0.85, *P* = 0.40) and an insignificantly lower intake rate than producers (*t* = -1.23, *P* = 0.23).

Due to the low number of attacks by *A. socialis* and the resulting small sample size for loners (*N* = 6), producers (*N* = 6) and scroungers (*N* = 9), we only provide descriptive statistics for *A. socialis*: loners achieved 0.0054 ± 0.0012 mg/min, producers gained 0.0048 ± 0.0016 mg/min and scroungers had the highest prey extraction efficiency (0.0071 ± 0.0015 mg/min). This pattern resembled that of *A. ergandros*.

Discussion

For three subsocial crab spider species, all of which do not build webs and thus cannot rely on the function of webs in managing group foraging, we demonstrate that grouping nonetheless leads to increased predatory success, accompanied by the capture of larger prey. Explicitly, we compared the capture rates, attack latencies and prey size

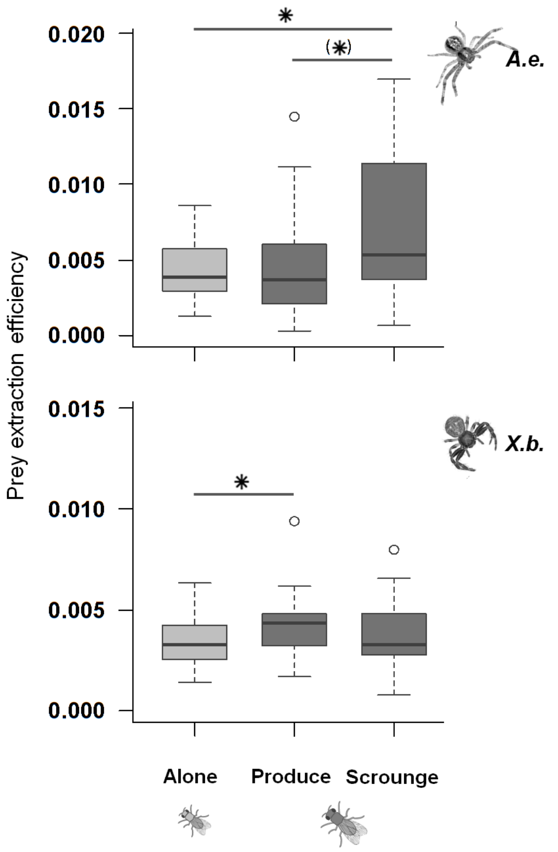

Figure 5 | The prey extraction efficiency (i.e. the weight gain in mg per min spent feeding) of *Australomisidia ergandros* and *Xysticus bimaculatus*, measured in groups receiving both small and large prey items. In the boxplot graph, the extraction efficiencies of individuals feeding alone on small and producers and scroungers feeding in groups on large prey are compared. The asterisks mark (marginally) significant differences in extraction efficiency.

preferences between singles and groups - and obtained remarkably similar results in favour of group foraging across all three species. In concert, these effects are thought to counteract the costs of food competition faced by group members, such that group living is persistently advantageous (Rubenstein 1978; Ranta et al. 1993; Krause & Ruxton 2002). We accordingly suggest that the faster capture of more and larger prey generally promotes group retention across group-living crab spiders. Besides the investigated species *Australomisidia ergandros*, *Australomisidia socialis* and *Xysticus bimaculatus*, the only other group-living crab spider is *Australomisidia inornata*. As this thomisid shares a comparable ecology and life history with the crab spiders used in this study (Evans 1995; Szymkowiak 2014; Dumke 2017), it likely derives similar advantages from foraging in groups.

The finding that crab spider groups were more successful in prey capture than single is consistent with numerous studies on group-living spiders that do build webs, irrespective of whether the web-builders studied were colonial, subsocial or social (Lubin 1974; Nentwig 1985; Uetz 1988; Rypstra 1989; Yip et al. 2008; Harwood & Avilés 2013). Yet, a substantial difference between these web-builders and our crab spiders lies in the means by which the increase in prey capture success is achieved. Colonial web-building spiders benefit from higher capture rates owing to the accumulation of individual capture webs: the interconnected webs form a three-dimensional structure that is more effective than a single web in trapping insects (Lubin 1974; Uetz 1988). Likewise, web structure seems to play an important role in enhancing the capture rates of (sub-) social web builders (Nentwig 1985; Guevara et al. 2011; Harwood & Avilés 2013). The Neotropical social spider *Anelosimus eximius*, for instance, captures a greater variety of prey types than solitary species because it accesses the flyways of larger insects with capture threads measuring several meters (Nentwig 1985). These ‘knockdown threads’ are constructed and maintained through the groups’ corporate web-building effort (Nentwig 1985; Pasquet & Krafft 1992).

In contrast, the here reported increase in prey capture success for crab spider groups compared to singles is not attributable to the structure of a communal web. Nor is it the result of density effects, as we standardized the hunting space per spider across singles and groups.

Considering that group-living crab spiders hunt actively by ambush (Ruch et al. 2014; Ruch et al. 2015), we instead suggest that our experimental groups achieved higher capture rates and shorter attack latencies via passive spatial effects of grouping and/or local enhancement (Brockmann & Barnard 1979; Waite 1981; Brown 1988). For instance, a prey item provided to groups may have been caught as it tried to escape the attack of one spider, but thus unwarily came within the range of another. This spatial effect resembles the ‘beater effect' found in waterfowl, penguins or storks (Brockmann & Barnard 1979). Moreover, the activity of individuals who already perceived the presence of prey may have attracted the attention of additional group members, resulting in more and faster captures. This effect, termed local enhancement, has been confirmed in cliff swallows and moreover in wasps (Waite 1981; D'Adamo et al. 2000).

We occasionally observed, but did not systematically record behavioral events that corresponded to these explanations. Hence, we are unable to conclusively assess whether spatial effects and/or local enhancement improved the prey capture success in our experimental groups. In natural environment, it also needs to be considered that group-living crab spiders prey upon insects on the surface of their nests (Figure 1; Main 1988; Evans 1995) – and that the 'beater effect' is unlikely to occur with winged insects, which would escape a spiders' grasp by leaving into the air. Yet besides flying insects, the natural prey spectrum of all group-living crab spiders includes worker ants. These march across the nest surface, thus allowing for spatial effects and local enhancement (Main 1988; Evans 1995; Ruch et al. 2014b). In general, future studies are needed to clarify the likely complex ecological relationships between group-living crab spiders and ants, which could also act as prey scavengers (Uetz 1992).

Group-living crab spiders may further increase their predatory success through cooperative hunting as in web-building spiders, mammalian predators and birds of prey (Bednarz 1988; Pasquet & Krafft 1992; Creel & Creel 1995; Kim et al. 2005; MacNulty et al. 2014). In particular, by subduing prey conjointly, they may expand their prey spectrum to include large prey unavailable to solitary attackers (Packer & Ruttan 1988). However, the *Drosophila* flies offered to A. *ergandros* and *X. bimaculatus* in this study were rarely attacked by multiple individuals, and singles were well able to capture both small and large prey types. The pattern of prey preference we found - that groups attacked higher amounts of large prey than singles - consequently does not reflect a beneficial expansion in the prey spectrum for groups of *A. ergandros* and *X. bimaculatus*. In *A. socialis*, by contrast, singles seemed to be restricted in their ability to capture large *Acheta* crickets, which were successfully attacked by groups. Still *A. socialis* groups rarely engaged in communal attacks, such that we attribute the captures of large crickets in *A. socialis* groups to the above discussed, passively derived advantages of foraging in groups (i.e. to possible spatial effects and/or local enhancement). Overall, we thus reject that cooperative hunting - to the extent that group members actively work together (Downes 1995) - explains the faster capture of more and larger prey in any of the crab spider groups in our study. Nonetheless, we acknowledge the possibility that group-living crab spiders hunt cooperatively at extreme prey sizes. *A. ergandros*, for example, collectively seizes *Musca domestica* flies of twice its body size (Ruch et al. 2015; Dumke et al. 2016).

Even though communal prey capture was rare in our experiment, group members frequently fed communally on the prey of solo attackers. In first instance, one could presume that this group feeding is the result of intraspecific kleptoparasitism, i.e. that group members competitively attempt to obtain food shares (Brockmann & Barnard 1979; Ward & Enders 1985; Pékar et al. 2005). However, we found in all three species that singles chose small over large prey, while individuals in groups had no preference. This pattern argues against the presumption of intraspecific kleptoparasitism: kleptoparasitic scenarios entail that group members - but not singles – prefer small prey items, since these items are better defendable (Brockmann & Barnard 1979; Packer & Ruttan 1988; Pékar et al. 2005).

In contrary, the pattern that crab spider groups captured greater amounts of large prey than singles could indicate a cooperative behavioral adaptation to group foraging: individuals within groups may more readily attack sharable prey so as to maximize group gain and minimize food competition (Rypstra & Tirey 1991; Pekár et al. 2005). Consistently, non-attacking group members should then also refrain from joining to feed on small prey items (Rypstra & Tirey 1991; Ranta et al. 1993; Pekár et al. 2005). In strong agreement, we found for all three species that group feeding occurred predominantly on large prey. Prey-size selective group feeding appears to be the rule in several group-living species of the web-building *Anelosimus* genus (Rypstra & Tirey 1991; Yip et al. 2008; Guevara et al. 2011).

Finally, we show that group members were differently effective in extracting prey biomass depending on the foraging tactic they employed. In *X. bimaculatus*, producing (i.e. the capture of large prey to be shared) seemed most effective. However, these producer gains are likely to be offset by the costs of energy loss and injury risk producing entails, ultimately resulting in equal payoffs to producing, scrounging and feeding alone (following Pékar et al. 2005). In a previous study, we raised the question of what mechanism constrain scrounging behavior in *X. bimaculatus* (Dumke 2017). To this effect, our present findings indicate that producing, scrounging and feeding alone present stable coexisting, risk-prone and risk-averse foraging strategies in *X. bimaculatus* (Packer & Ruttan 1988; Giraldeau & Caraco 2000).

In *A. ergandros* and potentially *A. socialis*, on the other hand, scrounging individuals most efficiently extracted biomass, suggesting they had preferential access to profitable feeding areas (Pekár et al. 2005) and/or exploited the digestive enzymes of producers (Schneider & Bilde 2008). Since scrounging individuals additionally avoid all hunting costs, their strategy should promise especially high foraging payoffs. This lends great relevance and justification to past and future reserach into the persistence of producers and scroungers in spider groups (Pruitt & Riechert 2009; Dumke et al. 2016).

To our knowledge, none of the here demonstrated group-foraging advantages have formerly been demonstrated in group-living spiders that lack capture webs. In fact, the absence of group-foraging advantages in the web-less but subsocial huntsmen spider *Delena cancerides* has led researchers to hypothesize that in the absence of a communal web, group foraging may not promote group retention (Rowell & Avilés 1995; Yip & Rayor 2011; Avilés & Guevara 2017). By verifying several mechanism and behavioral adaptations by which group-living crab spiders attain reduced food competition in favour of group retention our study refutes this previous assumption.

ACKNOWLEDGEMENTS

We thank our field assistants for their great help with spider collection across Australia: Ina Geedicke, K.J., Giselle Muschett and Pauline Scholzgart. We extend our special thanks to Nicolai J. Tatarnic and Nerida Wilson for their hospitality in Perth, and to Leigh W. Simmons and his lab group for providing lab space, equipment and a social work environment at UWA. For financial support, we acknowledge the Int. Macquarie Research Excellence Scholarship (Australia) and the doctoral scholarship ‘Promotionsförderung’ of the Konrad-Adenauer Foundation (Germany).

REFERENCES

Agnarsson I, Avilés L, Coddington JA, Maddison WP (2006). Sociality in theridiid spiders: repeated origins of an evolutionary dead end. Evolution 60: 2342-2351.

Avilés, L. (1997). Causes and consequences of cooperation and permanent-sociality in spiders. In: Choe JC, Crespi BJ (eds) *The evolution of social behavior in insects and arachnids*. Cambridge University Press: Cambridge, pp. 476-498.

Avilés L, Guevara J (2017). Sociality in spiders. In: Rubenstein DR, Abbott P (eds) *Comparative social evolution*. Cambridge University Press: Cambridge, pp. 188-223.

Bednarz JC (1988). Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). Science 239: 1525.

Brockmann HJ, Barnard C (1979). Kleptoparasitism in birds. Animal Behaviour 27: 487-514.

Brown CR (1988). Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. Animal Behaviour 36: 780-792.

Creel S, Creel NM (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour 50: 1325-1339.

D'Adamo P, Corley J, Sackmann P, Lozada M (2000). Local enhancement in the wasp *Vespula germanica*. Are visual cues all that matter? Insectes Sociaux 47: 289-291.

Downes M (1995). Australasian social spiders: what is meant by “social”? Records of the Western Australian Museum 25.

Duffy JE (1996). Eusociality in a coral-reef shrimp. Nature 381: 512.

Dumke M, Herberstein ME, Schneider JM (2016). Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. Proceedings of the Royal Society of London B: 20160114.

Dumke M (2017). Extended maternal care and offspring interactions in the subsocial Australian crab spider

Xysticus bimaculatus. Australian Journal of Zoology 64: 344-352.

Evans TA (1995). Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. Records of the Western Australian Museum 52: 151-158.

Evans TA (1998). Offspring recognition by mother crab spiders with extreme maternal care. Proceedings of the Royal Society B 265: 129-134.

Evans TA, Main BY (1993). Attraction between social crab spiders: silk pheromones in *Diaea socialis*. Behavioral Ecology 4: 99-105.

Giraldeau L-A, Caraco T (2000). *Social foraging theory*. Princeton University Press: Princeton.

Guevara J, Gonzaga MO, Vasconcellos-Neto J, Avilés L (2011). Sociality and resource use: insights from a community of social spiders in Brazil. Behavioral Ecology 22: 630-638.

Harwood G, Avilés L (2013). Differences in group size and the extent of individual participation in group hunting may contribute to differential prey-size use among social spiders. Biology Letters 9: 20130621.

Hultgren KM, Hurt C, Anker A (2014). Phylogenetic relationships within the snapping shrimp genus *Synalpheus* (Decapoda: Alpheidae). Molecular Phylogenetics and Evolution 77: 116-125.

Jones TC, Parker PG (2000). Costs and benefits of foraging associated with delayed dispersal in the spider *Anelosimus studiosus* (Araneae, Theridiidae). Journal of Arachnology 28: 61-69.

Kim KW, Krafft B, Choe JC (2005). Cooperative prey capture by young subsocial spiders. Behavioral Ecology and Sociobiology 59: 92-100.

Krafft B, Pasquet A (1991). Synchronized and rhythmical activity during the prey capture in the social spider *Anelosimus eximius* (Araneae, Theridiidae). Insectes Sociaux 38: 83-90.

Krause J, Ruxton GD (2002). *Living in groups*. Oxford University Press: Oxford.

Kullmann EJ (1972). Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). The American Zoologist 12: 419-426.

Lubin Y (1974). Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zoological Journal of the Linnean Society 54: 321-339.

Lubin Y, Bilde T (2007). The evolution of sociality in spiders. Advances in the Study of Behavior 37: 83-145.

MacNulty DR, Tallian A, Stahler DR, Smith DW (2014). Influence of group size on the success of wolves hunting bison. Plos One 9: e112884.

Main BY (1988). The biology of a social thomisid spider. In: Austin AD, Heather NW (eds) *Australian arachnology*. Australian Entomological Society: Brisbane, pp 55–73.

Majer M, Svenning J-C, Bilde T (2015). Habitat productivity predicts the global distribution of social spiders. Frontiers in Ecology and Evolution 3: 101.

McCreery HF, Breed M (2014). Cooperative transport in ants: a review of proximate mechanisms. Insectes Sociaux 61: 99-110.

Nentwig W (1985). Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). Behavioral Ecology and Sociobiology 17: 79-85.

Overmyer SL, Jeanne RL (1998). Recruitment to food by the German yellowjacket, *Vespula germanica*. Behavioral Ecology and Sociobiology 42: 17-21.

Packer C, Ruttan L (1988). The evolution of cooperative hunting. The American Naturalist 132: 159-198.

Pasquet A, Krafft B (1992). Cooperation and prey capture efficiency in a social spider, *Anelosimus eximius* (Araneae, Theridiidae). Ethology 90: 121-133.

Pekár S, Brabec M (2016). Marginal models via GLS: a convenient yet neglected tool for the analysis of correlated data in the behavioural sciences. Ethology 122: 621-631.

Pekár S, Hrušková M, Lubin Y (2005). Can solitary spiders (Araneae) cooperate in prey capture? Journal of Animal Ecology 74: 63-70.

Pruitt JN, Riechert SE (2009). Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. Evolution 63: 2966-2973.

Ranta E, Rita H, Lindstrom K (1993). Competition versus cooperation: success of individuals foraging alone and in groups. The American Naturalist 142: 42-58.

Roa R (1992). Design and analysis of multiple-choice feeding-preference experiments. Oecologia 89: 509-515.

Rowell D, Avilés L (1995). Sociality in a bark-dwelling huntsman spider from Australia, *Delena cancerides* Walckenaer (Araneae: Sparassidae). Insectes Sociaux 42: 287-302.

Rubenstein DR (1978). On predation, competition, and the advantages of group living. In: Bateson PPG, Klopfer PH (eds) *Social behavior. Perspectives in ethology, vol. 3*. Springer: Boston, pp 205-231.

Rubenstein DR, Abbot P (2017). *Comparative social evolution*. Cambridge University Press: Cambridge.

Ruch J, Dumke, M, Schneider JM (2015). Social network structure in group-feeding spiders. Behavioral Ecology and Sociobiology 69: 1429-1436.

Ruch J, Herberstein ME, Schneider JM (2014a). Families hunt more successfully: effect of group composition on hunting and communal feeding. Animal Behaviour 91: 171-178.

Ruch J, Riehl T, Michalik P (2014b). Re-description of *Xysticus bimaculatus* L. Koch, 1867 (Araneae, Thomisidae) and characterization of its subsocial lifestyle. ZooKeys 427: 1–19.

Rypstra AL (1989). Foraging success of solitary and aggregated spiders: insights into flock formation. Animal Behaviour 37: 274-281.

Rypstra AL, Tirey RS (1991). Prey size, prey perishability and group foraging in a social spider. Oecologia 86: 25-30.

Schneider J (1995). Survival and growth in groups of a subsocial spider (*Stegodyphus lineatus*). Insectes Sociaux 42: 237-248.

Schneider JM, Bilde T (2008). Benefits of cooperation with genetic kin in a subsocial spider. PNAS 105: 10843-10846.

Szymkowiak P (2014). Revision of Australian species of the genus *Diaea* (Araneae: Thomisidae) with redefinition of their taxonomic status. Annales Zoologici 64: 333-477.

Trumbo St (2012). Patterns of parental care in invertebrates. In. Royle NJ, Smiseth PT, Kölliker M (eds) *The evolution of parental care*. Oxford University Press: Oxford, pp. 81–100.

Uetz GW (1988). Group foraging in colonial web-building spiders. Behavioral Ecology and Sociobiology 22: 265-270.

Uetz GW (1989). The “ricochet effect” and prey capture in colonial spiders. Oecologia 81: 154-159.

Uetz GW (1992). Foraging strategies of spiders. Trends in Ecology & Evolution 7: 155-159.

Vanthournout B, Greve M, Bruun A, Bechsgaard J, Overgaard J, Bilde T (2016). Benefits of group living include increased feeding efficiency and lower mass loss during desiccation in the social and inbreeding spider *Stegodyphus dumicola*. Frontiers in Physiology 7: 18.

Ventura L, Smith DR, Lubin Y (2017). Crowding leads to fitness benefits and reduced dispersal in a colonial spider. Behavioral Ecology 28: 1384-1392.

Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA (1991). Producers, scroungers, and group foraging. The American Naturalist 137: 847-863.

Waite R (1981). Local enhancement for food finding by rooks (Corvus frugilegus) foraging on grassland. Ethology 57: 15-36.

Ward PI, Enders MM (1985). Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. Behaviour 94: 167-182.

Whitehouse MEA, Lubin Y (2005). The functions of societies and the evolution of group living: spider societies as a test case. Biological Reviews 80: 347-361.

Yip EC, Powers KS, Aviles L (2008). Cooperative capture of large prey solves scaling challenge faced by spider societies. PNAS 105: 11818-11822.

Yip EC, Rayor LS (2011). Do social spiders cooperate in predator defense and foraging without a web? Behavioral Ecology and Sociobiology 65: 1935-1947.

Yip EC, Rayor LS (2014). Maternal care and subsocial behaviour in spiders. Biological Reviews 89: 427-449

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Generalised estimation equations. In: *Mixed effects models and extensions in ecology with R*. Springer: New York, p. 246.

CHAPTER 4

Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider

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Published in *Proceedings of the Royal Society of London B* 283: 20160114, doi: 10.1098/rspb.2016.0114
April 2016

Abstract

In groups of socially foraging animals, feeding behaviour may change with group size in response to varying cost-benefit trade-offs. Numerous studies have described group-size effects on group-average feeding behaviour, particularly emphasizing an increase in scrounging incidence for larger groups, where individuals (scroungers) feed from the food sources others (producers) discovered. However, individual variation in feeding behaviour remains unconsidered in the vast majority of these studies even though theoretical models predict individuals to specialize in feeding tactic and anticipate higher scrounger-type frequencies in larger groups. We combined group-level and individual-level analyses of group-size effects on social foraging in the subsocial spider *Australomisidia ergandros*. Lending novel experimental support to model predictions, we found that individuals specialize in feeding tactic and that higher scrounging and lower producing incidence in larger groups were mediated through shifts in the ratio of feeding types. Further, feeding-type specialization was not explained by innate individual differences in hunting ability as all feeding types were equally efficient in prey capture when foraging alone. Context adaptivity of feeding behaviour might allow this subsocial species to succeed under varying socioecological conditions.

Introduction

The ecological determinants of group living fall into two major categories: anti-predator and foraging trade-offs (Alexander 1974; Krause & Ruxton 2002). Individuals in larger groups commonly benefit from a reduced per capita risk of being predated owing to phenomena known as the 'many-eyes hypothesis' or the 'dilution effect' (Krause & Ruxton 2002). Conversely, costs of food competition increase with group size and hence present counteracting selective pressures on group living (Grand & Dill 1999; Giraldeau & Caraco 2000). A negative relationship between group size and foraging is, however, not universal (Shen et al. 2014). In some species, food acquisition can improve with increasing group size owing to cooperation between individuals, thus promoting sociality. This seems to hold true especially for groups of predators that benefit from a reduced per capita cost of attacking and succeed more frequently in subduing prey when hunting in bigger packs (Macdonald 1983; Giraldeau & Caraco 2000). Improved foraging in larger groups has been demonstrated for cooperatively hunting mammals such as African wild dogs (Creel & Creel 1995) and bison-hunting wolves (MacNulty et al. 2014), but also for communally feeding spiders (Whitehouse & Lubin 2005; Yip et al. 2008).

Critically viewed, the above-mentioned studies describe only parts of the biological phenomena influencing group formation as they portray selective pressures on sociality at the level of averaged group-size effects (Sih et al. 2009; Morand-Ferron et al. 2011). However, the payoffs of group living are often not evenly distributed between the members of a social group (Dall et al. 2012). Individuals vary in their average level of behaviour, their 'behavioural type', and given this variation, the impacts of group size probably operate on individual level (Sih et al. 2004). More specifically, a group-size effect, such as improved foraging in larger groups, might result from a shift in the expression or frequency of behavioural types rather than from a uniform behavioural change that all individuals undergo. Therefore, linking group-level and individual-level effects of group size is essential for a comprehensive understanding of the evolutionary processes leading to sociality (Morand-Ferron et al. 2011; Dall et al. 2012; Sih et al. 2012).

Revisiting the relationship between group size and foraging trade-offs from this individual perspective, much of the literature describes a particular intraspecific pattern of behavioural types: the existence of 'producers' and 'scroungers' in groups of socially foraging animals (Barnard & Sibly 1981; Packer & Ruttan 1988; Vickery et al. 1991). Whenever only a few members of the group are necessary to create a collective good, e.g. a food source, individuals may specialize in either producing, where the individual actively acquires the food source, or scrounging, where the individual joins to consume parts of the food source other members acquired (Barnard & Sibly 1981). These producer-scrounger dynamics are presumed to be highly influential on the ecology of group living, as scrounging behaviour can exert a substantial cost on social living (Giraldeau & Caraco 2000).

Producer-scrounger models predict that the proportion of producers and scroungers alters as group size increases, with higher frequencies of scroungers in larger groups (Packer & Ruttan 1988; Vickery et al. 1991). Although the theory of producer-scrounger dynamics is well developed, surprisingly few studies have experimentally tested the influence of group size on feeding behaviour from an individual level (but see Coolen 2002).

Here, we present an experimental approach that combines group-level and individual-level analyses of group-size effects on producer-scrounger dynamics in the subsocial crab spider *Australomisidia ergandros*. These spiders make an excellent model for studying the ecology of social foraging. They naturally occur in groups of varying sizes and feed communally on large insects that only one to a few individuals captured (Ruch et al. 2013; Ruch et al. 2014a), whereby the scene for the emergence of producing and scrounging tendencies is set (Packer & Ruttan 1988). We focused our study on the relationship between group size, group-level effects on social foraging and individual specialization in the three possible feeding tactics: producing, scrounging and feeding alone. Specifically, we tested the model prediction that average feeding behaviour alters with increasing group size, showing higher incidence of scrounging in larger groups. By measuring individual behaviour over repeated trials, we furthermore tested the hypothesis that group-size effects on social foraging are mediated through shifts of behavioural types rather than through uniform behavioural changes of all individuals.

In some social spiders, individual differences in behaviour have been shown to result from innate phenotypic differences, thus persisting across context and subsequently being termed 'animal personalities' (Pruitt et al. 2008). For *A. ergandros* and other subsocial spiders, where group living is temporary (Ruch et al. 2014a; Ruch et al. 2014b), a persistence of the non-attacking scrounger type when not surrounded by group members would pose a substantial disadvantage for survival. We therefore extended our study to the persistence of feeding behaviour in a non-social context and examined innate individual differences in hunting ability as a possible factor explaining individual feeding type.

Material and Methods

Study species

Australomisidia ergandros (former *Diaea ergandros*, revised by Szymkowiak 2014) is an annual, subsocial crab spider inhabiting leaf nests in Eucalyptus trees along the Great Dividing Range from Victoria to Queensland, Australia. Group size within the nests ranges from five to 45 spiderlings (27 ± 10.81, *N* = 39 nests; Ruch et al. 2014a), usually the offspring of one female that provides maternal care by feeding her young (Evans 1998). After the mother's death, the spiderlings continue living jointly until maturation over a time period of five to seven months (Evans 1998; Evans & Goodisman 2002). During this post-maternal social period, they display cooperative behaviour by contributing to nest construction and feeding communally on large prey (Unglaub et al. 2013; Ruch et al. 2014a).

Collection and group establishment

We collected 25 *A. ergandros* nests containing juvenile spiders from Eucalyptus trees between Yass and Murrumbateman, NSW, Australia in February 2015. During that time of year, *A. ergandros spiderlings* are very young (four to six weeks after hatching), and the likelihood of having immigrant spiderlings within the nest is low (Evans & Goodisman 2002). Hence, we can assume that spiderlings from the same nest are related; an essential condition for studying *A. ergandros* feeding interactions as foreign spiderlings affect the group's social foraging structure (Ruch et al. 2015). The nests were removed from their host trees by cutting off supporting branches and were bagged separately for transport to the laboratory at the Macquarie University Sydney in NSW, Australia.

In the laboratory, we dissected the nests and counted the number of spiderlings within. In cases where the number of individuals exceeded 15 (*N* = 16 nests), we visually selected six, ten or 14 similar-sized spiderlings to compose an experimental group. These spiderlings were colour-marked individually (© Plaka Farbe) and jointly transferred into Petri dishes containing Eucalyptus leaves to offer shelter. We chose to create groups as opposed to using natural nests to achieve a sufficient number of replicates for group sizes. We established 15 experimental groups, equally divided over three group-size treatments: small (S) with six individuals, medium (M) with 10 individuals and large (L) with 14 individuals. Petri dish size was chosen depending on group size, with diameters of 80 mm for small, 100 mm for medium and 120 mm for large groups. Likewise, we varied the number of provided Eucalyptus leaves. The specific group sizes and the corresponding Petri dish sizes were chosen in order to optimally standardize spiderling density.

Groups were given a 14 day habituation phase to encourage silk weaving before we tested them in a series of repeated feeding trials. Throughout this phase, the groups were fed a diet of *Drosophila* or *Musca domestica* flies equal to the diet provided during the experiment. In six groups, one spiderling died prior to the start of the trials. Consequently, we redefined group-size treatments as ranges: small with five to six individuals, medium with nine to 10 individuals and large with 13-14 individuals. We excluded groups from the study if they fell out of these ranges over the course of the experiment owing to the death of further spiders. This was the case in one group per treatment.

Communal feeding experiment

To investigate the effect of group size on feeding behaviour and the existence of behavioural types, we assessed each individual's feeding behaviour in 10 consecutive communal feeding trials over 36 days. This duration is equivalent to approximately 10% of *A. ergandros's* lifespan. Every fourth day, the groups were presented with large alive *Drosophila* or *M. domestica* flies to provide the possibility of communal feeding. Testing every fourth day ensured that the groups, which were not fed between the trials, were sufficiently hungry to attack. To homogenize food availability across treatments, small groups were offered one, medium groups two, and large groups three flies. On average, three to four *A. ergandros* spiderlings feed on the captured prey (Ruch et al. 2015). Thus, the feeding possibility f_i per individual and trial, defined as the potentially available feeding spots, hovered around $f_i \approx 0.8$ for all group sizes. Two days after the 10th feeding trial, all individuals were weighted to determine the individual end mass measures (Table 1).

Trials were commenced by placing the adequate number of CO_2-anaesthesized flies into the Petri dishes. After a few seconds, the flies started moving, consequently noted and captured. In each trial, we documented: (i) the ID of the individuals that captured a fly and (ii) the ID of all spiderlings feeding at a fly every 30 min for 3h. Based on this data, we determined a series of feeding parameters describing individual feeding behaviour on its different axes (Table 1).

Single feeding experiment

To test for persistence of individual attacking behaviour across context (following Kralj-Fiser & Schneider 2012) and thereby for innate individual differences in hunting ability, we assessed each spiderling's prey capture performance in a single-feeding experiment after communal feeding trials. We therefore separated all individuals into individual Petri dishes (40 mm diameter) and standardized hunger level by starving the spiderlings for four days. In the subsequent test, we placed a big *Drosophila* fly into each Petri dish and continuously monitored spiderling behaviour for 90 min. We determined each spiderling's attack success (binary: yes/no) and where applicable the attack latency, quantified as the time span from the moment the spiderling oriented itself towards the prey until the successful attack. To approximate food intake rate, calculated as consumed mg per minute, we measured the time each spiderling spent feeding after the attack and weighted the spiderlings before and after the experiment to the fourth decimal with an electronic balance (Mettler Toledo Classic MS).

Data analyses

Statistical analyses were carried out in R (R Core Team 2014). We excluded individuals from the analyses if their feeding time value (Table 1) was below a threshold of 7 (25% quantile of the set of individual feeding time parameters) and therefore, insufficient to reflect feeding type tendency. Owing to this restriction, final sample size comprised $N = 90$ spiderlings ($N_{small} = 16$, $N_{medium} = 31$, $N_{large} = 43$).We analysed the effect of group size on feeding behaviour using binomial generalized estimating equations (GEEs) and fitted an exchangeable correlation structure to the within-group observations. Similar to mixed modelling, GEEs account for dependence in data, but an important difference is that GEEs do not require distributional assumptions, so that potentially misleading estimates through distributional miss-specification can be avoided (Zuur et al. 2009).

Table 1 | Parameters describing individual feeding behaviour in the communal feeding experiment for the subsocial crab spider *Australomisidia ergandros*

Parameter[a]	Definition	Data analyses
Time measurements		
feeding.time	total no. of 30 min intervals the ind. was observed feeding over the 10 trials, $\max_{\text{feeding time}} = 60$ min	group-size effect, cluster differences
produce.time	proportion of feeding time the ind. spent producing (= feeding communally on a self- captured fly)	group-size effect, cluster analysis, cluster differences
alone.time	proportion of feeding time the ind. spent feeding alone (= feeding alone on a self-captured fly)	group-size effect, cluster analysis, cluster differences
scrounge.time	proportion of feeding time the ind. spent scrounging (= feeding communally on a fly others captured)	group-size effect, cluster analysis, cluster differences
Frequency measurements		
feeding.freq	total no. of trials the ind. was observed feeding, $\max_{\text{feeding frequency}} = 10$	cluster differences
produce.freq	proportion of feeding frequency the ind. spent producing	group-size effect, cluster differences
alone.freq.	proportion of feeding frequency the ind. spent feed. alone	group-size effect, cluster differences
scrounge.freq	proportion of feeding frequency the ind. spent scrounging	group-size effect, cluster differences
Mass measurements		
body mass[b]	ind. body mass two days after the 10th trial in mg	group-size effect
mass rank	ranked value of an ind. body mass within its group, divided by the number of group members	group-size effect

[a] all parameters (except feeding time & frequency and body mass) take proportional values to allow for comparison of ind.

[b] measured with the electronic balance Mettler Toledo New Classic MS.

In case of heteroscedasticity, we used generalized least-squares (GLS) and applied the constant variance function varIdent. In separate models, each parameter of interest (Table 1) was treated as the response and group size as the explanatory variable. We added body mass and mass rank as covariates to all our models to factor in possible mass correlated behavioural variation. Model selection was done by stepwise elimination of the least significant predictors and refitting the model until all remaining predictors were significant.

We visually chose similar-sized spiderlings for our experiments as their small size did not allow precise mass determination. However, we do not interpret end mass differences between spiderlings, measured after the communal feeding experiment, as an indicator of fitness differences. End mass variation probably reflects variation that already existed at the start of the experiment but was visually not detectable. This argument is supported by an analysis in which we tested for change in mass rank after communal feeding trials and before single feeding trials (14 days).We found no significant change (paired Wilcoxon signed-rank test, $V = 419.5$, $N = 78$, $P = 0.6466$). Thus, incorporating the mass measurements as co-variates in our models is justified. We do not discuss body mass effects on feeding behaviour here as these will be investigated in a future study with targeted experimental design, where body mass is determined before measuring feeding behaviour.

To establish the existence of behavioural types, we used cluster analysis - a technique that aims at identifying groups of similar elements (here: similarly behaving individuals) in data sets (Halkidi et al. 2001). We applied a fuzzy clustering algorithm with Euclidean distance measure on a set of feeding parameters (Table 1). Group ID was included as a cluster variable to account for group-dependency. Elements clustered via fuzzy algorithms obtain a probability degree of belonging to each cluster rather than getting assigned with a membership level of either 0 or 1 (Halkidi et al. 2001). We selected the fuzzy method over hard clustering, because our data were visually not well separated and thus might be best modelled probabilistically. For cluster validation, we calculated the average silhouette width s, ($-1 < s < 1$), a goodness-of-fit measure of how appropriate the data have been clustered with values close to 1 indicating natural groupings (Rousseeuw 1987; Kaufmann & Rousseeuw 1991). We compared the silhouette width between a clustering into two and a clustering into three clusters, appropriate to the three axes of feeding behaviour, to find the clustering that explained individual variation best.

To characterize the discovered groupings, descriptive statistics of feeding parameters per cluster are given as mean ± SE. To analyse pairwise cluster differences in feeding behaviour, we performed non-parametric Mann-Whitney U-tests as normal distribution of parameters could not be achieved. The effect of group size on behavioural type frequency was analysed based on a contingency table of individual cluster membership per group size using the Freeman-Halton extension of Fisher's exact probability test.

In the analysis of the single feeding experiment, our main interest was the existence of innate individual differences in hunting ability between feeding types. Specifically, we tested whether individuals with scrounging tendencies in the communal feeding experiment showed lower attack tendencies in the single feeding experiment compared with non-scroungers. We used GEEs with scrounger-cluster membership as a predictor, group ID as a grouping variable and attack success or attack latency as the response variable. Individual body mass was included as a covariate. Sample size comprised $N = 78$ individuals as a few spiderlings died between experiments.

Results

Group-level effects

Effect of group size on producing

Group size had a significant effect on the percentage of feeding time individuals spent producing, which generally decreased with increasing group size (Figure 1; Table 2). Large groups spent significantly less of their overall feeding time producing than medium groups (*produce.time* M / L: $\chi^2 = 12.49$, $P = 0.0004$) and tended to spend less than small groups (*produce.time* S / L: $\chi^2 = 2.61$, $P = 0.106$). Hardly any difference existed between small and medium groups (Figure 1). Similarly, individuals in larger groups showed fewer incidences of producing behaviour (*produce.freq* S: 0.35 ± 0.07, M: 0.25 ± 0.03, L: 0.21 ± 0.03), but this effect was not significant (Table 2).

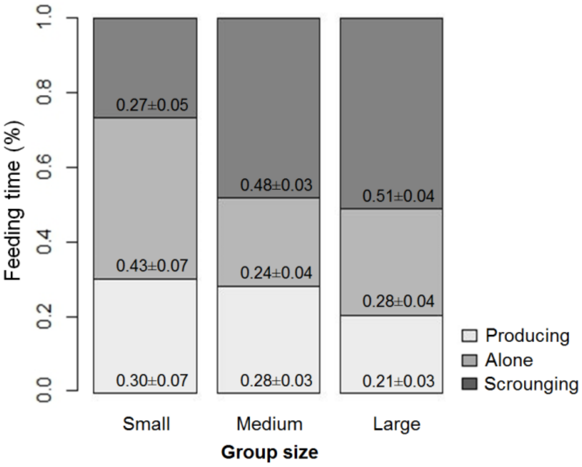

Figure 1 | Stacked percentage bars show the relative difference in the proportion of feeding time spent producing, feeding alone and scrounging (given as mean ± SE) between the group size treatments.

Effect of group size on feeding alone

Group size also affected the spiderlings' tendency to feed alone (Figure 1). While the GEE analysis showed marginal significance in the overall group-size effect on the percentage of feeding time that was spent alone (Table 2), the overall group-size effect on feeding alone frequency was significant (Table 2). Here, individuals in small groups fed alone considerably more often than individuals in medium and in large groups (*alone.freq* S / M: $\chi^2 = 6.78$, $P = 0.0092$; S / L: $\chi^2 = 5.91$, $P = 0.015$), whereas medium groups did not differ significantly from large groups.

Effect of group size on scrounging

As predicted, scrounging behaviour significantly increased with group size (Figure 1; Table 2). Comparing each possible pair of treatments, scrounging was considerably more pronounced in medium groups and large groups - in both time (*scrounge.time* S / M: $\chi^2 = 14.54$, $P = 0.0001$; S / L: $\chi^2 = 21.79$, $P < 0.0001$) and frequency (*scrounge.freq* S / M: $t = 5.56$, $P < 0.0001$; S / L: $t = 4.25$, $P = 0.0001$). Individuals in medium and large groups spent on average twice as much of their feeding time scrounging than individuals in small groups (Figure 1) and the same applies to the scrounging percentage of feeding frequency (*scrounge.freq* S: 0.31 ± 0.05, M: 0.57 ± 0.03, L: 0.59 ± 0.04). Following the general pattern, medium and large groups did not differ in these parameters.

Individual-level effects

Existence of behavioural types

The fuzzy cluster analysis indicated that the variation in individual feeding behaviour was best expressed by three clusters that were clearly separated with cluster-specific silhouette widths close to 1 (Figure 2A). Consequently, the average silhouette width of the overall grouping was $s = 0.628$, indicating high clustering validity. All clusters were well pronounced in terms of their number of members (Figure 2A). These findings suggest the existence of three behavioural types as such a cluster pattern would not emerge if all individuals on average behaved similarly (Kaufmann & Rousseeuw 1991). The characteristics of these behavioural types can be best described with graphical and statistical comparisons of feeding parameter means between the clusters.

In cluster 1, individuals spent more than 50% of their feeding time and feeding frequency producing (Figure 3), thus differing considerably from cluster 2 (*produce.time* c1 / c2: $Z = 5.69$, $P < 0.0001$; *produce.freq* c1 / c2: $Z = 5.39$, $P < 0.0001$) and cluster 3 individuals (pro*duce.time* c1 / c3: $Z = 6.58$, $P < 0.0001$; *produce.freq* c1 / c3: $Z = 6.12$, $P < 0.0001$). By contrast, no significant difference in producing behaviour was found between clusters 2 and 3 (Figure 3).

Cluster 2 stood out from the other clusters in the average tendency to feed alone. Unlike in clusters 1 and 3, feeding alone made up the largest proportion of feeding time and feeding frequency (Figure 3). These differences were significant between clusters 1 and 2 (*alone.time* c1 / c2: $Z = 25.68$, $P < 0.0001$; *alone.freq* c1 / c2: $Z = 25.65$, $P < 0.0001$) and between clusters 2 and 3 (*alone.time* c2 / c3: $Z = 6.42$, $P < 0.0001$; *alone.freq* c2 / c3: $Z = 6.36$, $P < 0.0001$).

In cluster 3, scrounging behaviour accounted for over 60% of feeding time and feeding frequency (Figure 3). These values proved to be significantly higher than in cluster 1 (*scrounge.time* c1 / c3: $Z = 26.57$, $P < 0.0001$; *scrounge.freq* c1 / c3: $Z = 25.38$, $P < 0.0001$) and cluster 2 (*scrounge.time* c2 / c3: $Z = 26.40$, $P < 0.0001$; *scrounge.freq* c2 / c3: $Z = 25.73$, $P < 0.0001$). Cluster 1 and cluster 2 individuals did not differ in scrounging tendency (Figure 3).

Table 2 | Model analyses of group-size effect on social foraging behaviour of the subsocial crab spider *A. ergandros*.

Response	Analysis[a]	Test statistics	*P*-value[b]
produce.time	GEE, binomial error structure, exchangeable correlation	Wald, $\chi^2_2 = 16.49$	**$P = 0.0003$**
produce.freq	GEE, binomial error structure, exchangeable correlation	Wald, $\chi^2_2 = 1.63$	$P = 0.44$
alone.time	GEE, binomial error structure, exchangeable correlation	Wald, $\chi^2_2 = 4.99$	*$P = 0.0830$*
alone.freq	GEE, binomial error structure, exchangeable correlation	Wald, $\chi^2_2 = 7.73$	**$P = 0.0210$**
scrounge.time	GEE, binomial error structure, exchangeable correlation	Wald, $\chi^2_2 = 18.17$	**$P = 0.0001$**
scrounge.freq	GLS, binomial error structure, exchangeable correlation, varIdent for homogeneity	*L*-ratio = 21.41 d.f. = 2	**$P < 0.001$**

We tested for significant differences in different feeding parameters (Table 1) between three group-size treatments: small with five to six individuals, medium with 9-10 individuals and large with 13-14 individuals.

[a] the explanatory variables of all models are group size, body mass and mass rank.

[b] significant *p*-values for the effect of group size are indicated in bold, trends in italic.

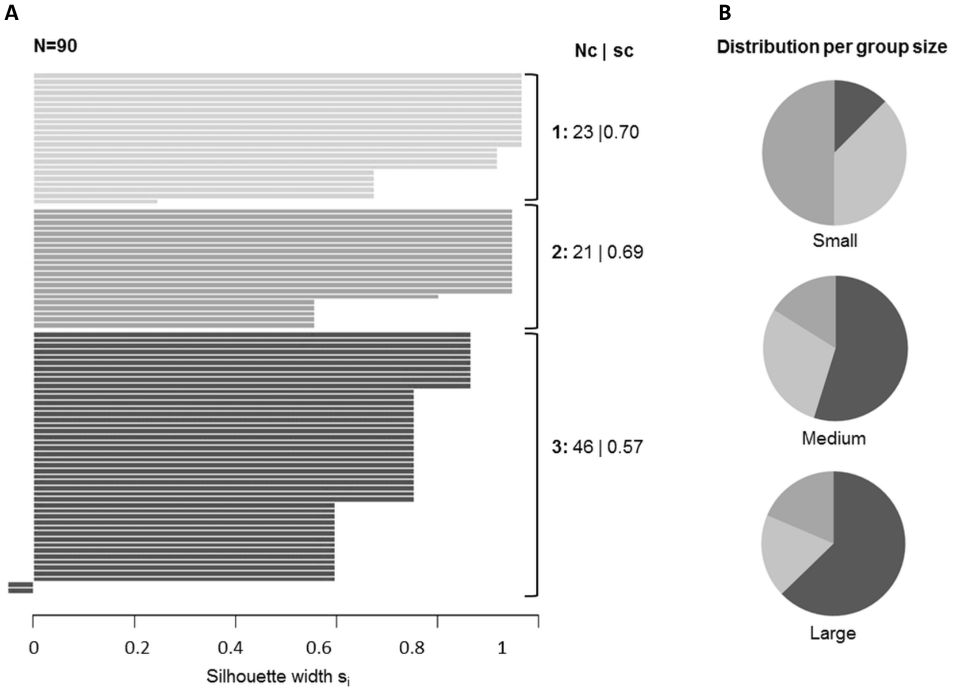

Figure 2 | A: Silhouette plot for cluster validation; it shows how well each individual lies within its assigned cluster. Each grouping of bars represents a cluster, each bar stands for the membership level (s_i) of an individual to its assigned cluster. N_c denotes the number of individuals within the cluster, sc the average silhouette width of the cluster. **:** The pie charts illustrate the percentage of individuals assigned to cluster 1 (light grey), 2 (grey) and 3 (dark grey) per group-size treatment.

Summarizing the results, cluster 1 characterized the expected producer-type and cluster 3 the expected scrounger-type. Cluster 2 individuals represented a third 'loner' behavioural type. The clusters did not differ in absolute feeding time (c1: 18.57 ± 1.44, c2: 17.29 ± 1.53, c3: 18.04 ± 0.8), implying that all behavioural types result in equal success in terms of per capita food availability. In cluster 2, however, absolute feeding frequency (c1: 5.48 ± 0.39, c2: 5 ± 0.37, c3: 6.52 ± 0.25) was notably lower (*feeding.freq* c2 / c3: $Z = 23.55$, $P = 0.0003$). This indicates that loners secure their food share through rarer, but longer feeding events - whereas the opposite applies to scroungers.

Frequency of behavioural types per group size

All three behavioural types were found in any of the group sizes (Figure 2B), but the quantitative ratio altered significantly between group size treatments (Fisher-Freeman-Halton, $P = 0.0058$). In particular, the percentage of producers that a group contained decreased with increasing group size (S: 0.31 ± 0.14, M: 0.28 ± 0.08, L: 0.19 ± 0.02), while the percentage of scroungers increased (S: 0.13 ± 0.08 M: 0.55 ± 0.12, L: 0.63 ± 0.06). In addition, small groups contained proportionally much more loners than the other group size treatments (Figure 2B).

Individual differences in hunting ability

The analysis of feeding behaviour of single spiders did not reveal any difference in hunting ability between spiderlings assigned to the scrounger-type and spiderlings assigned to either one of the two other behavioural clusters, the producer- type and the loner-type. There was no effect of cluster membership on attack success, meaning that scroungers did not attack significantly more or less flies than non-scroungers when facing the fly alone ($\chi^2 = 0.17$, $P = 0.68$). Similarly, no difference was found in the attack latency of scroungers and non-scroungers ($\chi^2 = 0.14$, $P = 0.71$). We therefore extended our GEE analysis to testing for behavioural type differences (scrounger / non-scrounger) in the time until the spiderlings' first attempt to grasp the fly. In the event of a successful attack, we tested for differences in *intake rate* (consumed mg per minute). Consistent with the above results,

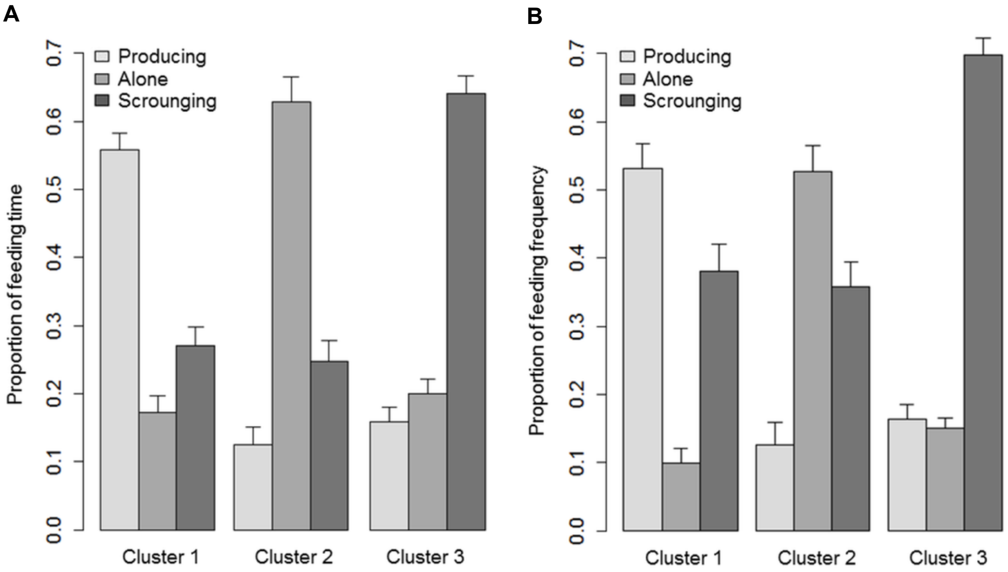

Figure 3 | Barplots describing cluster characteristics. **A:** Barplot A shows differences between the individuals assigned to clusters 1, 2 or 3 in the proportions of feeding time they spent producing, feeding alone and scrounging (time measurements; Table 1). **B:** Analogously, barplot B shows differences in the producing, feeding alone and scrounging proportion of feeding frequency (frequency measurements; Table 1).

scroungers and non-scroungers differed in neither of these two parameters (*time until first attempt*: $\chi^2 = 0.20$, $P = 0.66$; *intake rate*: $\chi^2 = 0.23$, $P = 0.63$).

Discussion

We found that group size significantly affected social foraging behaviour in the communally feeding spider *Australomisidia ergandros*. On group level, scrounging behaviour increased with group size, while producing and feeding alone behaviour decreased. Small groups were especially distinguished by low scrounging and high feeding alone tendencies. Large groups stood out through considerably low producing as well as high scrounging tendencies, whereas medium groups represented an intermediate stage. It has been argued that a positive relationship between group size and scrounger-tactic use corresponds to lower per capita prey density in larger groups, so that scrounging becomes increasingly necessary to obtain sufficient food (Coolen 2002). Here, however, scrounging increased with group size, irrespective of this pressure as we experimentally controlled for it. Independence between scrounging and prey density was also found in nutmeg mannikins (*Lonchura punctulata*; Coolen 2002). Therefore, scrounging incidence might be primarily influenced by other group-size-dependent factors.

In isolation, the above findings do not allow for individual-level interpretations as they portrait group-average changes in social foraging behaviour (Sih et al. 2009). However, group members could still diverge substantially in feeding tactic preference (Sih et al. 2004; Dall et al. 2012, Sih et al. 2012). We investigated individual-level effects and found strong evidence for the stable coexistence of three alternative feeding types: producers, loners and scroungers. Although all feeding types were present in all group sizes, their frequency altered with group size concurring with the group-level effects on feeding behaviour. This implies that the impacts of group size on social foraging operate on an individual-specific level in this subsocial spider, with group size influencing the ratio of behavioural types within the group.

Our study thus provides novel experimental support for predictions of producer-scrounger models by Packer & Ruttan (1988) and Vickery et al. (1991), which presume individuals to specialize in feeding tactic and anticipate higher scrounger-type frequencies in larger groups. Further, our results support the existence of 'loners', matching Packer & Ruttan's (1988) expectation of a solitary feeding type within foraging societies. In agreement with these models, laboratory research showed that nutmeg mannikins (*L. punctulata*) specialize in feeding tactics and increase their use of the scrounger tactic with group size (Coolen et al. 2001; Coolen 2002) but group-size dependency in the mix of behavioural types was not directly investigated.

Outside the context of social foraging, the finding that behavioural type ratio alters with group size is not entirely new. In Scottish blackface sheep (*Ovis aries*), where individuals display variability along the bold-shy continuum, behavioural type positively influences an individual's propensity to move away from conspecifics. Bold sheep leave at smaller group sizes than shy sheep and hence, larger foraging groups feature a higher frequency of the shy behavioural type (Michelena et al. 2009). Moreover, Pruitt & Riechert (2009) reported a positive association between colony size and frequency of an aggressive, 'asocial' phenotype in the socially polymorphic spider *Anelosimus studiosus*. However, their results suggest that the greater proportion of asocial spiders increases capture success (Pruitt &Riechert 2011) and thus, a scrounging tendency of the asocial phenotype seems unlikely.

It has been proposed that individuals within foraging societies choose feeding tactic depending on predation risk, feeding efficiency and/or individual phenotypic differences (Barnard & Sibly 1981; Barta & Giraldeau 1998; Anders 2001). Our experimental groups were not exposed to predation risk but scrounger-type frequency still increased with group size. However, we cannot neglect a possible impact of predation risk on scrounging. Predation risk has been shown to affect scrounger-tactic use in multiple bird species (Barta et al. 2004) and is assumed to be group-size-dependent in group-living spiders (Yip et al. 2008; Unglaub et al. 2013). Testing the effect of predator presence on behavioural-type frequency across group sizes *in A. ergandros* would be an interesting extension to the research presented here.

Improved feeding efficiency probably explains the increase in scrounger-type frequency found in this study. In this context, Packer &Ruttan (1988) propose that the advantage of avoiding the costs of attacking outweighs the improvement in food acquisition through producing behaviour as group size increases. Consequently, in larger groups, proportionally more individuals can benefit from the costly prey capture of a few producers and the group's feeding efficiency is enhanced (also discussed in Rypstra 1993). In line with the theory, we found that both the percentage of feeding time spent producing and the producer-type frequency declined with larger group size. We could not provide a measure of average feeding efficiency (such as mean individual weight gain) for different group sizes. However, a recent study of group size and predation risk in *A. ergandros* by Unglaub et al. (2013) further supports feeding efficiency as the likely mechanism influencing the scrounger-type frequency. In that study, larger groups comprising 10 and 25 individuals were found to grow better than smaller groups irrespective of predator presence.

This gives rise to the idea of 'beneficial scrounging' as a factor promoting group living. Such dynamics, however, can only be stable as long as prey biomass is sufficient to saturate all feeding individuals (Packer & Ruttan 1988; Rypstra 1993). The number of communal feeders exceeding this equilibrium is presumably higher than the group sizes investigated in Unglaub et al. (2013) and in this study. For even larger group sizes, scrounging might become increasingly costly, so that the scrounger-type frequency would again decline (Giraldeau & Caraco 2000). Accordingly, research on African subsocial and social spiders reports negative effects of group size on feeding efficiency (Whitehouse & Lubin 1999; Ruch et al. 2009).

Our finding that all behavioural types were present in all group sizes further points to the relevance of a factor besides feeding efficiency, that specifically influences which individuals specialize in producing or feeding alone even when scrounging would be equally (or more) efficient. For social spiders, it has been suggested that individuals tend to be scroungers when they are larger than the group average and thus unlikely to be hindered (Ward 1986). Alternatively, we argue that the costs of the producer-tactic are lower for larger individuals because they need to invest proportionally less venom to subdue the prey (Foelix 2010). Hence, the threshold to attack might be lower in larger individuals, which may drive producing tendencies. The solitary feeding type is unlikely to be an artefact of 'loners' compulsorily monopolizing a fly because most other group members already feed on another. The highest loner-frequency was found in small groups, which received only one fly. This indicates a group size effect on the threshold to feed alone. Response-threshold variation is believed to promote task differentiation in insect societies and can be mediated by morphological size differences as well as group size (Duarte et al. 2011; Dall et al. 2012).

Possibly consistent with the above assumptions, Ruch et al. (2015) reported that body mass relative to group members influenced feeding interactions in *A. ergandros* groups, with small and large individuals being more involved in communal feeding events than medium-sized spiders. The individuals tested in our study also differed in body mass, at least as measured at the end of the communal feeding trials, but our experimental design did not allow for a specific analysis of body mass effects on social foraging. Relative body mass is therefore a likely predictor of an individual's feeding type in this system and should be investigated in a subsequent study.

We found no evidence for innate individual differences in hunting ability, which thus cannot explain the existence of different individual feeding types. On their own, all individuals were equally efficient and likely to attack prey. Based on this result, we further disfavor considering feeding types as behavioural expressions of personalities in *A. ergandros*. The personality definition demands behavioural consistency in time and context (Pruitt et al. 2008), but although we found individual feeding behaviour to be temporally stable, scrounger attacking behaviour did not persist across context. Our individual- level results from the communal feeding trials underline this assertion, as individuals assigned to a certain feeding type did not exclusively produce, feed alone or scrounge. From an ecological and evolutionary perspective, context-adaptivity of feeding behaviour makes sense in the light of the life history of a subsocial spider where, after adulthood dispersal, individuals depend on procuring food for themselves or in the case of females for their offspring (Whitehouse & Lubin 2005).

Conclusion

The subsocial crab spider *A. ergandros* shows behavioural specialization and between-individual polymorphism in feeding tactic use. Group-size effects on social foraging, such as for example higher scrounging and lower producing incidence in larger groups, are explained on this individual level, being mediated through ratio shifts of feeding types. We thus give first experimental evidence in accordance with established individual-level predictions from producer- scrounger models. We suggest that feeding efficiency is a likely ecological determinant of feeding-type ratio and that an individual's feeding type may further depend on body size differences between group members. In this context, relative body size variation may correlate with attack-threshold variation, driving feeding type polymorphism. The flexibility of feeding behaviour under novel, non-social conditions stands in line with these assumptions and may further be evolutionary adaptive, allowing individuals to succeed under different socioecological conditions.

ACKNOWLEDGEMENTS

M.D. is supported by a PhD scholarship of the Konrad-Adenauer Foundation. We thank K.J. for help with spider collection. Moreover, we thank Jasmin Ruch for sharing her knowledge on *A. ergandros* as well as for helpful advice concerning the study design.

REFERENCES

Alexander RD (1974). The evolution of social behavior. Annual Review of Ecology, Evolution, and Systematics 5: 325-383.

Anders NP (2001). Predator behaviour and prey density: evaluating density-dependent intraspecific interactions on predator functional responses. Journal of Animal Ecology 70: 14-19.

Barnard CJ, Sibly RM (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29: 543-550.

Barta Z, Giraldeau L-A (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. Behavioral Ecology and Sociobiology 42: 217-223.

Barta Z, Liker A, Monus F (2004). The effects of predation risk on the use of social foraging tactics. Animal Behaviour 67: 301-308.

Coolen I, Giraldeau LA, Lavoie M (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Animal Behaviour 61: 895-903.

Coolen I (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in Nutmeg Mannikins (*Lonchura punctulata*). Behavioral Ecology and Sociobiology 52: 232-238.

Creel S, Creel NM (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour 50: 1325-1339.

Dall SRX, Bell AM, Bolnick DI, Ratnieks FLW (2012). An evolutionary ecology of individual differences. Ecology Letters 15:1189-1198. 14.

Duarte A, Weissing FJ, Pen I, Keller L (2011). An evolutionary perspective on self-organized division of labor in social insects. Annual Review of Ecology, Evolution, and Systematics 42: 91-110.

Evans TA (1998). Offspring recognition by mother crab spiders with extreme maternal care. Proceedings of the Royal Society of London B 265: 129-134.

Evans TA, Goodisman MA (2002). Nestmate relatedness and population genetic structure of the Australian social crab spider *Diaea ergandros* (Araneae: Thomisidae). Molecular ecology 11: 2307-2316.

Foelix R (2010) *Biology of spiders*. Oxford University Press: New York, pp. 88-217.

Giraldeau L-A, Caraco T (2000) *Social foraging theory*. Princeton University Press: Princeton, pp. 51-196.

Grand TC, Dill LM (1999). The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? Animal Behaviour 58: 443-451.

Halkidi M, Batistakis Y, Vazirgiannis M (2001). On clustering validation techniques. Journal of Intelligent Information Systems 17: 107-145.

Kaufman L, Rousseeuw PJ (1991) *Finding groups in data: an introduction to cluster analysis*. John Wiley & Sons: Hoboken, pp. 64-198.

Kralj-Fiser S, Schneider JM (2012) Individual behavioural consistency and plasticity in an urban spider. Animal Behaviour 84: 1-8.

Krause J, Ruxton GD (2002). *Living in groups*. Oxford University Press: New York, pp. 6-54.

Macdonald DW (1983) The ecology of carnivore social behaviour. Nature 301: 379-384.

MacNulty DR, Tallian A, Stahler DR, Smith DW (2014). Influence of group size on the success of wolves hunting bison. PLos ONE 9: e0112884.

Michelena P, Sibbald AM, Erhard HW, McLeod JE (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. Behavioral Ecology 20: 145-152.

Morand-Ferron J, Wu G-M, Giraldeau L-A (2011). Persistent individual differences in tactic use in a producer-scrounger game are group dependent. Animal Behaviour 82: 811-816.

Packer C, Ruttan L (1988). The Evolution of cooperative hunting. The American Naturalist 132: 159-198.

Pruitt JN, Riechert SE, Jones TC (2008). Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. Animal Behaviour 76: 871-879.

Pruitt JN, Riechert SE (2009). Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. Evolution 63: 2966-2973.

Pruitt JN, Riechert SE (2011). How within-group behavioural variation and task efficiency enhance fitness in a social group. Proceedings of the Royal Society of London B 278: 1209-1215.

Rousseeuw PJ (1987) Silhouettes: a graphical aid to the interpretation and validation of cluster-analysis. Journal of Computational and Applied Mathematics 20: 53-65.

Ruch J, Heinrich L, Bilde T, Schneider JM (2009). The evolution of social inbreeding mating systems in spiders: limited male mating dispersal and lack of pre-copulatory inbreeding avoidance in a subsocial predecessor. Biological Journal of the Linnean Society 98: 851-859.

Ruch J, Herberstein, ME, Schneider JM (2014a). Families hunt more successfully: effect of group composition on hunting and communal feeding. Animal Behaviour 91: 171-178.

Ruch J, Herberstein ME, Schneider JM (2014b). Offspring dynamics affect food provisioning, growth and mortality in a brood-caring spider. Proceedings of the Royal Society of London B 281: 20132180.

Ruch J, Dumke M, Schneider JM (2015). Social network structure in group-feeding spiders. Behavioral Ecology and Sociobiology 69: 1429-1436.

Rypstra AL (1993) Prey size, social competition, and the development of reproductive division of labor in social spider groups. The American Naturalist 142: 868-880.

Shen S-F, Akcay E, Rubenstein DR (2014) Group size and social conflict in complex societies. The American Naturalist 183: 301-310.

Sih A, Bell A, Johnson JC (2004) Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19: 372-378.

Sih A, Hanser SF, McHugh KA (2009) Social network theory: new insights and issues for behavioral ecologists. Behavioral ecology and sociobiology 63: 975-988.

Sih A, Cote J, Evans M, Fogarty S, Pruitt J (2012). Ecological implications of behavioural syndromes. Ecology Letters 15: 278-289.

Szymkowiak P (2014). Revision of Australian species of the genus *Diaea* (Araneae: Thomisidae) with redefinition of their taxonomic status. Annales Zoologici 64: 333-477.

Unglaub B, Ruch J, Herberstein ME, Schneider JM (2013). Hunted hunters? Effect of group size on predation risk and growth in the Australian subsocial crab spider

Diaea ergandros. Behavioral Ecology and Sociobiology 67: 785-794.

Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA (1991). Producers, scroungers, and group foraging. The American Naturalist 137: 847-863.

Ward PI (1986) Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. Behaviour 97: 213-225.

Whitehouse MEA, Lubin Y (1999) Competitive foraging in the social spider *Stegodyphus dumicola*. Animal Behaviour 58: 677-688.

Whitehouse ME & Lubin Y (2005). The functions of societies and the evolution of group living: spider societies as a test case. Biological Reviews 80: 347-361.

Yip EC, Powers KS, Aviles L (2008). Cooperative capture of large prey solves scaling challenge faced by spider societies. PNAS 105: 11818-11822.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer Press: New York, pp. 295-342.

CHAPTER 5

Stable cooperation among social predators: female defectors are outplayed by male providers

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Submitted

Abstract

Cooperation is highly susceptible to the invasion of ‘defectors’, but nonetheless persists in numerous societies from microbes to humans. To explain cooperation stability despite defection, theoretical models often assume conditional tactic use (i.e. individuals cooperate conditional upon the cooperation of others). We employed social foraging theory to propose an alternative scenario, where unconditional cooperators (producers) outplay defectors (scroungers) ‘by default’. For socially foraging predators, we assume that cooperators and defectors differ consistently in their cooperative tendency to acquire and offer prey – but not in their competitive ability to obtain prey shares. Provided that the frequency of defectors fluctuates over lifetime, we consequently predict that cooperators overall reap exceptional payoffs: when defectors are frequent, defectors must compete over the rarely offered food, such that cooperators reap higher payoffs - and when cooperators are frequent, cooperators likely reap similar payoffs than defectors, as they likely take food offers before having paid the costs of cooperating (i.e. the costs of prey capture). We empirically tested our assumption on the characterising behavioral tendencies of cooperators and defectors in the sub-social crab spider *Australomisidia ergandros*, where groups contain ‘producer’-individuals and ‘scrounger’-individuals. Between homogeneous groups of producers or scroungers only, we compared foraging behavior, and also fitness payoffs, over several weeks. In validation of our assumption, scroungers among their peers hesitantly attacked and did not offer prey - thus suffering weight loss and mortality - whereas producers regularly shared prey in groups of their own. With social network analysis, we further investigated the proximate determinants of the demonstrated feeding- type characteristics in *A. ergandros*. Remarkably, we found that males were significantly more cooperative than females.

Introduction

Animals that forage in groups can benefit substantially from the pooling of individual efforts to obtain food resources. In non-predatory foragers, grouping increases feeding efficiency as group members share information about the location and quality of food patches (Barnard & Sibly 1981; Clark & Mangel 1984; Giraldeau & Caraco 2000) and in predatory foragers, individuals accomplish greater foraging success when hunting together (Malcolm & Marten 1982; Heinsohn & Packer 1995). Either way, social foraging is beneficial because the food acquisitions by some lead to the feeding of many, so that the per-capita feeding rates are maximized at minimal per-capita costs (Vickery et al. 1991; Giraldeau & Caraco 2000). By satisfying this norm, social foraging qualifies as cooperation (Nowak 2006).

Possible mechanisms driving the evolution of (foraging) cooperation include reciprocity and kin selection (Hamilton 1964; Trivers 1971; West et al. 2007; Taborsky 2013). Under reciprocity, individuals cooperate conditionally - meaning they cooperate dependent on the cooperative behavior previously exercised by others - and thereby as a function of the likelihood to receive a direct benefit (i.e. the return favor; Taborsky 2013). Cooperation evolves in a positive feedback loop ('a cooperation for a cooperation for a cooperation…') of these direct benefits (Trivers 1971; Nowak & Sigmund 2005). Under kin selection, individuals receive indirect benefits from helping relatives in addition to possible direct benefits (inclusive fitness; Hamilton 1964). Cooperation under kin selection evolves once the inclusive benefits exceed the costs of cooperating (Hamilton 1964; Nowak 2006; West et al. 2007).

Fundamental rules of Darwinian selection, however, leave the maintenance of cooperation highly exposed to the invasion of exploitative behavior (Nowak et al. 1994; Doebeli & Hauert 2005; Imhof et al. 2005; Nowak 2006). As emphasized by game theory (e.g. in the prisoner's dilemma or the snowdrift game), individuals facing cooperation will reap the highest payoffs by defecting (Dawes 1980; Doebeli & Hauert 2005; Imhof et al. 2005), that is foregoing the costs of cooperating but still receiving the benefits of being helped. In consequence, selection should lead to a spread of defectors within social groups. Strikingly, the rise of defection will promote even more defection ('a defection for a defection for a defection…') in reciprocal systems (Nowak & Sigmund 1992). In kin-selected systems, this downtrend may be buffered by the additional indirect benefits from helping relatives, but it would require an unnaturally high degree of relatedness to compensate for sheer defection (Griffin & West 2002).

Significant scientific attention has been devoted to understanding how cooperation is maintained despite this susceptibility to defection (Frank 1995; Egas & Riedl 2008; Boyd et al. 2010; Krams et al. 2013; McNamara & Doodson 2015). Yet, although nature provides numerous examples of cooperative systems, the evolutionary scenarios leading to stable cooperation have mostly been studied in theoretical models (Dugatkin 1997; Doebeli & Hauert 2005; Pruitt & Riechert 2009).

In the context of social foraging, producer-scrounger-models serve this purpose. Producing refers to the cooperative behavior of acquiring food that is shared, whereas scrounging means the defective behavior of exploiting others' food acquisitions (Barnard & Sibly 1981). Given that individuals specialize in one of these foraging tactics (e.g. due to phenotypic differences; Vickery et al. 1991), the spread of scroungers is predicted to be constrained by negative-frequency dependent selection: if scroungers become increasingly frequent, producers will reap higher payoffs (despite the costs of acquiring food) because scroungers must compete over the acquired food (Vickery et al. 1991; Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000).

Conversely, if producers become increasingly frequent, scroungers will reap higher payoffs because they avoid the costs of acquiring food at low competition (Vickery et al. 1991; Giraldeau & Beauchamp 1999; Giraldeau & Caraco 2000). This frequency-dependence in payoffs will maintain the coexistence of producers and scroungers, and will thus maintain cooperation in social foraging groups. The course of the above dynamics can be traced in a function graph of the per capita payoffs to producers (cooperators) and scroungers (defectors) relative to the frequency of defectors in the social foraging group (Figure 1A; based on Giraldeau and Beauchamp 1999).

From a game-theoretical viewpoint, the situation between socially foraging cooperators and defectors at a given feeding event resembles an *N* person snowdrift game (Doebeli & Hauert 2005; Santos et al. 2012). In this game, cooperating confers a benefit to the cooperator even when all other group members defect (Santos et al. 2012). Defecting when all others defect instead confers zero benefits to every group member (Doebeli & Hauert 2005). Correspondingly, acquiring food confers the 'finder's share' (Vickery et al. 1991) to the socially foraging cooperator among defectors, who would starve in the absence of cooperators.

Importantly, the snowdrift game emphasizes that individuals should ideally apply a conditional policy, inverse to that of reciprocally cooperative systems: 'defect if others are likely to cooperate, but cooperate if others are likely to defect' (after Doebeli & Hauert 2005; Santos et al. 2012). Such conditional tactic use would outplay pure tactics provided that the frequency of defectors fluctuates over repeated feeding events (Vickery et al. 1991): while cooperators would reap higher payoffs than defectors at those times where defectors are frequent and vice versa, 'conditional' individuals would reap the higher payoffs at any time and defector frequency. In sum, they would achieve greater fitness (cf. respective upper curves in Figure 1A). In contrast to the frequency-dependent scenario predicted by producer-scrounger-models, conditional tactic use can prevent the evolutionary spread of defectors altogether, creating entirely stable levels of cooperation.

In social foraging groups, fluctuations in the frequency of defectors are not unusual. Fission-fusion dynamics and predation- or age-related mortality alter group composition over lifetime, setting the stage for the emergence of conditional tactic use (Heinsohn & Packer 1995; Couzin 2006). Obstructively, however, conditional foraging tactic use is thought to require advanced social cognition: the ability to perceive, memorize and strategize based on information about the previous social interactions in the group (Nowak et al. 1994). For that reason, conditionality in foraging behavior is considered to be rather unlikely (Nowak et al. 1994; Nowak & Sigmund 2005; but see Rutte & Taborsky 2008; Morand-Ferron et al. 2011).

In respect of the above, we here model an alternative, non-cognitive scenario that may create entirely stable levels of cooperation in socially foraging predators. In this scenario, cooperators outplay defectors - albeit being specialized and not applying a conditional policy. Inspired by earlier experimental observations (Barnard & Sibly 1981; Pruitt & Riechert 2009; Dumke et al. 2016), we assume that socially foraging cooperators and defectors differ in their tendencies to (i) acquire and (ii) intentionally offer food (their cooperative tendency) but are similar in their ability to feed on food acquired and offered by others (their competitive ability).

At times when defectors are frequent, we then conventionally expect defectors to compete over the few food sources acquired and offered by the cooperators, such that cooperators obtain higher payoffs. At times when defectors are amongst themselves, we even expect that food is not acquired or offered at all, such that defectors reap zero payoffs (Figure 1A & B). At times when cooperators are frequent, on the other hand, we expect all cooperators to attempt to acquire food until one to a few cooperators are successful. Thereupon, we expect the remaining cooperators to feed on the food offered by the successful.

In non-predatory foragers where the crucial costs of cooperating arise from the search for food (Barnard & Sibly 1981; Clark & Mangel 1984; Morand-Ferron et al. 2011), this makes no difference: cooperators will have paid the crucial costs of cooperating anyway, and will still reap much lower payoffs than defectors (Figure 1A). In predatory foragers, however, those cooperators that feed on food offered by others will not have paid the crucial costs of cooperating, which arise from capturing and killing the prey (Packer & Ruttan 1988; Heinsohn & Packer 1995; Dumke et al. 2016). It follows that, at times when they are

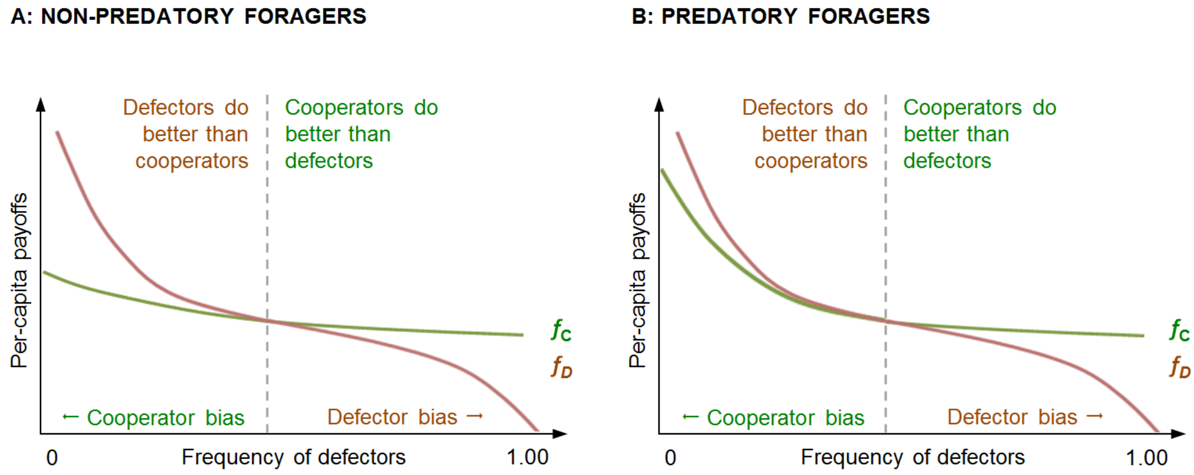

Figure 1 | The per-capita payoffs to specialized cooperators and defectors in relation to the defector-frequency in social foraging groups at a given feeding event. The model is based on Giraldeau & Beauchamp (1999). **A**: The per-capita payoffs to cooperators (green curve fc) and defectors (brown curve fd) relative to the frequency of defectors in non-predatory foragers. The frequency of defectors (x-axis) is expressed as a decimal percentage. The per-capita payoffs to cooperators remain stable across different defector-frequencies because cooperators always pay the crucial costs of cooperating. The per-capita payoffs to defectors decrease with increasing defector-frequency because of increasing competition. **B**: The per-capita payoffs to cooperators (f_c) and defectors (f_d) in predatory foragers. The per-capita payoffs to defectors are as in A, but the per-capita payoffs to cooperators increase with decreasing defector-frequency, approaching the per-capita payoffs to defectors. This is because cooperators are increasingly likely to 'miss' the crucial costs of killing the prey, while being able to feed on it. Given fluctuating defector-frequencies, the advantage to cooperators is in sum larger than the advantage to defectors.

frequent, cooperators are likely to reap similar payoffs than defectors (Figure 1B).

In mathematical terms, our scenario predicts that the per-capita costs for unconditional cooperators in social predators are negatively frequency dependent (and not as usually assumed constant): the more cooperators, the lower the probability for one to actually pay the cost of cooperating. This dynamic significantly increases the per-capita payoff to cooperators at times when cooperators are frequent, thus diminishing the advantage of defectors (Figure 1B). Given fluctuating frequencies of defectors over repeated feeding events, cooperators will in sum achieve greater fitness, just like 'conditional' individuals would have had. In terms of evolutionary selection, cooperators will outplay defectors - even though acting purely upon intrinsic tendencies.

For empirical support, we tested our model assumption about the characteristic behavioral tendencies of foraging cooperators and defectors in the group-hunting crab spider *Australomisidia ergandros*. Individuals of this species specialize in foraging tactic at stable group compositions: producers (i.e. cooperators) mostly capture prey that is shared, and scroungers (i.e. defectors) mostly feed on prey captured by others (Dumke et al. 2016). In an initial laboratory experiment, we determined the feeding types of *A. ergandros* individuals in field-collected kin groups. Subsequently, we manipulated group composition by composing kin groups with scrounger frequencies of zero or one (producer-groups and scrounger-groups). We then explored the effect of group composition on social foraging behavior and individual fitness payoffs in repeated feeding trials.

If producers and scroungers in *A. ergandros* differed solely in their cooperative tendency - i.e. if producers had a stronger tendency to (i) acquire and (ii) intentionally offer prey - we expected (i) attacking behavior to be more pronounced and (ii) prey sharing to be greater in producer-groups than in scrounger-groups. The latter finding would also validate the assumption that producers are well able to feed on prey acquired and offered by others. We furthermore predicted greater fitness payoffs for producer-group members compared to scrounger-group members. This finding would confirm the assumption of unconditional and consistent tactic use, and it would support the model prediction of a grave difference in the payoffs to cooperators amongst themselves versus defectors amongst themselves (cf. Figure 1A & B).

In the event that cooperators achieve greater fitness than defectors, the logical question arises as to why defectors persist at all. One possible explanation might be that defecting is proximately coupled with phenotypic traits that are subject to positive selection. In pursuit of this approach, we examined possible proximate causes of feeding type variation in *A. ergandros* (Morand-Ferron et al. 2011; Dumke et al. 2016). Explicitly, we applied network analysis to social foraging to test for sex differences in the individual tendency to produce.

Methods

Group composition effects

Australomisidia ergandros communally inhabits leaf nests on Eucalyptus trees throughout South-Eastern Australia. Nest groups comprise the offspring of a single female, which founds and then expands the nest over a period of extended maternal care until her death (Ruch et al. 2014b). We collected 29 A. *ergandros* nests from a population along Yass River Road in New South Wales, Australia (34°55'20.50''S, 149°6'15.53''E) in February 2016. At this time of year, the spiderlings are very young and the presence of immigrants, who may negatively influence the extent of social foraging, is improbable (Ruch et al. 2014a; Ruch et al. 2015). For our experiments, we transferred the original nests to the laboratory at Macquarie University in Sydney.

To investigate group composition effects, we first assessed the feeding types of individuals within 'initial' groups (phase 1) and subsequently composed and tested 'sorted' groups of producers or scroungers only (phase 2). The formation of the initial groups was dictated by special requirements (Supp. information S1, S2). Basically, we randomly selected up to 30 individuals per original nest and split these individuals into two to three initial groups of ten ($N_{\text{nests}} = 10$, $N_{\text{groups}} = 25$). Each selected individual received a unique color mark (© Plaka-Farbe) and was weighed to the nearest 0.01 mg on an electronic balance (Mettler Toledo New Classic MS). Each group was then transferred to a petri dish of 100 mm diameter: the test arena for the feeding-type assessment. An acclimation period of four days ensured that the spiders weaved silk threads (which amplify vibrations by prey) but were not food-deprived to an extent where cannibalism occurs (Evans 1999).

Phase 1

We assessed feeding types with a modified version of the 'communal feeding experiment' originally used by Dumke et al. (2016) to establish feeding tactic specialization in *A. ergandros*. For each initial group, we completed a series of trials, in which we offered living *Musca domestica* flies and observed the foraging behavior of every group member (details in Dumke et al. 2016). We extended the three-day time span between trials by one day to increase the probability of attacks. However, we limited the number of trials per group to seven to keep the data manageable for the quantification of feeding types within the two days before individuals were regrouped.

Each fly was weighed before being placed into the petri dish and either removed after two hours if not captured, or after two hours post capture. Per trial and group, we documented the attack latency, the attacker IDs and the IDs of the feeding individuals in 10 minute intervals over three hours. From these data, we then determined the feeding frequency of each individual (i.e. the number of trials it was feeding) and calculated the proportions to which it produced and scrounged. We thus obtained comparable quantifications of feeding-type tendencies (Dumke et al. 2016). All individuals except those that died during the assessment (56 of 250 ind.) were weighed two days after the last trial to assess *weight gain*$_1$ (= log (*end weight*/*start weight*) after Crawley 2007).

Phase 2

Following phase 1, we regrouped individuals into 'sorted' groups of producers or scroungers only. Producer-groups were formed by selecting the nine to ten individuals with the highest producing tendencies from the pool of individuals per original nest. Scrounger-groups were formed analogously from that same pool (S1). Thus, we achieved paired relatedness between producer-groups and scrounger-groups, so as to control for nest origin and nest experience (matched pairs design; Heath 2002). We further warranted comparability of producer-groups and scrounger-groups in the individuals' physical state (details in S2). Owing to mortality (in three nests) or restricted possibilities to ensure balanced conditions between groups (in two nests), we could establish five producer-scrounger group pairs with nine individuals per group.

To explore group composition effects on social foraging behavior and individual fitness payoffs, we tested each sorted group over another seven feeding trials. The trials were conducted in the same manner as for the feeding type assessment. From the recorded data (attack latency, IDs of attackers, IDs of feeding individuals), we calculated a set of variables that quantified social foraging behavior (data points per trial and group; Table 1). To examine individual fitness payoffs, we checked the petri dishes for dead individuals and noted their identity prior to every trial. As an additional fitness payoff measure for those individuals still alive at the end of phase 2, we determined individual *weight gain*$_2$ (= log(*end weight*$_2$/*start weight*$_2$)).

Sex differences

To examine sex differences, we collected another eight nests from Yass River Road in June 2016. Around this time, *A. ergandros* individuals reach the subadult stage, at which sex can be visually determined (Evans 2000). Three nests contained subadult males and females in sufficient numbers, so that we formed three groups of each ten males and ten females from the same natal nest (in total: $N_{\mathrm{males}} = 30$, $N_{\mathrm{females}} = 30$). All group members were weighed and color marked before they were tested in another, extended feeding type assessment over ten trials.

Based on the IDs of attackers and feeding individuals recorded in these trials, we generated social network graphs that visualized the foraging interactions within the groups (Croft et al. 2008; Farine & Whitehead 2015; Ruch et al. 2015): individuals were represented by 'nodes'; a directed line ('edge') was drawn from one node to another if the specific individual had produced for the other. The lines received weights reflecting the frequency of the respective interaction. We quantified individual producing tendencies using the node-level metric *out-strength*: the weight sum of all outgoing edges from a particular node (Farine & Whitehead 2015). This metric comprehensively reflects an individual's producing tendencies, as it incorporates the frequency and the spread of producing behavior. To visualize social networks and calculate each individual's *out-strength*, we used the software UCINET 6 (Borgatti et al. 2002).

Statistical analyses

All model analyses were performed in R version 3.2.2 (R Core Team 2015) and all social network analyses were conducted in UCINET 6 (Borgatti et al. 2002).

Group composition effects

We modelled the effect of group composition on social foraging behavior separately for each response variable (Table 1) with binomial or gamma GEEs (generalized estimation equations). GEEs are adequate to analyse data from repeated measurements over time within the same groups because they allow adjustment for the dependence of these measurements (Zuur et al. 2009). Defining the dependence structure of our data, we employed sorted-group ID as a grouping variable and specified the temporal correlation AR-1. Group composition constituted the explanatory variable of interest, fly weight and group size were included as additional variables to control for prey mass and mortality. An exception was the model for the *scrounging degree*, in which group size was controlled by the variable itself (Table 1). We assessed the significance of group composition effects by dropping each explanatory variable in turn and then comparing the full model to its nested models based on Wald test statistics. The least significant variable was removed, and the model comparisons were repeated until all remaining variables were significant.

Mortality was compared between producer-groups and scrounger-groups using a Chi-squared test. The difference between group compositions in individual *weight gain*$_2$ was analysed in a GLS (generalized least squares) model that incorporated an exchangeable correlation structure with sorted-group ID as the grouping variable (Table 1).

Sex differences

A node-based Monte Carlo randomization test was conducted to determine whether the observed difference in mean *out-strength* between sexes deviated significantly from the difference expected if producing associations occurred randomly and hence independent of sex. The observed data were shuffled in 10,000 node-label randomizations that preserved group membership. The sum of the differences between mean male *out-strength* (σ_m) and mean female *out-strength* (σ_f) within groups was used as the test statistic A (calculated as $A = \sum_{i=1}^{3} \overline{\sigma_{m_i} - \sigma_{f_i}}$, where i denotes the group identity). To produce a probability value, we compared the observed test statistic to the distribution of random test statistics drawn from the 10,000 Monte Carlo simulations (after Croft et al. 2008).

Results

Group composition effects

Attacking behavior

In detail, we compared three components of attacking behavior between producer-groups and scrounger-groups: success, latency and joint participation (Figure 2A; Table 1). The effect of group composition on *attack success* was not significant even though producer-groups (p) captured more prey than scrounger-groups (s). Over seven feeding trials per group, we recorded 27 successful attacks in producer-groups and 21 successful attacks in

Table 1 | The effect of group composition on social foraging behavior and individual fitness payoffs in *A. ergandros*

Variable	Variable definition	Analysis	Test statistics	*P*-value
Social foraging behavior (data per trial and group)				
Attack success	Specified as 1 if prey was successfully attacked, i.e. subdued and eaten (binomial)	GEE (binomial family)	Wald $\chi^2 = 0.87$	$P = 0.352$
For successful attacks ($N_P = 27$, $N_S = 21$):				
Attack latency	Time in minutes until the first individual attacked (maximum 60 min)	GEE (gamma family)	Wald $\chi^2 = 6.77$	**$P = 0.0093$**
Joint attacks	Specified as 1 if two or more individuals participated in the attack (binomial)	GEE (binomial family)	Wald $\chi^2 = 2.80$	*$P = 0.0941$*
Scrounging degree	Number of non-attackers that fed with attackers in relation to the total number of non-attackers	GEE (cbind, binomial family)	Wald $\chi^2 = 28.20$	**$P < 0.0001$**
Individual fitness payoffs (data per individual)				
Mortality	Specified as 1 if the individual died during the experiment ($N_P = 45$, $N_S = 45$)	Chi-squared test	$\chi^2 = 4.41$	**$P = 0.0463$**
Weight gain	= *log (end weight$_2$ / start weight$_2$)*, for all living individuals that were weighted excl. two outliers ($N_P = 37$, $N_S = 30$)	GLS (Gaussian)	*L*-ratio $\chi^2 = 4.85$	**$P = 0.0277$**

Significant *P*-values are indicated in bold, trends in italic. The abbreviations ‘p’ and ‘s’ in the statements of sample sizes mean producer-groups and scrounger-groups, respectively. The lower-case number ‘2’ in the formula for weight gain indicates that individual weight was taken in the 2nd experimental phase.

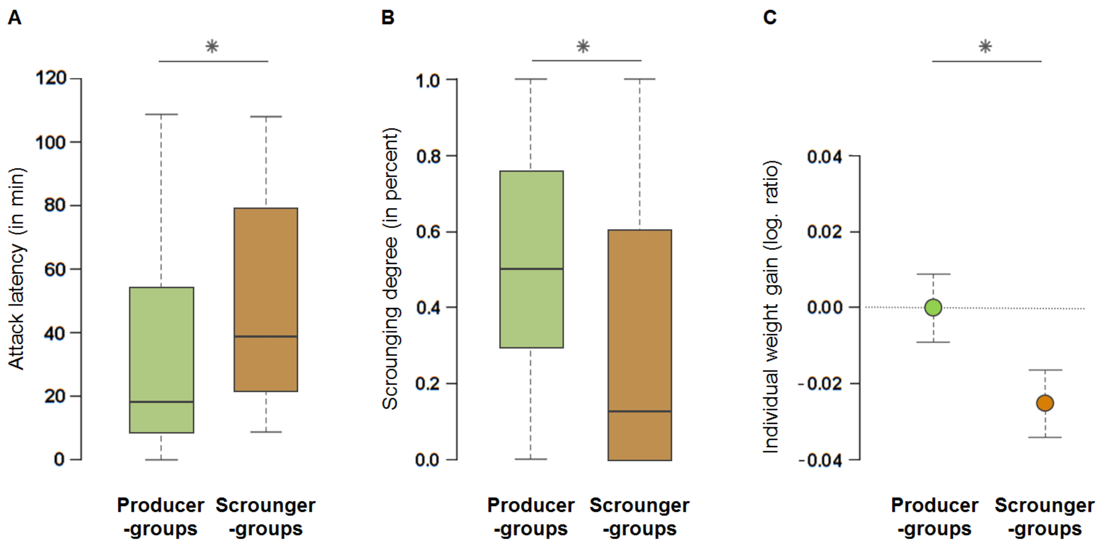

Figure 2 | Group composition effects on social foraging behavior and individual fitness payoffs. **A** & **B**: The effects of group composition (producer-group 'p' or scrounger-group 's') on *attack latency* (A) and the extent of prey sharing (B); only successful attacks are considered (p: *N* = 27, s: *N* = 21). The boxplots show median, upper and lower quartiles and interquartile range (1.5 times). **C**: The effect on individual *weight gain* (p: *N* = 38, s: *N* = 31) presented as mean (circle) ± SE (whiskers). The asterisk marks a significant difference between group compositions as revealed by statistical analyses (see also Table 1).

scrounger-groups (mean number of *successful attacks*/group ± SE; p: 5.40 ± 0.51, s: 4.20 ± 0.97).

The expected distinctions between producer-groups and scrounger-groups were found when evaluating the successful attacks. Primarily, group composition had a strong effect on *attack latency* (Figure 2A; Table 1): prey was captured notably faster in producer-groups than in scrounger-groups (mean *attack latency* ± SE; p: 34.04 ± 6.08 min, s: 49.76 ± 7.09 min). Moreover, producer-groups tended to perform more joint attacks (Table 1). 70.37% of the 27 attacks in producer-groups were performed by more than one individual, whereas this applied to only 33.33% of the 21 attacks in scrounger-groups (mean number of *joint attacks* /group ± SE; p: 3.80 ± 0.49, s: 1.40 ± 1.17).

Prey sharing behavior

Producer-groups and scrounger-groups differed significantly in the extent of prey sharing, which we measured per attack as the *scrounging degree* (Figure 2B; Table 1). As expected, prey sharing was much more pronounced in producer-groups, where 48.99 ± 5.90% (mean ± SE) of the respective non-attackers fed on a given prey item. This proportion fell to 27.67 ± 8.68% in scrounger-groups. The difference in prey sharing between group compositions was also reflected by absolute values (mean number of feeding non-attackers ± SE; p: 3.15 ± 0.42, s: 1.62 ± 0.40).

Individual fitness payoffs

Individual fitness payoffs were measured as *mortality* and, whenever applicable, individual *weight gain*. *Mortality* was considerably lower in producer-groups (Table 1): only three producer-group members (6.68%) died compared to eleven scrounger-group members (24.44%; mean number of deaths/group ± SE; p: 0.60 ± 0.40, s: 2.20 ± 0.66). Consistently, there was a significant effect of group composition on the *weight gain* of still living individuals (Figure 2C; Table 1). On average, producer-group members kept their weight, while scrounger-group members lost weight (mean individual *weight gain* (as log. ratio) ± SE; p: 0.000 ± 0.077, s: -0.026 ± 0.080). The absolute per-capita weight change amounted to 0.01 ± 0.07 mg (mean ± SE) for producer-group members and -0.21 ± 0.07 mg (mean ± SE) for scrounger-group members.

Sex differences

We tested for differences between sexes in the tendency to cooperate (i.e. produce) in three sub-

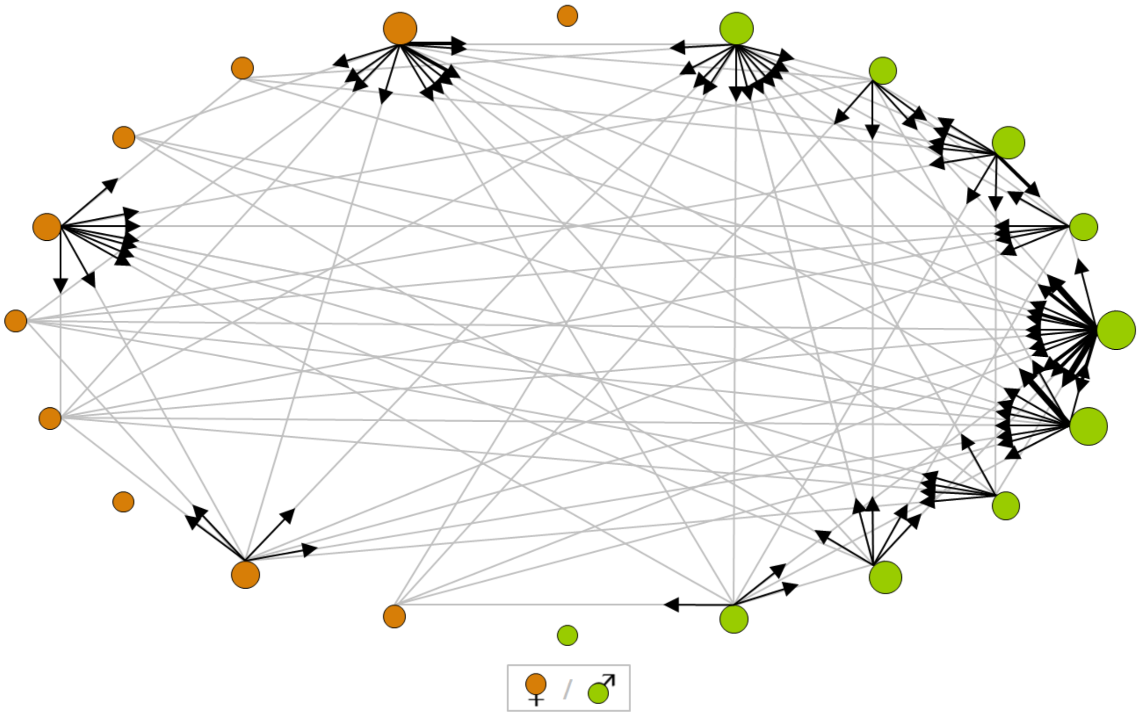

Figure 3 | A social network reflecting the different producing tendencies of males and females in *Australomisidia ergandros*. The graph shows the foraging interactions in one exemplary group of ten males (green nodes) and ten females (brown nodes) recorded over ten repeated feeding trials. A line between two nodes indicates that one individual shared prey with the other; the respective arrow indicates who produced for whom. The number of outgoing arrows per node reflects the producing tendency of the particular individual in terms of spread over different group members. The node size reflects the trial frequency to which the individual produced.

adult offspring groups of each ten males and ten females. We found that males had significantly higher producing tendencies than females (Monte Carlo test, $P = 0.045$; Figure 3). Specifically, the individual *out-strength* (σ), a network measure incorporating the frequency and the number of group members an individual produced for, was higher for males (m) than for females (f) in all groups (sex-specific mean ± SE; g1: $\sigma_m = 15.98 \pm 4.27 > \sigma_f = 10.10 \pm 2.94$, g2: $\sigma_m = 9.20 \pm 3.23 > \sigma_f = 7.80 \pm 3.10$, g3: $\sigma_m = 7.70 \pm 2.06 > \sigma_f = 2.50 \pm 1.41$).

The sum of the within group differences in sex-specific means amounted to $A = 12.39$. Equal or higher values for this test statistic A were achieved in only 450 of 10,000 Monte Carlo randomizations of the data (interval for A with 10,000 randomization = [-13.86, 14.07], mean random $A = 0.07$). Overall, this implies that the detected network pattern of producing behavior (Figure 3) would unlikely occur if the tendency to cooperate was independent of sex.

Discussion

Our study links theoretical considerations with empirical evidence to investigate how cooperation may resist the invasive spread of defectors in social foraging groups. For socially foraging predators, we propose that unconditional cooperators (producers) will outplay unconditional defectors (scroungers), provided that cooperators differ from defectors in their cooperative tendency but not in their competitive ability. The results of our laboratory experiment using the group-foraging spider *Australomisidia ergandros* clearly support our model assumptions.

We revealed that attacking behavior was considerably more pronounced, and that prey sharing was significantly greater in producer-groups than in scrounger-groups. These results offer convincing evidence that *A. ergandros* producers have a stronger tendency to acquire and to offer prey (i.e. a stronger cooperative tendency) compared to *A.*

ergandros scroungers. The greater extent of prey sharing in producer-groups further confirms that producers have a similar ability as scroungers to feed on prey acquired and offered by others (i.e. a similar competitive ability). Most importantly, the existence of pronounced scrounging behavior in producer-groups indicates the predicted option for cooperators to reap defector-like payoffs when being frequent.

Concerning the concept that an individual's cooperative tendency is the sum of two components - first, the tendency to acquire food and second, the tendency to intentionally offer food - our experiment was designed to verify whether cooperators score high and defectors low in both components. However, the concept also implies the appearance of feeding types with divergent scores, for instance with a high tendency to acquire but a low tendency to offer food. A prior study demonstrated such a feeding type in *A. ergandros*: the 'loner', who frequently captures but rarely shares prey (Dumke et al. 2016). The existence of loner-types further validates our model assumption - and is compatible with our model predictions. These model predictions refer entirely to the foraging interactions among producers and scroungers, which should (and in *A. ergandros* evidently do) occur whether loners are present or not (Packer & Ruttan 1988; Dumke et al. 2016).

In accordance with another prediction of our model (cf. Figure 1B), the measured per-capita fitness payoffs to producer-group members were higher than those to scrounger-group members, who suffered weight loss and mortality in consequence of minor foraging success. Notably, a few scrounger-group members did capture prey, but the overall pattern of behavior observed in the scrounger-groups nonetheless reflected consistent defector-tactic use: scroungers attacked late and rarely shared - neither the costs of prey capture nor the prey itself. Prospectively, this unconditional tactic use ensures that scroungers reap negative fitness payoffs when being frequent.

Previous studies investigating the frequency-dependence of payoffs to cooperators and defectors arrived at similar results, especially concerning the success of defector-groups. Using a theoretical approach, Avilés (2002) demonstrated reduced productivity for groups with high frequencies of 'freeloaders' - individuals that displayed low cooperative tendencies. Avilés (2002) proposed that the freeloaders' failure to cooperate was responsible for this effect. We experimentally confirmed reduced prey sharing in scrounger-groups, thereby lending strong support to Aviles' assertion. Likewise, empirical work on group-living *Anelosimus studiosus* spiders by Pruitt & Riechert (2009) showed that groups of mostly 'asocial' individuals were not as efficient in prey consumption as groups of mostly 'social' individuals. In contrast to our crab spiders, however, 'social' *A. studiosus* individuals were shown to be less aggressive towards prey than 'asocial' individuals (Pruitt et al. 2008). Therefore, the lower foraging success in 'asocial' groups could not, as in our study, be attributed to less pronounced attacking behavior. Alternatively, Pruitt and Riechert (2009) suggested that asocial individuals earned negative frequency-dependent payoffs because they lost foraging time over resolving conflicts with their alike group members.

In cooperator-dominated groups, on the other hand, both Avilés (2002) and Pruitt & Riechert (2009) reported a sizable advantage for defectors over cooperators. Within groups of mostly social *A. studiosus* spiders, asocial individuals gained more weight (Pruitt & Riechert 2009), and the general model by Avilés (2002) predicted greater fitness for rare freeloaders than for frequent cooperators. In fact, substantial advantages for defectors over cooperators at high cooperator-frequencies are central to most studies that reconcile frequency-dependence with cooperation; whether in the context of social foraging (Barnard & Sibly 1981; Giraldeau & Beauchamp 1999), communal brood care (Dobata & Tsuji 2013) or joint territory defence (Heinsohn & Packer 1995; Riehl & Frederickson 2016).

The distinctiveness of our model hinges on the (predator-specific) prediction that there is no frequency at which defectors reap significantly higher per-capita payoffs than cooperators (Figure 1B). In other words, we propose that the tactic of cooperators is 'by default' more resistant to frequency fluctuations. Therefore, cooperators overall likely enjoy a fitness advantage. Their feeding type should be subject to positive selection, and cooperation will be entirely stable. As outlined above, our empirical results validate the basic model assumption on which we base this essential prediction. However, to conclusively confirm our model and the predicted greater fitness for cooperators compared to defectors, it remains for future experiments to determine the per capita payoffs to cooperators and defectors within groups along a gradient of defector-frequencies.

Ultimately, selection for (or against) foraging cooperation does not exactly act on feeding types, but rather on the phenotypic traits that underlie feeding-type specialization (Barta & Giraldeau 1998; Sih et al. 2004; Morand-Ferron et al. 2011). To this effect, our study revealed that in *A. ergandros*, feeding types are sex-dependent. Spider males tended to be cooperators, while females adopted the defector-role. Similar sex differences were demonstrated in the prey sharing behavior of African wild dogs (Malcolm & Marten 1982), but it is beyond the scope of this discussion to fathom an evolutionary explanation for sex roles in socially foraging predators.

Instead, we wish to elaborate on how our study reflects on a puzzling and eponymous characteristic of our model species: In *A. ergandros*, which is only mildly inbred and has unbiased sex ratios, males were shown to contribute to nest construction (Evans 2000; Evans & Goodisman 2002). We show that additionally, males contribute even more than females to prey capture. In contrast, male work does not occur in the subsocial congener *A. socialis*, which is inbred and has female biased sex ratios (Evans 2000). Furthermore, male work is also not assumed for social spiders, which too exhibit inbreeding and female bias (Aviles 1993; Aviles et al. 2000; Lubin & Bilde 2007). In this respect, our results suggest that the evolution of permanent sociality along with female-biased sex ratios in *A. ergandros* is counteracted by the fitness detriments that groups with female bias (i.e. defector-biased groups) would experience in terms of social foraging payoffs.

Obviously, our model species is characterised by high relatedness of group members, easing the evolution of intentional cooperation through kin selection (Hamilton 1964; West et al. 2007). For example, the advantage to food-offering producers at high defector-frequencies may only be significant because of additional indirect benefits to feeding relatives (Giraldeau & Caraco 2000). Whether the mechanisms proposed here apply and work independently of indirect benefits of cooperating is a compelling question to be addressed in future studies.

ACKNOWLEDGEMENTS

We thank Giselle Muschett and Ina Geedicke for their assistance in the field, as well as Jasmin Ruch and James C. O'Hanlon for their great help, advice and guidance regarding the experiment to test sex differences. We also are indebted to Lutz Fromhage for his thoughtful comments, which greatly aided in developing the paper. This work was funded by the International Macquarie Research Excellence Scholarship (Macquarie University, Australia), the doctoral stipend “Promotionsförderung” of the Konrad-Adenauer-Foundation (Germany) and the stipend “Hamburglobal” for studies abroad (University Hamburg, Germany).

REFERENCES

Aviles L (1986). Sex-ratio bias and possible group selection in the social spider *Anelosimus eximius*. The American Naturalist 128: 1-12.

Aviles L (1993). Interdemic selection and the sex ratio: a social spider perspective. The American Naturalist 142: 320-345.

Avilés L (2002). Solving the freeloaders paradox: genetic associations and frequency-dependent selection in the evolution of cooperation among nonrelatives. PNAS 99: 14268-14273.

Aviles L, Mc Cormack J, Cutter A, Bukowski T (2000). Precise, highly female–biased sex ratios in a social spider. Proceedings of the Royal Society of London B 267: 1445-1449.

Barnard CJ, Sibly RM (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour 29: 543-550.

Barta Z, Giraldeau L-A (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. Behavioral Ecology and Sociobiology 42: 217-223.

Borgatti, S.P., Everett, M.G. & Freeman, L.C. (2002). UCINET 6 for Windows. Analytic Technologies 185, Harvard.

Boyd R, Gintis H, Bowles S (2010). Coordinated punishment of defectors sustains cooperation and can proliferate when rare. Science 328: 617-620.

Clark CW, Mangel M (1984). Foraging and flocking strategies: information in an uncertain environment. The American Naturalist 123: 626-641.

Couzin ID (2006). Behavioral ecology: social organization in fission–fusion societies. Current Biology 16: R169-R171.

Crawley MJ (2007). Proportion data. In: Crawley MJ (ed) *The R book*. John Wiley & Sons:Sussex, pp. 569-591

Croft DP, James R, Krause J (2008). *Exploring animal social networks*. Princeton University Press: Princeton.

Dawes RM (1980). Social dilemmas. Annual review of psychology 31: 169-193.

Dobata S, Tsuji K (2013). Public goods dilemma in asexual ant societies. PNAS 110: 16056-16060.

Doebeli M, Hauert C (2005). Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. Ecology Letters 8: 748-766.

Dugatkin LA (1997). Theoretical perspectives on the evolution of cooperation. In: Dugatkin LA (ed) *Cooperation among animals*. Oxford University Press: Oxford, pp. 14-44

Dumke M, Herberstein ME, Schneider JM (2016). Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider. Proceedings of the Royal Society of London B 283: 20160114.

Egas M, Riedl A (2008). The economics of altruistic punishment and the maintenance of cooperation. Proceedings of the Royal Society of London B 275: 871-878.

Evans TA (2000). Male work and sex ratio in social crab spiders. Insectes Sociaux 47: 285-288.

Evans TA (1999). Kin recognition in a social spider. Proceedings of the Royal Society of London B 266: 287-292.

Evans TA, Goodisman MA (2002). Nestmate relatedness and population genetic structure of the Australian social crab spider *Diaea ergandros* (Araneae: Thomisidae). Molecular Ecology 11: 2307-2316.

Farine DR, Whitehead H (2015). Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology 84: 1144-1163.

Frank SA (1995). Mutual policing and repression of competition in the evolution of cooperative groups. Nature 377: 520-522.

Giraldeau L-A, Caraco T (2000). *Social foraging theory*. Princeton University Press: Princeton.

Giraldeau L, Beauchamp G (1999). Food exploitation: searching for the optimal joining policy. Trends in Ecology & Evolution 14: 102-106.

Griffin AS, West SA (2002). Kin selection: fact and fiction. Trends in Ecology & Evolution 17: 15-21.

Hamilton WD (1964). The genetical evolution of social behaviour I and II. Journal of Theoretical Biology 7: 1-52.

Hamilton WD (1967). Extraordinary sex ratios. Science 156: 477-488.

Heath D (2002). Tests for two related samples. In: Heath D (ed) *An introduction to experimental design and statistics for biology*. CRC Press: Boca Raton, pp. 253-268.

Heinsohn R. Packer C (1995). Complex cooperative strategies in group-territorial African lions. Science 269: 1260.

Imhof LA, Fudenberg D, Nowak MA (2005). Evolutionary cycles of cooperation and defection. PNAS 102: 10797-10800.

Krams I, Kokko H, Vrublevska J, Āboliņš-Ābols M, Krama T, Rantala MJ (2013). The excuse principle can maintain cooperation through forgivable defection in the Prisoner's Dilemma game. Proceedings of the Royal Society of London B 280: 20131475.

Lubin Y. Bilde T(2007). The evolution of sociality in spiders. Advances in the Study of Behavior 37: 83-145.

Malcolm JR, Marten K (1982). Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behavioral Ecology and Sociobiology 10: 1-13.

McNamara JM, Doodson P (2015). Reputation can enhance or suppress cooperation through positive feedback. Nature communications 6: 6134

Morand-Ferron J, Wu G-M, Giraldeau L-A (2011). Persistent individual differences in tactic use in a producer-scrounger game are group dependent. Animal Behaviour 82: 811-816.

Nowak MA (2006). Five rules for the evolution of cooperation. Science 314: 1560-1563.

Nowak MA, Bonhoeffer S, May RM (1994). Spatial games and the maintenance of cooperation. PNAS 91: 4877-4881.

Nowak MA, Sigmund K (1992). Tit for tat in heterogeneous populations. Nature 355: 250-253.

Nowak MA, Sigmund K (2005). Evolution of indirect reciprocity. Nature 437: 1291-1298.

Packer C, Ruttan L (1988). The evolution of cooperative hunting. The American Naturalist 132: 159-198.

Pruitt JN, Riechert SE (2009). Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. Evolution 63: 2966-2973.

Pruitt JN, Riechert SE, Jones TC (2008). Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. Animal Behaviour 76: 871-879.

Riehl C, Frederickson ME (2016). Cheating and punishment in cooperative animal societies. Philosophical Transactions of the Royal Society B 371: 20150090.

Ruch J, Herberstein ME, Schneider JM (2014a). Families hunt more successfully: effect of group composition on hunting and communal feeding. Animal Behaviour 91: 171-178.

Ruch J, Herberstein ME, Schneider JM (2014b). Offspring dynamics affect food provisioning, growth and mortality in a brood-caring spider. Proceedings of the

Royal Society of London B 281: 20132180

Ruch J, Dumke M, Schneider JM (2015). Social network structure in group-feeding spiders. Behavioral Ecology and Sociobiology 69: 1429-1436.

Rutte C, Taborsky M (2008). The influence of social experience on cooperative behaviour of rats (*Rattus norvegicus*): direct vs generalised reciprocity. Behavioral Ecology and Sociobiology 62: 499-505.

Santos MD, Pinheiro FL, Santos FC, Pacheco JM (2012). Dynamics of N-person snowdrift games in structured populations. Journal of Theoretical Biology 315: 81-86.

Sih A, Bell A, Johnson JC (2004). Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology and Evolution 19: 372-378.

Sih A, Bell A, Johnson JC (2004). Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution 19: 372-378.

Taborsky M (2013). Social evolution: reciprocity there is. Current Biology 23: R486-R488.

Trivers RL (1971). The evolution of reciprocal altruism. The Quarterly Review of Biology 46: 35-57.

Vickery WL, Giraldeau L-A, Templeton JJ, Kramer DL, Chapman CA (1991). Producers, scroungers, and group foraging. The American Naturalist 137: 847-863.

West SA, Griffin AS, Gardner A (2007). Evolutionary explanations for cooperation. Current Biology 17: R661-R672.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer: New York.

Supporting Information

S1

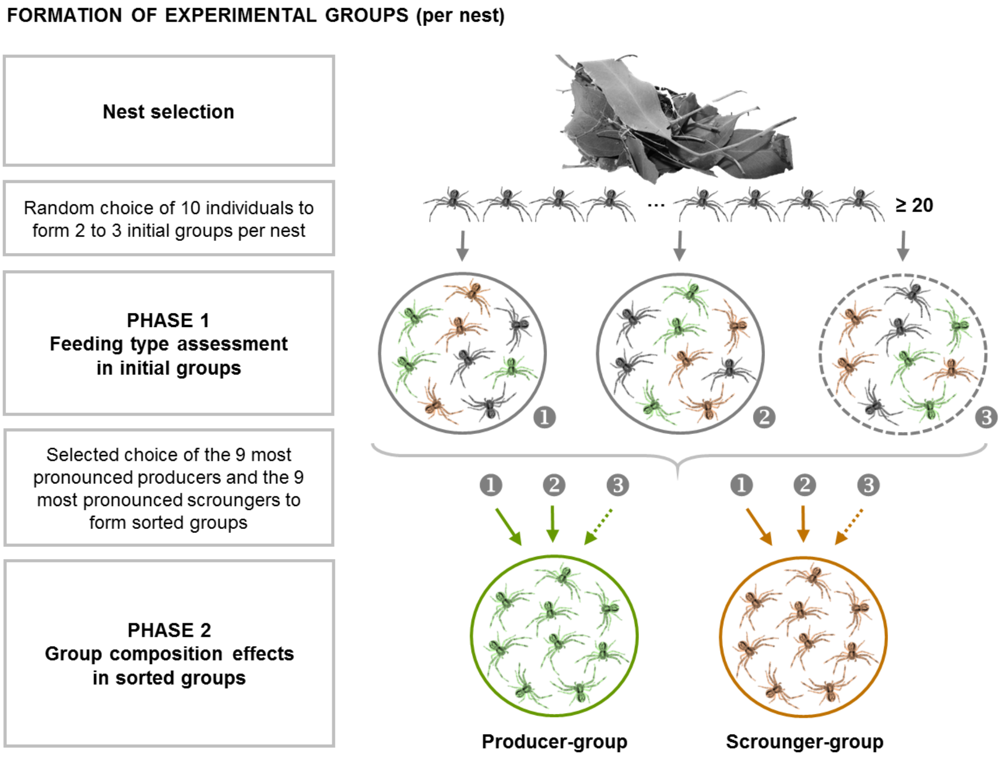

Figure S1 | The formation of groups for the group composition experiment. We formed two to three 'initial' groups per nest for 'phase 1', the assessment of individual feeding types (N_{nests} = 10). We then regrouped individuals into 'sorted' groups, according to the feeding type they exhibited in the initial groups (green: producers, brown: scroungers). In the sorted producer-groups and scrounger-groups, we tested for group composition effects on social foraging behavior and individual fitness payoffs.

S2

Special requirements of group formation

The experimental procedure that we followed to investigate group composition effects in *Australomisidia ergandros* consisted of two phases: firstly, the assessment of feeding types (producer or scrounger) in 'initial' groups, and secondly, the assessment of group composition effects in groups composed of producers or scroungers only (see also S1). To be able to compose and compare these sorted groups from the pool of assessed feeding types, several requirements had to be considered in the formation of initial groups: For comparability, the sorted producer-groups and scrounger-groups had to be of equal sizes. This required the identification of similar numbers of producers and scroungers in the initial groups. Furthermore, all experimental groups had to fulfill the natural condition of within-group relatedness. To meet these requirements, we selected nests with at least 20 individuals of a body size large enough to be color-marked (N_{nests} = 10). We formed two to three initial groups per nest (Figure S1), such that every group contained nine to ten randomly selected, but still related individuals (N_{groups} = 25). We assessed feeding types in this group size, as a previous study demonstrated balanced feeding-type ratios for that group size (details in Dumke et al. 2016). To keep all variables but group composition constant between the two experimental phases, we also assessed group composition effects in groups of nine to ten.

Comparability of producer-groups and scrounger-groups

We ensured that a producer-group and its related scrounger-group were comparable in terms of the number of individuals chosen from each initial group as well as similar in average individual weight gain$_1$ and average individual weight after the first phase (end weight1). With this, we aimed to avoid group composition bias in the individuals' physical state. We statistically tested for the similarity of paired groups in these traits with Wilcoxon signed-rank tests.

CHAPTER 6

General discussion
of social foraging and exploitative behaviour in group-living crab spiders

General discussion

The advantages and downsides of social foraging, with particular reference to exploitative foraging behaviour ('scrounging'), have been widely studied in theory and by experiment. In the latter case, flocks of ground-feeding birds have served as the prime model organisms to examine group living in the light of cooperative and exploitative foraging interactions among group members (e.g. Barnard & Sibly 1981; Giraldeau & Lefebvre 1986; Coolen et al. 2001; Morand-Ferron et al. 2011; David et al. 2014). Spice finches (*Lonchura punctulata*), for example, were investigated in terms of group size effects on scrounging incidence (e.g. Coolen 2002), frequency dependence of scrounger payoffs (e.g. Mottley & Giraldeau 2000) and individual specialisation in foraging tactic use (e.g. Morand-Ferron et al. 2011). The frequency-dependence of scrounger payoffs was further examined in house sparrows (*Passer domesticus*; Barnard & Sibly 1981) and wild Carib grackles (*Quiscalus lugubris*; Morand-Ferron et al. 2007). In addition, feral pigeons (*Columbia livia*) and zebra finches (*Taeniopygia guttata*) were used to explore the phenotypic determinants of an individuals' tendency to apply one social foraging tactic over another (Giraldeau & Lefebvre 1986; David & Giraldeau 2011).

Mechanism promoting social foraging and constraining exploitation

To explain the evolution and retention of group living in terms of (1) social foraging advantages and (2) exploitation susceptibility, the above (and several other) studies firstly acknowledge that flocking increases the foraging efficiency of individuals (see also Waite 1981; Brown et al. 1991; Galef & Giraldeau 2001). Secondly, these studies propose that scrounging is regulated via foraging-tactic adjustment. The payoffs of scrounging decrease as the scrounging frequency within the group increases - in response, individual flock members reduce their use of the scrounger tactic and switch to producing. Through behavioural adjustment, they thus largely evade the detrimental effects of scrounging behaviour (Morand-Ferron & Giraldeau 2010; Morand-Ferron et al. 2011).

Experimental research that addresses similar questions in predatory species, on the other hand, is rare, possibly owing to the difficulty to experimentally manipulate predator groups (but see Pruitt & Riechert 2009 for an example in the socially foraging spider *Anelosimus studiosus*). However, predator groups are especially susceptible to exploitation, because scroungers evade the significant costs of prey capture. In view of that, the general objective of this thesis was to experimentally investigate social foraging and exploitative foraging behaviour in predators. Using group-living crab spiders as the predatory model organism, the overall aim was to identify probable mechanisms that promote and regulate group foraging.

In combination, my findings point to an evolutionary solution that warrants beneficial social foraging in group-living crab spiders - despite the challenging incidence of scrounger specialisation (which is established in **Chapter 4**). As in the well-studied avian species, this solution is based on two mechanisms: (1) the advantages of group formation in terms of foraging efficiency (as shown in three of four group-living crab spiders in **Chapter 2** & **3**) and (2) the negative frequency dependence in scrounger payoffs (established for the specially disposed thomisid *Australomisidia ergandros* in **Chapter 4** & **5**).

Yet, in contrast to the producer-scrounger systems of several avian species, I demonstrate for *A. ergandros* that scroungers are consistently specialised: they pursue their defective foraging tactic when being in a group (**Chapter 4**), regardless of the groups' scrounger frequency (**Chapter 5**). At high scrounger frequencies, they thus reap negative payoffs. Conversely, producers cooperatively share their food procurements (**Chapter 3** & **5**). At low scrounger frequencies, an innate producer is therefore likely to obtain prey shares; at high scrounger frequencies it is likely to attack (**Chapter 5**). As to the mechanism that constrains exploitation, scrounging should consequently be kept in check via frequency-dependent selection rather than via short-term behavioural adjustment. In opposition, the characteristic tactic of producers is adjustable, but by default (**Chapter 5**).

(1) Foraging advantages of grouping

Regarding the first mechanism - foraging advantages of grouping - in more detail, my findings support that offspring group living in crab spiders is promoted by benefits of maternal food provisioning even after the nutritional independence of the young (**Chapter 2**). Moreover, the results of **Chapter 3** suggest that offspring grouping beyond maternal care is promoted because groups attain greater predatory success.

Maternal food provisioning

The benefits of maternal provisioning I revealed in **Chapter 2** (i.e. the increased offspring fitness) affirm that group living in crab spiders evolved on the subsocial route, where groups originate as the progeny of a single foundress or breeding pair that engages in parental care (**Chapter 1**; Lin & Michener 1972). The same route is presumed for the web-building subsocial and social spiders (Kullmann 1972; Brach 1977; Lubin & Bilde 2007; Yip & Rayor 2014). Of course, it needs to be noted that I only demonstrated the advantages of maternal food provisioning in one subsocial crab spider, *Xysticus bimaculatus*. However, *A. ergandros* mothers were previously shown to capture prey for their young, and even to provide themselves as a food source (Evans et al. 1995; Evans 1998b). In *A. socialis*, the mother lives and forages with her offspring for up to five months - a phenomenon equally indicative of foraging benefits through extended maternal care (Main 1988; Evans & Main 1993).

Interestingly, the progression towards cooperative group living via prolonged brood care is presumed for a broad range of organisms. In most social birds, groups form and are retained owing to parental care and consequently delayed offspring dispersal (Cockburn 2006; Cant 2012). Foraging advantages, in particular, are obtained through offspring provisioning by either one or both parents (maternal, paternal and biparental care; Ar & Yom- Tov 1978; Owens 2002; Cockburn 2006). At a higher social stage, brood care is exerted by more than two individuals, for example older siblings (helpers at the nest, a form of cooperative brood care; Emlen et al. 1986; Koenig & Dickinson 2004; Cockburn 2006).

Cooperative brood care

Offspring provisioning is also thought to have formed the baseline for the evolution of cooperative brood care in invertebrates (Lin & Michener 1972; Tallamy 1984; Cant 2012), where the possibility to increase the survival of broods through food provisioning - besides other modes of care - has likewise encouraged the extension of brood care to non-direct relatives (Anderson 1984; Bourke 1988, Salomon & Lubin 2007). This includes individuals provisioning the later offspring of their parents as well as individuals provisioning the offspring of their siblings or of other kin. In the Hymenoptera (ants, bees and wasps), the extension of care has culminated in complex eusocial societies with nonreproductive workers (Trivers & Hare 1976; Anderson 1984; Bourke 1988; Wilson & Hölldobler 2005; Nowak et al. 2010). In spiders, cooperative brood care has been observed, but rarely empirically confirmed. One exception is the social spider *Stegodyphus dumicola* (Eresidae), where adult but virgin females regurgitate food and are eaten by the brood of their reproducing sisters (Salomon & Lubin 2007). A recent study provides evidence for task differentiation in this system: virgin females are more likely to engage in prey capture, while mothers more often tend the egg sacs (Junghanns et al. 2017).

The evolutionary factors that endorse helping behaviour in brood care, up to the sacrifice of own reproduction, include advantages of propagating the genes of siblings (kin selection; Hamilton 1964; Queller & Strass-mann 1998; Wilson 2005; Hughes et al. 2008). Moreover, there is abundant evidence that environmental pressures select for cooperative breeding in invertebrates. Invertebrate group living is usually associated with the construction of protective nests (Anderson 1984; Wilson 2005).

If predation or few opportunities to found a new retreat minimise dispersal success, providing care to siblings or their descendants may be more beneficial than dispersal (Gadagkar 1990; Jones & Parker 2000; Peer & Taborsky 2007; Nowak et al. 2010). As an example, risky dispersal appears to have favoured cooperative breeding in Ambrosia beetles (Xyleborini), where some females remain and care for subsequent broods and do not reproduce in the natal gallery after reaching adulthood (Peer & Taborsky 2007). These factors - kin grouping, nest building and risky dispersal - are also prevalent in subsocial crab spiders, but their biology largely excludes cooperative breeding.

In the group-living crab spiders of the genus *Australomisidia*, mothers do not seem to regularly produce more than one clutch of eggs - they are semelparous, unlike solitary crab spiders (Main 1988; Evans et al. 1995). This trait prohibits the evolution of alloparental brood care in the form of brood provisioning by older siblings. Besides, gravid females do disperse from their natal nest to found a new one, which excludes the possibility that non-reproducing siblings of these females may provide allomaternal care (Main 1988; Evans 1995). In *Xysticus bimaculatus*, on the other hand, different offspring age classes were occasionally found in one nest, and little is known about the dispersal behaviour of gravid females (Ruch et al. 2014c; **Chapter 2**). Investigating the existence of cooperative brood care in *X. bimaculatus* should therefore be subject to future studies.

Predatory success

While cooperation in brood provisioning is not apparent in subsocial crab spiders, foraging cooperation among same-aged offspring beyond prolonged maternal provisioning probably exists. Active or even coordinated foraging cooperation in predators (e.g. herding and taking turns in striking the prey as is known for wild dogs, lions or lionfish; Creel & Creel 1995; Heinsohn & Packer 1995; Rizzari & Lönnstedt 2014) evolves from simpler, often passive forms of cooperative group foraging (Packer & Ruttan 1988; Lönnstedt et al. 2014). In this respect, I demonstrate passively increased predatory success for groups compared to singles in **Chapter 3.** As therein discussed, it remains to be studied if such an increase in gross predatory success entails a net gain in foraging payoffs for the group member as compared to the solitary individual. Alternatively, this gross foraging advantage could just compensate for the costs of food competition arising in groups (Janson & Van Schaik 1988). In the latter case, the foraging payoffs of grouping will only equal the payoffs of foraging alone (Packer & Ruttan 1988). This possibility is supported by the finding that group members attacked small and large prey (i.e. alone consumed and jointly consumed prey) in equal numbers (**Chapter 3**), and further by the detection of a loner-type besides producers and scroungers (**Chapter 4**). Such concurrence indicates similar payoffs of feeding in groups and feeding alone (Nowak & Sigmund 2004). Social group living would then be eased, but primarily driven by other than foraging rewards (Avilés & Guevara 2017, **Chapter 3**).

As a side note, the respective payoffs of coexisting tactics are, as usual in evolutionary games, likely frequency dependent (Nowak & Sigmund 2004; Doebeli & Hauert 2005; Imhof et al. 2005). In this thesis, I examined the frequency dependence of producer and scrounger tactics in group feeds (**Chapter 5**). Similarly, it may be highly relevant to examine the frequency dependence of group feeding versus feeding alone within groups.

Cooperative hunting

With regards to active cooperation, I found that the foraging behaviour of at least some spiderlings had a cooperative character in terms of the choice of prey sizes (**Chapter 3**) and the intention to share (**Chapter 5**). In addition, I documented joint prey capture of very large prey in **Chapter 4** & **5** (i.e. *Musca domestica* flies; Figure 1; and see also Ruch et al. 2014a; Ruch et al. 2015). Yet, I did not examine hunting cooperation among attackers. Attackers could greatly benefit from communal prey capture if the necessary amount of venom is shared, at least if prey items yield enough biomass to satiate all participants.

This possibility of cooperation remains a focus for future reserach into social foraging in spiders:

experimental analyses that relate attacker numbers, prey sizes and paralysis latencies could offer insight into whether group-living spiders inject venom relative to prey size and the number of attackers (Pekár et al. 2005; Jackson & Nelson 2012). Venom production is assumably very costly (Kuhn-Nentwig *et al.* 2011), but is particularly important for non-webbuilding spiders, which receive little structural support in prey capture (Jackson & Nelson 2012). Hence, group living and communal attacking in crab spiders (but also in web builders) may be promoted by considerable advantages regarding venom production.

(2) Frequency dependence of scrounger payoffs

Cooperative foraging sets the stage for exploitation, and I found that several *A. ergandros* group members specialise as scroungers, while others are producers (**Chapter 4**). Two characteristics seem to define this particular feeding-type specialisation: the tendency to attack and the tendency to cooperate, with scroungers scoring low and producers scoring high in both (**Chapter 5**). Earlier in this discussion and in **Chapter 5**, I already explained how these characteristics may lead to frequency-dependent selection against scroungers. In the following, I therefore discuss the exploitative character of the scrounger-type in detail. To moreover judge the general applicability of the here stated producer-scrounger characteristics, I ask whether behaviour types with such characteristics also coexist in other species.

Feeding type characteristics

A. ergandros scroungers do possess the general ability to seize prey (**Chapter 4**) but in groups exhibit a characteristically high threshold to attack (**Chapter 5**). Thereby, they evade the costs of prey capture - and they furthermore gain more weight per minute feeding time than producers (see 'prey extraction efficiency' in **Chapter 3**). This is not to be explained by individual variation in the power of digestive enzymes that are injected into the prey: when innate scroungers are forced to attack, they attain a similar weight gain per minute than the other feeding types (see 'food intake' in **Chapter 4**).

The difference in food intake between individuals that produce or scrounge on the same fly may thus indicate that *A. ergandros* scroungers exploit the digestive enzymes of their producer siblings (**Chapter 3**). Likely to prevent enzyme exploitation, individuals of the social spider *Stegodyphus mimosarum* inject less enzymes when group-feeding (Ward & Enders 1985). However, *Stegodyphus mimosarum* societies as well as crab

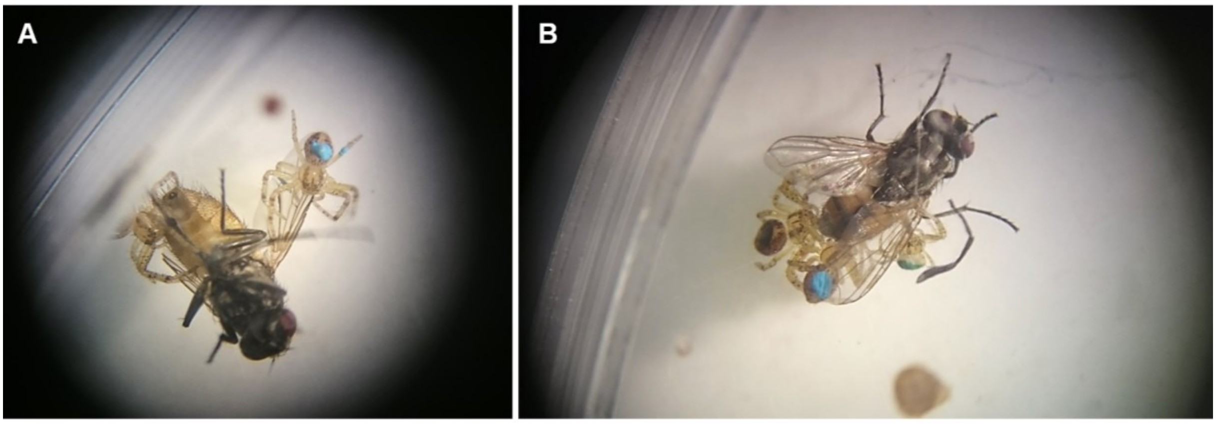

Figure 1 | A communal attack on a *Musca domestica* fly performed by three juveniles of the subsocial crab spider species *Australomisidia ergandros*. The individuals were marked to assess individual participation in attacking and feeding behaviour (**Chapter 4**). As the pictures were taken, the fly was still capable of moving **A**: The first individual that attacked the fly (by grasping its wing) was the light blue marked individual. The second individual attacked a few seconds later on the abdomen of the prey (second individual marked with a black color dot, not visible). **B**: The light blue marked individual has changed position to also grasp the abdomen and potentially inject venom and enzymes. A third individual has joined the attack by holding on to one of the legs of the fly. Another fly leg has been lost.

spider groups are composed of kin. As a matter of fact, crab spiders groups mainly contain siblings (but possibly of more than one father; Evans & Goodisman 2002) and *Stegodyphus mimosarum* societies are highly inbred. Therefore, substantial indirect fitness benefits may generally relax the costs of exploitation (Schneider & Bilde 2008).

Because innate *A. ergandros* producers probably share prey intentionally and innate scroungers neither readily attack nor share (**Chapter 5**), they can be considered cooperators and defectors. The coexistence of cooperators and defectors is common in nature (Doebeli et al. 2004). In street dogs, (*Canis lupus familiaris*), pack members cooperate in inter-group conflicts by participating in threatening group displays - or they defect by avoiding to take part in these displays. These behaviour types result from individual differences in the tendency to cooperate, with high-ranking and young pack members cooperating more often (Bonanni et al. 2010). In the context of social foraging, chimpanzees (*Pan troglodytes*) exhibit individual differences in the tendency to participate in hunting as well as in the tendency to share prey (Boesch 1994, Boesch 2002). In lions (*Panthera leo*), females consistently apply either a cooperative hunting strategy, or a defective foraging tactic where they contribute less or nothing to the groups effort (Heinsohn & Packer 1995). Many further examples are reviewed in Riehl & Frederickson (2016). This abundance of individual differences in cooperative behaviour stresses the applicability of the theoretical considerations on the maintenance of cooperation in **Chapter 5**, as these are based on the central assumption that individuals differ in their cooperative tendency.

Group size effect

Chapter 4 postulates that scrounging increases with group size, mediated through shifts in the ratio of specialised feeding types. At first sight, this appears to be contradictive to the finding that *A. ergandros* scroungers consistently pursue their foraging tactic across group compositions (**Chapter 5**). If individual specialisation in scrounging alters with group size, why does it not shift in response to feeding-type composition?

The probable explanation lies in the defining feeding-type characteristics, as well as in the different numbers of prey items provided to small, medium and large groups in **Chapter 4**. To control for prey density, larger groups received more prey items. This mirrors the natural situation, because larger groups build bigger nests and hence use wider foraging areas (Evans 1995; Evans 2000; but see also Ward 1986; Yip et al. 2008). If a producer in a larger group then attacks a prey item and cooperatively shares it, innate producers may join to feed instead of attacking the other items. Thus, the likelihood of experimentally detecting an innate producer is lower in larger groups. Put another way: the likelihood that an innate producer actually does produce naturally decreases with group size (Caraco & Giraldea 1991; Vickery et al. 1991).

Phenotypic determinants

The crab spider *A. ergandros* exhibits sex dependence in the individual tendency to cooperate in foraging (**Chapter 5**). Males tend to procure and readily share their prey with any other group member, irrespective of sex. Yet, this foraging cooperation is not irrespective of kin. Group living crab spiders have kin recognition (Evans 1999), and kin groups on prey items feed in larger numbers (Ruch *et al.* 2014a). Experimentally introduced non-kin group members are integrated into the social foraging network of groups depending on their body size (Ruch et al. 2015). Thus, in addition to an individuals' sex, its body size and condition may determine its attack threshold, its tendency to share and/or its joining behaviour. Ruch et al. (2015) did not analyse whether well-integrated non-kin individuals were producers or scroungers, but the data would allow post hum analysis.

Sex dependence in the individual tendency to cooperate, where males invest more than females, is very unusual for group living spiders. Again, this finding rather matches findings in avian species, where male helpers contribute more to brood care than female helpers (reviewed in Cockburn 2006). One explanation is that these helper males mate within their group of origin and through rearing group members increase their own reproductive success (Greenwood 1980; Clutton-Brock et al. 2002). The same may apply here - if *A. ergandros* males (at least before dispersal) mate in their offspring group, as occurs in *A. socialis* (Main 1988) and most permanently social spiders (Bilde et al. 2005; Ruch et al. 2009). To this effect, the few study findings on population genetic structure and gene flow, male mating dispersal and inbreeding, or polyandry and nestmate relatedness in *A. ergandros* are some-what ambiguous (Evans & Goodisman 2002).

To elucidate the 'genetics of foraging cooperation' in *A. ergandros,* I propose a study of nestmate relatedness and the 'genetic network' between nests within locales, with comparison to the other group-living crab spider species.

Environmental and interspecific influences

I investigated social foraging and exploitative behaviour of Australia's group-living crab spiders in an environmentally controlled, laboratory setting. However, to comprehensively understand not only the foraging advantages of group living but group living per se, one also needs to consider that subsocial crab spiders, other group living Araneae and virtually all animal societies face environmental conditions and interspecific influences that have shaped their social structure (Lin & Michener 1972; Anderson 1984; Krause & Ruxton 2002; Koenig & Dickinson 2004; Wilson & Hölldobler 2005; Nowak et al. 2010; Majer et al. 2015; Rubenstein & Abbot 2017). Group-living crab spiders share their nest with commensals (Evans 1998a), and nests are intruded by natural enemies (Unglaub et al. 2013). Nests are constructed from tree foliage, and the host tree species are prone to defoliation by insect invaders (Ohmart & Edwards 1991). Furthermore, the group living Thomisidae predate on and forage alongside ants (Main 1988; Evans 1995; Ruch *et al.* 2014c), that are well-fortified and themselves form highly organised colonies. The environmental factors and interspecific relationships that may have promoted group living in crab spiders are yet to be revealed.

REFERENCES

Anderson M (1984). The evolution of eusociality. Annual Review of Ecology and Systematics 15: 165-189.

Ar A, Yom-Tov Y (1978). The evolution of parental care in birds. Evolution 32: 655-669.

Avilés L, Guevara J (2017). Sociality in spiders. In: Rubenstein DR, Abbott P (eds) *Comparative social evolution*. Cambridge University Press: Cambridge, pp. 188-223.

Barnard CJ, Sibly RM (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. Animal Behaviour 29: 543-550.

Bilde T, Lubin Y, Smith D, Schneider JM, Maklakov AA (2005). The transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. Evolution 59: 160-174.

Boesch C (1994). Cooperative hunting in wild chimpanzees. Animal Behaviour 48: 653-667.

Boesch C (2002). Cooperative hunting roles among Tai chimpanzees. Human Nature 13: 27-46.

Bonanni R, Valsecchi P, Natoli E (2010). Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs. Animal Behaviour 79: 957-968.

Bourke AF (1988). Worker reproduction in the higher eusocial Hymenoptera. The Quarterly Review of Biology 63: 291-311.

Brach V (1977). *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution 31: 154-161.

Brown CR, Brown MB, Shaffer ML (1991). Food-sharing signals among socially foraging cliff swallows. Animal Behaviour 42: 551-564.

Cant MA (2012). Cooperative breeding systems. In: Royle NJ, Smiseth PT, Kölliker M (eds.) *The evolution of parental care*. Oxford University Press: Oxford, pp. 206-255.

Caraco T, Giraldea L-A (1991). Social foraging: producing and scrounging in a stochastic environment. Journal of Theoretical Biology 153: 559-583.

Clutton-Brock T, Russell A, Sharpe L, Young A, Balmforth Z, McIlrath G (2002). Evolution and development of sex differences in cooperative behavior in meerkats. Science 297: 253-256.

Cockburn, A. (2006). Prevalence of different modes of parental care in birds. Proceedings of the Royal Society of London B 273: 1375-1383.

Coolen I (2002). Increasing foraging group size increases scrounger use and reduces searching efficiency in Nutmeg Mannikins (*Lonchura punctulata*). Behavioral Ecology and Sociobiology 52: 232-238.

Coolen, I., Giraldeau, L.-A. & Lavoie, M. (2001). Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Animal Behaviour 61: 895-903.

Creel S, Creel NM (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. Animal Behaviour 50: 1325-1339.

David M, Giraldeau L-A (2011). Zebra finches in poor condition produce more and consume more food in a producer-scrounger game. Behavioral Ecology 23: 174-180.

David M, Le Hô M, Laskowski KL, Salignon M, Gillingham MA, Giraldeau L-A (2014). Individual differences in behavioral consistency are related to sequential access to resources and body condition in a producer-scrounger game. Frontiers in Ecology and Evolution 2: 19.

Doebeli M, Hauert C (2005). Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. Ecology Letters 8: 748-766.

Doebeli M, Hauert C, Killingback T (2004). The evolutionary origin of cooperators and defectors. Science 306: 859-862.

Emlen ST, Emlen JM, Levin SA (1986). Sex-ratio selection in species with helpers-at-the-nest. The American Naturalist 127: 1-8.

Evans TA, Main, BY (1993). Attraction between social crab spiders: silk pheromones in *Diaea socialis*. Behavioral Ecology 4: 99-105.

Evans TA, Wallis EJ, Elgar MA (1995). Making a meal of mother. Nature 376: 299-299.

Evans TA (1995).Two new species of social crab spiders of the genus *Diaea* from eastern Australia, their natural history and distribution. Records of the Western Australian Museum 52: 151–158.

Evans TA (1998a). Factors influencing the evolution of social behaviour in Australian crab spiders (Araneae: Thomisidae). Biological Journal of the Linnean Society 63: 205-219.

Evans TA (1998b). Offspring recognition by mother crab spiders with extreme maternal care. Proceedings of the Royal Society of London B 265: 129-134.

Evans TA (1999). Kin recognition in a social spider. Proceedings of the Royal Society of London B 266: 287-292.

Evans TA (2000). Male work and sex ratio in social crab spiders. Insectes Sociaux 47: 285-288.

Evans TA, Goodisman MA (2002). Nestmate relatedness and population genetic structure of the Australian social crab spider *Diaea ergandros* (Araneae: Thomisidae). Molecular Ecology 11: 2307-2316.

Gadagkar R (1990). Evolution of eusociality: the advantage of assured fitness returns. Philosophical Transactions of the Royal Society of London B 329: 17-25.

Galef BG, Giraldeau L-A (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Animal Behaviour 61: 3-15.

Giraldeau L-A, Lefebvre L (1986). Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. Animal Behaviour 34: 797-803.

Greenwood PJ (1980). Mating systems, philopatry and dispersal in birds and mammals. Animal behaviour 28: 1140-1162.

Hamilton WD (1964). The genetical evolution of social behaviour. II. Journal of Theoretical Biology 7: 17-52.

Heinsohn R, Packer C (1995). Complex cooperative strategies in group-territorial African lions. Science 269: 1260-1262

Hughes WO, Oldroyd BP, Beekman M, Ratnieks FL (2008). Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science 320: 1213-1216.

Imhof LA, Fudenberg D, Nowak MA (2005). Evolutionary cycles of cooperation and defection. PNAS 102: 10797-10800.

Jackson RR, Nelson XJ (2012). Specialized exploitation of ants (Hymenoptera: Formicidae) by spiders (Araneae). Myrmecol News 17: 33-49.

Janson CH, Van Schaik CP (1988). Recognizing the many faces of primate food competition: methods. Behaviour 105: 165-186.

Jones TC, Parker PG (2000). Costs and benefits of foraging associated with delayed dispersal in the spider *Anelosimus studiosus* (Araneae, Theridiidae). Journal of Arachnology 28: 61-69.

Junghanns A, Holm C, Schou MF, Sørensen AB, Uhl G, Bilde T (2017). Extreme allomaternal care and unequal task participation by unmated females in a cooperatively breeding spider. Animal Behaviour 132: 101-107.

Koenig WD, Dickinson JL (2004). *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press: Cambridge.

Krause J, Ruxton GD (2002). *Living in groups*. Oxford University Press: Oxford.

Kuhn-Nentwig L, Stöcklin R, Nentwig W (2011). Venom composition and strategies in spiders: is everything possible? Advances in Insect Physiology 40: 1-86.

Kullmann, E.J. (1972). Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). The American Zoologist 12: 419-426.

Lin N, Michener CD (1972). Evolution of sociality in insects. The Quarterly Review of Biology 47: 131-159.

Lönnstedt OM, Ferrari MC, Chivers DP (2014). Lionfish predators use flared fin displays to initiate cooperative hunting. Biology Letters 10: 20140281.

Lubin Y, Bilde T (2007). The evolution of sociality in spiders. Advances in the Study of Behavior 37: 83-145.

Main BY (1988). The biology of a social thomisid spider. In: Austin AD, Heather NW (eds) *Australian arachnology* Australian Entomological Society: Brisbane. pp 55–73.

Majer M, Svenning J-C, Bilde T (2015). Habitat productivity predicts the global distribution of social spiders. Frontiers in Ecology and Evolution 3: 101.

Morand-Ferron J, Giraldeau L-A (2010). Learning behaviorally stable solutions to producer–scrounger games. Behavioral Ecology 21: 343-348.

Morand-Ferron J, Giraldeau L-A, Lefebvre L (2007). Wild Carib grackles play a producer–scrounger game. Behavioral Ecology 18: 916-921.

Morand-Ferron J, Wu G-M, Giraldeau L-A (2011). Persistent individual differences in tactic use in a producer-scrounger game are group dependent. Animal Behaviour 82: 811-816.

Mottley K, Giraldeau L-A (2000). Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. Animal Behaviour 60: 341-350.

Nowak MA, Sigmund K (2004). Evolutionary dynamics of biological games. Science 303: 793-799.

Nowak MA, Tarnita CE, Wilson EO (2010). The evolution of eusociality. Nature 466: 1057-1062.

Ohmart C, Edwards P (1991). Insect herbivory on Eucalyptus. Annual Review of Entomology 36: 637-657.

Owens IP (2002). Male-only care and classical polyandry in birds: phylogeny, ecology and sex differences in remating opportunities. Philosophical Transactions of the Royal Society of London B 357: 283-293.

Packer C, Ruttan L (1988). The evolution of cooperative hunting. The American Naturalist 132: 159-198.

Peer K, Taborsky M (2007). Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. Behavioral Ecology and Sociobiology 61: 729-739.

Pekár S, Hrušková M, Lubin Y (2005). Can solitary spiders (Araneae) cooperate in prey capture? Journal of Animal Ecology 74: 63-70.

Pruitt JN, Riechert SE (2009). Frequency-dependent success of cheaters during foraging bouts might limit their spread within colonies of a socially polymorphic spider. Evolution 63: 2966-2973.

Queller DC, Strassmann JE (1998). Kin selection and social insects. Bioscience 48: 165-175.

Riehl C, Frederickson ME (2016). Cheating and punishment in cooperative animal societies. Philosophical Transactions of the Royal Society of London B 371: 20150090.

Rizzari JR, Lönnstedt O (2014). Cooperative hunting and gregarious behaviour in the zebra lionfish, *Dendrochirus zebra*. Marine Biodiversity 44: 467-468.

Rubenstein DR, Abbot P (2017). *Comparative Social Evolution*. Cambridge University Press: Cambridge.

Ruch J, Heinrich L, Bilde T, Schneider JM (2009). The evolution of social inbreeding mating systems in spiders: limited male mating dispersal and lack of pre-copulatory inbreeding avoidance in a subsocial predecessor. Biological Journal of the Linnean Society 98: 851-859.

Ruch J, Herberstein, ME, Schneider JM (2014a). Families hunt more successfully: effect of group composition on hunting and communal feeding. Animal Behaviour 91: 171–178.

Ruch J, Herberstein ME, Schneider JM (2014b). Offspring dynamics affect food provisioning, growth and mortality in a brood-caring spider. Proceedings of the Royal Society of London B 281: 20132180.

Ruch J, Riehl T, Michalik P (2014c). Re-description of *Xysticus bimaculatus* L. Koch, 1867 (Araneae, Thomisidae) and characterization of its subsocial lifestyle. ZooKeys 427: 1–19.

Ruch J, Dumke M, Schneider JM (2015a). Social network structure in group-feeding spiders. Behavioral Ecology and Sociobiology 69: 1429-1436.

Salomon M, Lubin Y (2007). Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). Behavioral Ecology and Sociobiology 61: 1743-1750.

Schneider JM, Bilde T (2008). Benefits of cooperation with genetic kin in a subsocial spider. PNAS 105: 10843-10846.

Tallamy DW (1984). Insect parental care. BioScience 34: 20-24.

Trivers RL, Hare H (1976). Haploidploidy and the evolution of the social insect. Science 191: 249-263.

Unglaub B, Ruch J, Herberstein M, Schneider J (2013). Hunted hunters? Effect of group size on predation risk and growth in the Australian subsocial crab spider *Diaea ergandros*. Behavioral Ecology and Sociobiology 67: 785-794.

Vickery WL, Giraldeau LA, Templeton JJ, Kramer DL, Chapman CA (1991). Producers, Scroungers, and Group Foraging. The American Naturalist 137: 847-863.

Waite R (1981). Local enhancement for food finding by rooks (*Corvus frugilegus*) foraging on grassland. Ethology 57: 15-36.

Ward PI (1986). Prey Availability Increases Less Quickly than Nest Size in the Social Spider *Stegodyphus mimosarum*. Behaviour 97: 213-225.

Ward PI, Enders MM (1985). Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. Behaviour 94: 167-182.

Wilson EO (2005). Kin selection as the key to altruism: its rise and fall. Social Research 72: 159-166.

Wilson EO, Hölldobler B (2005). Eusociality: origin and consequences. PNAS 102: 13367-13371.

Yip EC, Powers KS, Aviles L (2008). Cooperative capture of large prey solves scaling challenge faced by spider societies. PNAS 105: 11818-11822.

Yip EC, Rayor LS (2014). Maternal care and subsocial behaviour in spiders. Biological Reviews 89: 427-449.

APPENDIX I

Social network structure in group-feeding spiders

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Published in *Behavioral Ecology and Sociobiology* 69: 1429-1436, doi: 10.1007/s00265-015-1955-4
September 2015

Behav Ecol Sociobiol
DOI 10.1007/s00265-015-1955-4

ORIGINAL PAPER

Social network structure in group-feeding spiders

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Received: 30 October 2014 / Revised: 28 May 2015 / Accepted: 5 June 2015

Abstract In group-living animals, an individual's fitness is predicted by non-random interactions with other group members and social network analysis has become a powerful tool to study these interactions. We experimentally studied the social network structure in group-foraging subsocial spiders that naturally live in kin groups but accept immigrants. Spiderlings were individually marked and we observed interactions during six foraging trials in groups comprising (i) siblings, (ii) siblings with two non-siblings, and (iii) assorted spiderlings. In this foraging context, we found a higher social network structure in sibling groups compared with assorted groups or sibling groups containing two non-siblings. We asked whether non-siblings in the treatment containing mostly siblings and two immigrants are excluded or less connected, which would explain the overall reduced social network structure of the whole group. We found that non-siblings were not generally excluded but that their presence negatively affected the network structure of the whole group. The connectivity of foreign individuals in this treatment was moreover predicted by their size relative to the other group members with very small and very large spiderlings being well connected. Our findings support the idea that siblings have an advantage over unrelated individuals and that the social network structure may play a role in the evolution of social behaviour in spiders.

Communicated by M. Elgar

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Keywords *Australomisidia ergandros* · *Diaea* · Spider sociality · Group dynamics · Scramble competition

Introduction

The evolution and maintenance of sociality have been major themes in evolutionary biology for many decades (Hamilton 1964; Hardin 1968; Émlen 1982; Brown 1983; Avilés 1997; Choe and Crespi 1997; Lubin and Bilde 2007). Strong connections between individuals in groups of gregarious animals seem to be important for the evolution of cooperation and sociality, and the social network approach has become a powerful tool to study animal interactions (Fewell 2003; Croft et al. 2004; Lusseau and Newman 2004; Krause et al. 2007). Individuals preferentially join groups and thus form non-random associations when they match certain phenotypic traits, such as body size or colour (Krause et al. 2007; Croft et al. 2009). Once living in a group, individual fitness benefits depend on non-random interactions with other group members, which in turn affect an individual's behaviour (Fewell 2003; Lion and van Baalen 2008; Kurvers et al. 2013; Marcoux and Lusseau 2013). In social insects, for example, most interactions for colony functions are non-random, which means that a few key individuals distribute more information than others (such as dancers and scouts in a foraging task group) (Fewell 2003).

The social network approach can predict interactions between group members and an individual's position within the network (Pike et al. 2008; Croft et al. 2009; Krause et al. 2010). In bottlenose dolphins (*Tursiops* spp.), for example, some individuals of a group could be identified as "brokers" who maintain links between sub-communities and play a crucial role for the social cohesion of a population (Lusseau and Newman 2004). In three-spined sticklebacks (*Gasterosteus* *aculeatus*), bold individuals have fewer but more evenly distributed interactions, while shy individuals preferentially associate with few group members (Pike et al. 2008). Similarly, Trinidadian guppies (*Poecilia reticulata*) associate with individuals depending on behavioural traits (Croft et al. 2009).

Social network position and therewith the groups' social network structure have fitness consequences for individuals. In female baboons (*Papio cynocephalus*), fully socially integrated individuals have higher reproduction rates (Silk 2007). In female chacma baboons (*Papio hamadryas ursinus*), females with stronger social bonds live longer (Silk et al. 2010) and benefit from enhanced offspring survival (Silk et al. 2009). Social bonds moreover increase the reproductive success of unrelated females in feral horses (Cameron et al. 2009). Furthermore, individual fitness does not only depend on social bonds but also on group size. In a social wasp, *Ropalidia marginata*, smaller colonies are more homogeneously connected than large ones, potentially leading to task specialization of individuals in large groups (Naug 2009).

While the abovementioned studies focus on how the position within a social network affects an individual's fitness, only few studies show that the structure of network interactions themselves affect fitness (Royle et al. 2012). In broods of great tits (*Parus major*), however, family fitness is highest in groups that had the highest social network structure and resolved conflicts most efficiently (Royle et al. 2012).

Conflict resolution and thus the social network structure may also play an important role in foraging societies, which are mainly affected by competition over food (Whitehouse and Lubin 1999). Subsocial and social spiders communally hunt and feed on large prey items (Avilés 1997; Lubin and Bilde 2007; Yip and Rayor 2014), and it has been shown that competition is reduced when group members are closely related (Schneider and Bilde 2008; Ruch et al. 2009).

In the subsocial crab spider *Diaea ergandros* (now *Australomisidia ergandros* (Szymkowiak 2014)), natural nests mainly contain not only kin, but also unrelated immigrants (Evans 1998a; Evans 1999), which affect the foraging dynamics. Group hunting and communal feeding can be more frequently found among family members compared with family groups containing few immigrants or completely unrelated spiders (Ruch et al. 2014a). Moreover, female-offspring interactions depend on group composition (Evans 1998b; Ruch et al. 2014b). In *A. ergandros* group-size predicts growth of individual group members, with individuals in larger groups having an advantage over those living in smaller groups (Unglaub et al. 2013). González-Tokman et al. (2014) showed that the body lipid content of solitary foraging *A. ergandros* spiderlings was reduced compared with their group-foraging siblings, indicating that group foraging is beneficial in this species. Moreover, family groups grow better, which can be linked to higher individual foraging times (Ruch et al. 2014a). However, so far, it is unclear how interactions between individuals of the foraging group affect growth of the involved individuals. In other communally foraging spiders, spiderling size predicts growth with larger spiderlings growing better than smaller ones (Whitehouse and Lubin 1999). We analysed social network interactions of group-feeding spiderlings (i) living with siblings, (ii) living with mainly siblings but few immigrants, and (iii) living with unrelated spiderlings to detect how immigrating spiderlings affect group-foraging dynamics and whether spiderling size predicts the position in the social network. We predict that small spiderlings would be better connected than larger ones as larger spiderlings could potentially monopolize prey. We moreover predict that siblings are more strongly connected, which results in less conflict.

Methods

We collected *A. ergandros* nests in March 2013 from *Eucalyptus* trees around Yass (34°55′20.50″S, 149°6′15.53″E) and Boorowa (34°25′53.31″S, 148°43′49.47″E). Nest mates are usually highly related in these spiders (***r***=0.44; Evans and Goodisman 2002), although immigrant spiders from other nests can be found (Evans 1998b). The spiders were collected when they were very young which reduces the likelihood of finding immigrant spiderlings within nests (Evans 1999), and we thus assume that spiders from the same nest are most likely related. We selected similar-sized spiderlings from their natal nests (*N*=17 nests) and separated them into three treatments comprising seven spiders. Groups consisted of (i) siblings (related spiders from the same nest *N*=11), (ii) siblings with two non-siblings (five spiderlings from the same nest and two non-siblings, *N*=11), or (iii) unrelated spiderlings ("assorted," each spiderling coming from a different nest, collected at least 1 km apart from each other, *N*=11).

Each spiderling was individually weighed using an electronic balance (Mettler Toledo New Classic MS), marked with non-toxic watercolour dots (© Plaka Farbe), and then placed into Petri dishes (10 cm diameter) with a leaf-shaped paper towel as shelter (*N*=231 spiderlings). Individuals were ranked (ranks 1–7, 1= smallest spiderling) according to their start mass to detect whether size relative to the other group members affects the position within a network. We moreover compared individual spiderling mass between the start and the end of the experiment (11 weeks after the spiderlings were placed into the Petri dishes) and calculated the relative mass increase corrected for start mass using the formula [(spiderling mass end−spiderling mass start)/(spiderling mass start)×100]. All spiders were immature and accordingly had sufficient growth to achieve.

Table 1 Summary of the calculated network parameters on both group level and individual level

Parameter	Character	Definition
Group level		
Average degree (*n*)	Unweighted	Average over the number of the individuals neighbours in the network, high values show high networking
Average distance (*d*)	Unweighted	Average over the number of edges between every possible pair of two individuals in the network, low values show high networking
Density (*D*)	Unweighted	Ratio between actual number of edges and theoretical possible number of edges in the network, high values show high networking
Average weighted degree (n_w)	Weighted	Average over the number of the individuals interactions in the network, high values show high networking
Average weighted feeding time/edge	Weighted	Average over the feeding times between every possible pair of two individuals within the network, high values show high networking
Individual level		
Local clustering coefficient (*c*)	Unweighted	Each individual's ratio of the number of edges between the neighbours of an individual to the theoretical possible number of edges between these neighbours, high values (max=1) show high levels of inner connectivity
Weighted degree (n_w)	Weighted	Each individual's total number of interactions, high values show high sociality
Relation degree (n_r)	Unweighted	Each individual's ratio between number of neighbours of an individual in the network and the total number of individuals in the network −1

Feeding experiment

After being placed into the Petri dishes, spiderlings had a 2-week habituation phase during which they were fed twice with a *Musca domestica* fly. For the experiment, we anaesthetized a fly with CO_2, weighed the fly, and placed it into the Petri dish where it started moving after a few seconds. We waited until the spiderlings had attacked the fly (for details, see Ruch et al. 2014a) and determined the number and ID of the feeding spiderlings every 15 min for 2 h (nine observations). The group-hunting activity and individual foraging times with respect to growth were analysed elsewhere (Ruch et al. 2014a). The 15-min interval results from the feeding behaviour of the spiders, which tend to continuously feed on a captured prey item without significant interruptions. As our measure for social interaction, we determined the identity of the individuals that fed simultaneously on the prey item as well as the duration and frequency of two or more individuals feeding together.

If the prey was not attacked within 2 h, we terminated the trial and tested the group on the next day. If spiderlings did not attack on the next day, they were tested once again on the subsequent day and in case of no attack they then had to wait until the next week. We aimed for seven successful feeding trials; however, not all groups attacked seven times over the duration of the experiment (Ruch et al. 2014a). For the network structure, we only analysed data recorded in the first six feeding trials for each group since we were able to record at least six successful trials for each group. Two groups in the sibling +2 and two groups in the assorted treatment had less

Table 2 Network parameters analysed on group level between the three treatments (siblings, siblings +2, assorted). Italic *P* values show significant variables

	Siblings	Siblings +2	Assorted	Test	*P*
Average degree (*n*)	5.37± 0.16	4.7±0.34	4.6±0.46	Kruskal–Wallis: X^2=2.12	0.35
Average distance (*d*)	1.07±0.02	1.09±0.04	1.13±0.05	Kruskal–Wallis: X^2=1.64	0.44
Density (*D*)	0.91±0.022	0.85±0.057	0.78±0.07	Kruskal–Wallis: X^2=1.55	0.46
Average weighted degree (n_w)	14.62±1.44	9.55±1.19	9.47±1.69	ANOVA: $F_{2,25}$=4.00	*0.03*
Average weighted feeding time/edge	177.1±17.75	146.2±16.18	102.8±10.84	ANOVA: $F_{2,25}$=5.90	*0.008*

Italic *P* values show significant variables

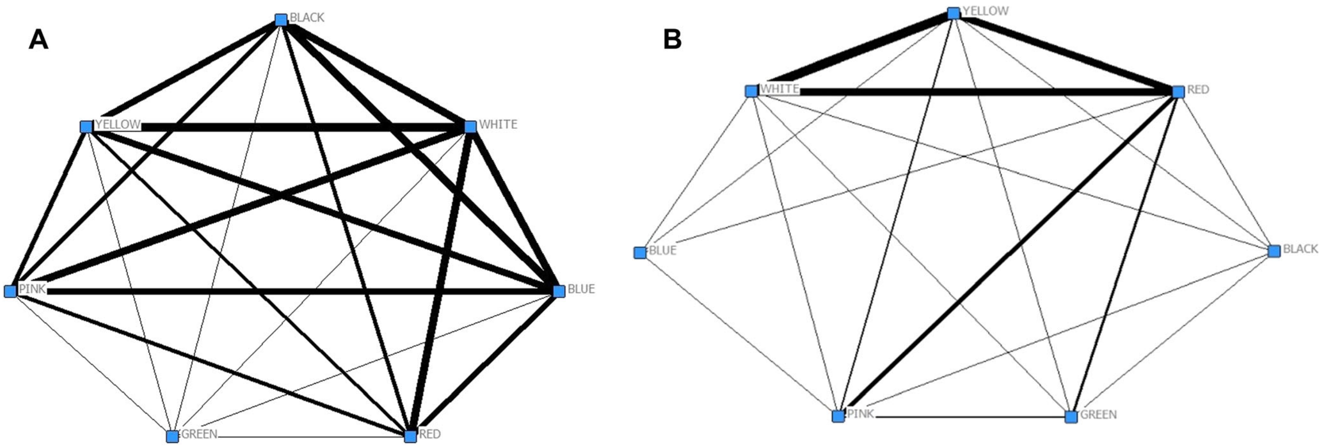

Fig. 1 Social network of an *Australomisidia ergandros* sibling-group (**a**) and a group of unrelated (assorted) spiderlings (**b**). *Blue nodes* represent individuals and black edges feeding interactions among them. The more often two individuals fed together, the thicker is the edge. The networks were chosen as suitable representatives of the differences in connectivity between related and unrelated spiderlings for they show—measured by the group parameters average weighted degree and average weighted feeding time per edge—both the second best connectivity within their treatment

than six successful feeding trials and were excluded from all analyses ($N_{\text{sibling}}=11$, $N_{\text{sibling }+2}=9$, $N_{\text{assorted}}=9$ groups). We corrected the relative mass increase for groups with higher successful trial numbers by dividing each individual's relative mass increase by the number of actual feeding events.

Based on the collected interactional data, we calculated network parameters (Table 1) (i) on group level for groups belonging to the three treatments, as well as parameters on individual level for (ii) individuals belonging to a certain group within the three treatments. We analysed both unweighted and weighted parameters. Our unweighted parameters describe the connectivity of groups and individuals without taking into account frequency or duration (time spent feeding) of interactions while our weighted parameters include either frequency of interactions (e.g., average weighted degree) or feeding times (e.g., average weighted feeding time/edge).

Statistical analyses

Network analyses were carried out with UCINET, a software package developed for the visualization and analysis of social network data. First, we compiled interaction matrices for each group of spiderlings out of the collected data. These matrices were imported into UCINETs integrated drawing tool NetDraw to generate network graphs visualizing the social interaction patterns within the various groups. The network graphs consist of "nodes," each representing an individual. "Edges" between these nodes show existing interactions. These networks, together with other provided calculative tools, were then used for the calculation of the parameters described above.

Statistical analyses of the network parameters were carried out with JMP 9.0 (SAS Institute Inc., Cary, NC, USA) and R version 2.15.3 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Continuous data were tested for normal distribution (Shapiro–Wilk test) as well as for equal variance. Parametric tests were applied when the data fulfilled the criteria of normal distribution of the residuals; otherwise, nonparametric tests were used. All statistical tests are two tailed ($\alpha=0.05$). Descriptive statistics are given as mean±SE.

Analysis of individual level parameters

The effect of treatment on the individual relation degree (unweighted) was analysed with a GEE (generalised estimation equation) with binomial error structure and exchangeable association structure with group ID as a grouping variable.

The effect of treatment and rank (as well as their interaction) on the individual weighted degree was fitted with a GLS (generalised least squares) with group ID as a grouping variable to control for measurements of the same group and exchangeable correlation structure. We corrected for unequal variances between treatments by applying the constant variance function (varIdent).

Table 3 Network parameters on individual level shown for the three treatments (siblings, siblings+2 non-siblings, assorted)

	Siblings	Siblings +2	Assorted
Local clustering coefficient (c)	0.94±0.032	0.89±0.026	0.85±0.032
Weighted degree (n_{w})	14.65±0.77	9.57±0.63	9.58±0.81
Relation degree (n_{r})	0.92±0.016	0.86±0.027	0.79±0.033

Table 4 Effect of treatment and rank on individuals' weighted degree

Response	Analysis	Explanatory variables	Test	*df*	*P*
Weighted degree	GLS with normal distribution, correlation structure specified as exchangeable (compound symmetry) for group ID and constant variance function for treatment *N*=28 groups, 189 individuals	Treatment (siblings, siblings+2 non-siblings, assorted)	*L* ratio=7.35	5	*0.025*
		Rank	*L* ratio=0.85	7	0.36
		Rank × treatment	*L* ratio=3.65	8	0.16

Test statistics, *df*, and *P* values of non-significant variables stem from the step when a variable was dropped from the model, and *df* vary depending on the number of remaining variables. Italic *P* values show significant variables that remained in the final model

The effect of treatment and individual relation degree and rank (as well as their interaction) on individual relative mass increase was fitted with a GLS with group ID as a grouping variable and exchangeable correlation structure. We fitted the model with the individual relation degree as this unweighted parameter of connectivity is independent from feeding times. We corrected for unequal variances between treatments by applying the constant variance function (varIdent).

Analysis of the treatment including two non-siblings

We analysed whether siblings differ in their connectivity towards all other group members from non-siblings towards all other group members in the sibling +2 treatment using a GEE with binomial error structure and exchangeable association structure (group ID as a grouping variable).

Relative mass increase was analysed with a GLS with origin (siblings/non-siblings) and individual relation degree and rank as well as the interactions between origin × individual relation degree and origin × rank as explanatory variables in the sibling + 2 treatment (group ID as a grouping variable and exchangeable correlation structure). We corrected for unequal variances for origin by applying the constant variance function (varIdent).

Results

Group level

Average degree, average distance, and density (unweighted group parameters) were not significantly different between treatments (Table 2). However, the average weighted degree (n_w, describing the frequency of communal feeding) and the average feeding time per edge (describing the duration of communal feeding) were significantly different between treatments. Groups comprising only siblings were generally more connected than the groups in the other two treatments (Table 2, Fig. 1). While all individuals had interactions in all group treatments as indicated by the similar average degree, the significant difference in the average weighted degree and average feeding time per edge shows that the interactions within sibling groups were more frequent, more intense, and more homogeneous.

Individual level

The local clustering coefficient was generally high, meaning that individuals of all treatments had repeated interactions with almost all other individuals of the group (Table 3). The individual relation degree was also high for most individuals and did not differ between individuals within the treatments (GEE, Wald test: $\chi^2_2=3.75$, $P=0.15$, $N_{\text{clusters}}=28$, $N_{\text{individuals}}=189$, Table 3).

However, individuals of the sibling treatment had a significantly higher weighted degree, meaning that their interactions with the other group members were more intense. Thus, they were generally better connected compared with groups of siblings including two non-siblings (sibling+2 non-siblings) and assorted spiderlings, whose interactions with their group members were comparatively less frequent and of shorter duration. Spiderling start mass (rank, 1=smallest, 7=largest spider) did not predict the weighted degree (Table 4).

Table 5 Effect of treatment (siblings, siblings+2 non-siblings, assorted), rank (1–7), and relation degree on individual relative mass increase

Response	Analysis	Explanatory variables	Test	*df*	*P*
Relative mass increase	GLS with normal distribution, correlation structure specified as exchangeable (compound symmetry) for group ID and constant variance function *N*=28 groups, 189 individuals	Treatment	*L* ratio=15.81	7	*<0.0001*
		Rank	*L* ratio=4.77	8	*0.028*
		Relation degree (n_r)	*L* ratio=5.90	8	*0.015*

The interaction terms were non-significant and removed from the final model. Italic *P* values show significant variables

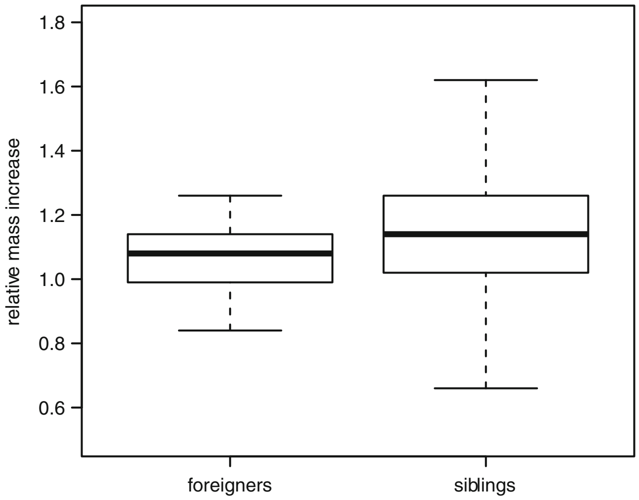

Fig. 2 Comparison of the relative mass increase between foreign individuals and siblings in the "sibling+2 non-siblings treatment." Siblings grew significantly better compared with the non-siblings of the group (see Table 6)

The relative mass increase was predicted by treatment, rank, and relation degree (Table 5). Spiderlings of the sibling treatment had a higher relative mass increase than spiderlings of the sibling +2 treatment and of the assorted treatment. Spiderlings with a high connectivity, described by the unweighted relation degree, were growing better than hardly connected ones independent of foraging time. Moreover, smaller spiderlings of each group were growing better than larger ones.

Sibling treatment including two non-siblings:

Spiders in the sibling +2 treatment showed a weaker overall connectivity compared with the sibling treatment indicated by the lower average weighted degree. We focused on the sibling +2 treatment to further explore patterns in the connectivity of the foreign individuals in comparison to the siblings within these groups.

Therefore, we investigated the underlying factors explaining the relation degree with a GEE including origin (sibling/foreign) and size rank as well as their interaction as explanatory variables. We found a significant interaction (GEE, Wald test $X^2=4.44$, $P=0.035$, $N_{\text{clusters}}=9$, $N_{\text{individuals}}=58$) suggesting that non-siblings were better connected when being either the smallest or largest individuals of the group, while medium-sized non-siblings were less connected. The siblings in this treatment were better connected when they were the smallest individuals of the group.

The relative mass increase was significantly higher for siblings than for non-siblings in this treatment, but was not explained by rank or relation degree (Fig. 2, Table 6).

Discussion

Understanding the evolutionary significance of animal social networks requires measuring their fitness effects on the level of groups and populations (Krause et al. 2007) as well as their fitness effects on individual group members (Fewell 2003). Another important approach is to identify the influencing factors on the social network structure of a group. We studied the social network structure of the subsocial crab spider *A. ergandros* in a foraging context depending on group composition (siblings, siblings with two non-siblings, assorted spiderlings) and found that "pure" families had the strongest social network structure as they were displaying high density and intensive connections (strong edges) between individuals. Families including two non-siblings were less connected compared with families containing exclusively siblings. We asked whether the latter is the result of the two non-siblings being excluded, which would reduce the average parameters describing the social network structure of the whole group and found that only medium sized non-siblings were less connected, but that small non-siblings were socially well included and that large non-siblings even showed a higher connectivity than large siblings in this treatment. This indicates that non-siblings are not generally separated, but that their presence—depending on their body mass relative to the other group members—negatively affects the network structure of the whole group by reducing the overall connectivity between siblings.

Table 6 Effect of origin (sibling/foreign) relation degree and rank on individuals' mass increase in the sibling+2 treatment only

Response	Analysis	Explanatory variables	Test	*df*	*P*
Relative mass increase	GLS with normal distribution, correlation structure specified as exchangeable (compound symmetry) for group ID and constant variance function for origin N=9 groups, 56 individuals	Origin	L ratio=4.50	4	*0.03*
		Rank	L ratio=2.45	6	0.11
		Relation degree	L ratio=2.84	5	0.09

Test statistics, *df*, and *P* values of non-significant variables stem from the step when a variable was dropped from the model, and *df* vary depending on the number of remaining variables. Italic *P* values show significant variables that remained in the final model. Interactions were not significant and test statistics not shown here

The social network structure likely affects the evolution of sociality (Kurvers et al. 2014). In populations with non-random interactions, kin selection has been suggested to be a key element promoting the evolution of sociality (Lion and van Baalen 2008). For example, natural fish shoals approached a novel foraging area earlier than assorted groups and thus had a foraging advantage (Morrell et al. 2008). Barnacle geese also preferentially associate with relatives when foraging (Kurvers et al. 2013), and in a colony of Bechstein's bats, related bats had significantly stronger and consistent social associations (Kerth et al. 2011). In guppies, however, relatedness does not explain the occurrence of strong social associations (Croft et al. 2012).

Our findings strongly support the idea that individuals in family groups have a fitness advantage over individuals in groups of unrelated individuals, which is mediated not only through increased foraging times (Ruch et al. 2014a) but also through better connectivity independent from foraging times (shown by a significant effect of the relation degree on relative mass increase). The differences in connectivity of differently sized non-siblings in *A. ergandros* indicate the existence of a factor influencing the social network structure on a second level after kinship, which is the effect of body mass. Our results suggest that the tolerance of related group members towards the inclusion of a foreigner, mirrored by the individual relation and weighted degrees of the latter, is affected by the foreigner's body mass. Group members display higher tolerance towards relatively small and relatively large unrelated spiders, which is shown by the high connectivity of foreign individuals being either ranked smallest or largest. It could be assumed that relatively small foreign individuals are not considered to be a severe feeding competition, and/or significantly reduce the individual predation risk (Lengyel 2007) and are therefore better accepted. Unlike predicted, large spiderlings did not monopolize prey. A possible explanation for the high connectivity of relatively large non-siblings could be a benefit for the group when it comes to prey capture. Large individuals might be able to capture larger prey on which the group members might feed communally. Consequently, medium-sized non-siblings would not promise a sufficient fitness increase and thus face a higher risk of being excluded from the group's social interactions.

Alternatively, large spiders may be dominant over smaller ones since body size generally determines dominance in animals including spiders. However, our findings contradict a potential dominance of larger spiders at least in the examined feeding context. Not only did we find that smaller spiderlings were growing better than larger ones but also that smaller spiderlings had a higher feeding network structure in the sibling treatment including two non-siblings. In the social spider *Stegodyphus dumicola*, contest competition seems to predict resource distribution, with larger spiders having an advantage over smaller ones (Whitehouse and Lubin 1999). In contrast, our results indicate that contest competition as in *S. dumicola* with high body mass being an advantage does not explain differences in growth in *A. ergandros*. In this species, individuals initiating an attack and having the longest feeding times grow best (Ruch et al. 2014a). Our findings therefore imply that in *A. ergandros*, scramble competition predicts how resources are shared. In scramble competition, growth strongly depends on the order of arrival at the resource (Whitehouse and Lubin 1999). Thus, the high connectivity of the small spiderlings—which grew best—might serve as a clear advantage in accessing food resources in this competition concept. While individuals compete during the process of food ingestion with no apparent advantage for a second individual to feed on prey already being fed on in *S. dumicola* (Amir et al. 2000), *A. ergandros* spiderlings seem to benefit from high connectivity and thus from sharing the resource.

In addition, relative body mass could be considered a significant determining factor on the social networking of *A. ergandros* groups, with heterogeneity in spiderling size positively influencing the density and weight of interactional relations. However, this does not explain the negative effects on the overall connectivity in groups of siblings containing two non-siblings. The finding that non-siblings were similarly connected but grew less than the respective siblings in this treatment suggests that reduced growth may be a result of an enzyme incompatibility (Schneider 1996). In this case, components of the digestive enzyme of unrelated individuals may interfere during communal feeding, which may reduce the overall digestive efficiency (Schneider 1996).

For future studies, it would be interesting to investigate which other factors influence network structure. Possible candidates might be personality composition (Pruitt and Riechert 2009; Pruitt and Riechert 2011), familiarity, and competitive asymmetries.

Acknowledgments We would like to thank Gerald Kerth, Mark Elgar, and an anonymous reviewer for helpful comments on the manuscript. JR was funded by an international scholarship of Macquarie University.

References

Amir N, Whitehouse MEA, Lubin Y (2000) Food consumption rates and competition in a communally feeding social spider, *Stegodyphus dumicola* (Eresidae). J Arachnol 28:195–200

Avilés L (1997) Causes and consequences of cooperation and permanent-sociality in spiders. In: Choe JC, Crespi BJ (eds) The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge, Massachusetts, pp 476–498

Brown JL (1983) Cooperation—a biologist's dilemma. In: Rosenblatt J (ed) Advances in the study of behavior. Academic Press, pp 1-37

Cameron EZ, Setsaas TH, Linklater WL (2009) Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci U S A 106:13850–13853

Choe JC, Crespi BJ (1997) Explanation and evolution of social systems. In: Choe JC, Crespi BJ (eds) The evolution of social behaviour in

Insects and Arachnids. Cambridge University Press, Cambridge, Massachusetts, pp 499–524

Croft DP, Hamilton PB, Darden SK, Jacoby DMP, James R, Bettaney EM, Tyler CR (2012) The role of relatedness in structuring the social network of a wild guppy population. Oecologia 170:955–963

Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R (2009) Behavioural trait assortment in a social network: patterns and implications. Behav Ecol Sociobiol 63:1495–1503

Croft DP, Krause J, James R (2004) Social networks in the guppy (*Poecilia reticulata*). Proc R Soc B 271:S516–S519

Émlen ST (1982) The evolution of helping: an ecological constraints model. Am Nat 119:29–39

Evans TA (1998a) Factors influencing the evolution of social behaviour in Australian crab spiders (Araneae: Thomisidae). Biol J Linn Soc 63:205–219

Evans TA (1998b) Offspring recognition by mother crab spiders with extreme maternal care. Proc R Soc B 265:129–134

Evans TA (1999) Kin recognition in a social spider. Proc R Soc B 266: 287–292

Evans TA, Goodisman MAD (2002) Nestmate relatedness and population genetic structure of the Australian social crab spider *Diaea ergandros* (Araneae: Thomisidae). Mol Ecol 11:2307–2316

Fewell JH (2003) Social insect networks. Science 301:1867–1870

González-Tokman D, Ruch J, Pulpitel T, Ponton F (2014) Cuticular antifungals in spiders: density- and condition dependence. Plos One 9: e91785

Hamilton WD (1964) The genetical evolution of social behaviour I & II. J Theor Biol 7:1–52

Hardin G (1968) The tragedy of the commons. Science 162:1243–1248

Kerth G, Perony N, Schweitzer F (2011) Bats are able to maintain long-term social relationships despite the high fission–fusion dynamics of their groups. Proc R Soc B

Krause J, Croft DP, James R (2007) Social network theory in the behavioural sciences: potential applications. Behav Ecol Sociobiol 62:15–27

Krause J, James R, Croft DP (2010) Personality in the context of social networks. Philos Trans R Soc B 365:4099–4106

Kurvers R, Adamczyk V, Kraus RHS, Hoffman JI, van Wieren SE, van der Jeugd HP, Amos W, Prins HHT, Jonker RM (2013) Contrasting context dependence of familiarity and kinship in animal social networks. Anim Behav 86:993–1001

Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M (2014) The evolutionary and ecological consequences of animal social networks: emerging issues. Trends Ecol Evol 29:326–335

Lengyel S (2007) Benefits of large broods by higher chick survival and better territories in a precocial shorebird. Behav Ecol Sociobiol 61: 589–598

Lion S, van Baalen M (2008) Self-structuring in spatial evolutionary ecology. Ecol Lett 11:277–295

Lubin Y, Bilde T (2007) The evolution of sociality in spiders. Adv Stud Behav 37:83–145

Lusseau D, Newman MEJ (2004) Identifying the role that animals play in their social networks. Proc R Soc B 271:S477–S481

Marcoux M, Lusseau D (2013) Network modularity promotes cooperation. J Theor Biol 324:103–108

Morrell LJ, Croft DP, Dyer JRG, Chapman BB, Kelley JL, Laland KN, Krause J (2008) Association patterns and foraging behaviour in natural and artificial guppy shoals. Anim Behav 76:855–864

Naug D (2009) Structure and resilience of the social network in an insect colony as a function of colony size. Behav Ecol Sociobiol 63:1023–1028

Pike TW, Samanta M, Lindstrom J, Royle NJ (2008) Behavioural phenotype affects social interactions in an animal network. Proc R Soc B 275:2515–2520

Pruitt JN, Riechert SE (2009) Frequency-dependent success of cheaters during foraging bouts might limit thier spread within colonies of a socially polymorphic spider. Evolution 63:2966–2973

Pruitt JN, Riechert SE (2011) How within-group behavioural variation and task efficiency enhance fitness in a social group. Proc R Soc B 278:1209–1215

Royle NJ, Pike TW, Heeb P, Richner H, Kolliker M (2012) Offspring social network structure predicts fitness in families. Proc R Soc B 279:4914–4922

Ruch J, Heinrich L, Bilde T, Schneider JM (2009) Relatedness facilitates cooperation in the subsocial spider, *Stegodyphus tentoriicola*. BMC Evol Biol 9

Ruch J, Herberstein ME, Schneider JM (2014a) Families hunt more successfully: effect of group composition on hunting and communal feeding. Anim Behav 91:170–177

Ruch J, Herberstein ME, Schneider JM (2014b) Offspring dynamics affect food provisioning, growth and mortality in a brood-caring spider. Proc R Soc B 281

Schneider JM (1996) Differential mortality and relative maternal investment in different life stages in *Stegodyphus lineatus* (Araneae, Eresidae). J Arachnol 24:148–154

Schneider JM, Bilde T (2008) Benefits of cooperation with genetic kin in a subsocial spider. Proc Natl Acad Sci U S A 105:10843–10846

Silk JB (2007) Social components of fitness in primate groups. Science 317:1347–1351

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc B 276:3099–3104

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010) Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol 20:1359–1361

Szymkowiak P (2014) Revision of Australian species of the genus *Diaea* (Araneae: Thomisidae) with redefinition of their taxonomic status. Ann Zool 64:333–477

Unglaub B, Ruch J, Herberstein ME, Schneider JM (2013) Hunted hunters? Effect of group size on predation risk and growth in the Australian subsocial crab spider *Diaea ergandros*. Behav Ecol Sociobiol 67:785–794

Whitehouse MEA, Lubin Y (1999) Competitive foraging in the social spider *Stegodyphus dumicola*. Anim Behav 58:677–688

Yip EC, Rayor LS (2014) Maternal care and subsocial behaviour in spiders. Biol Rev 89:427–449

DECLARATION

Certificate of Originality

English: I hereby declare that the contents of this thesis entitled "Social foraging and exploitative behaviour in group-living crab spiders" are a record of my own original work, except where other contributors are named. In detail, my contributions and those of others are listed in the below statement.

German: Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen verwendet habe. Mein Anteil an Konzeption, Durchführung und Berichtsabfassung, sowie die Beiträge Anderer sind im „Contribution Statement" im Einzelnen dargelegt.

Marlis Dumke
Hamburg, December 2017

Approvals

As all studies presented in this thesis were conducted on invertebrates, ethics approvals were not required. To collect the species *Australomisidia socialis* for Chapter 2, a 'Licence to take Fauna for Scientific Purposes' (Reg. 17) as well as a 'Scientific or other prescribed purposes licence to take native flora from Crown land' were obtained from the Department of Parks and Wildlife of the Government of Western Australia.

Contribution Statement

Chapter 1 | General Introduction

I, Marlis Dumke, wrote the general introduction. My doctoral supervisors Jutta M. Schneider and Marie E. Herberstein edited the general introduction.

Chapter 2 | Extended maternal care and offspring interactions in the subsocial Australian crab spider *Xysticus bimaculatus*

As a solo author paper, this chapter was conceived entirely and independently by me. Jay A. Stafstrom and Vincent Stangenberg assisted with spider collection during two field trips, which were organized and led by me. The manuscript was improved thanks to valuable comments made by Jutta M. Schneider, Marie E. Herberstein and two anonymous reviewers.

Chapter 3 | Advantages of social foraging in crab spiders: groups capture more and larger prey despite the absence of a web

The third chapter was written by me, with contributions to structure, content and writing style of the manuscript by Marie E. Herberstein and Jutta M. Schneider. All authors were equally involved with the design of the project. I organized and led four field trips to collect the spiders, Marie E. Herberstein, Giselle Muschett, Ina Geedicke and Pauline Scholzgart assisted with spider collection. Experiments and data analyses were carried out by me, except that Pauline Scholzgart helped with the experimental preparations and experiments on *Australomisidia socialis*. Leigh W. Simmons provided lab space and equipment at the University of Western Australia in Perth (WA).

Chapter 4 | Producers and scroungers: feeding-type composition changes with group size in a socially foraging spider

The reserach presented in this chapter was conducted by me. Marie E. Herberstein and Jutta M. Schneider contributed to the conceptual design of the study. Marie E. Herberstein further assisted with spider collection during a jointly organized fieldtrip. I performed all experiments and data analyses, and I wrote the paper. Marie E. Herberstein and Jutta M. Schneider made substantial suggestions to develop the manuscript. Ines Dumke provided feedback on the wording, and the paper was further improved by the comments of two anonymous reviewers.

Chapter 5 | Stable cooperation among social predators: female defectors are outplayed by male providers

This project was carried out by me, Jutta M. Schneider, the bachelor's student Tanja Rüthemann and Marie E. Herberstein. All authors contributed equally to the study design. I organized and led the field trips to collect spiders, with assistance from Giselle Muschett and Ina Geedicke. I performed the group-composition experiment and Tanja Rüthemann performed the sex-differences experiment. Jasmin Ruch and James C. O'Hanlon gave guiding advice. Descriptive analyses were performed by me and Tanja Rüthemann, statistical data analyses were carried out by me. I wrote the manuscript; Jutta M. Schneider and Marie E. Herberstein proposed amendments to the content. A discussion of the content with Lutz Fromhage helped to further develop the manuscript.

Chapter 6 | General Discussion

I wrote the general discussion. Marie E. Herberstein and Jutta M. Schneider made improving comments and suggestions.