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

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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 *X. 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 *X. bimaculatus* as a suitable model for investigating the regulation of communal feeding in group-living spiders.

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Introduction

Extended maternal care, defined as any posthatching maternal behaviour that enhances the fitness of the mother’s offspring (Clutton-Brock 1991; Klug et al. 2012), appears to be a prerequisite for the evolution of stable family groups and eusocial societies in invertebrates (Tallamy 1984; Lubin and 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 and 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 and Lubin 2011; Walter and 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 and Bilde 2007). These transitions particularly include the evolution of extended maternal care resulting in the initial formation of mother–offspring 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 and Lubin 2005; Avilés and Bukowski 2006; Schneider and 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 and 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 and 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
genus Australomisidia, 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 and 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) has 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 for 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 forests 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 versus 26.79% in
November). In further support, subadult and adult males were
exclusively found late in the year. X. bimaculatus is remarkably
similar in 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 (Nnests = 33) and 2016 (Nnests = 49) at Toohay Forest
(27°32'44.5"S, 153°02'47.3"E) and Mount Coo-Tha Forest
(27°27'41.4"S, 152°57'38.2"E) in Brisbane, Queensland. 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
(after 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
samples (treatment). This matched-pairs design
reduced variation between treatments in otherwise 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 the 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 hydei). 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 min, 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 min 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 formula

\[
\text{spiderling weight change} = \log(\text{final weight/initial weight})
\]

(Crawley 2007). 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 through 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 spiderlings, was taken into account in the calculation of the feeding parameters scrounger percentage and scrounger percentage for spiderling attacks (Table 1).

Statistical analyses
Descriptive statistics are given as mean ± s.e. 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 (Npairs = 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 summarising the behaviour of groups over the eight trials (number of attacks (Table 1) and spiderling mortality) were analysed using Poisson and binomial GLMMs (generalised 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 (Nnests = 7) or contained only subadult spiders (Nnests = 7). The early-instar nests were constructed from 5.98 ± 0.28 leaves (range = 2–14 leaves, Nnests = 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 containing 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

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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of attacks</td>
<td>Sum of attacks over the eight trials (per group)</td>
</tr>
<tr>
<td>Number of spiderling attacks</td>
<td>Sum of attacks over the eight trials (per group) being performed by one or more spiderlings</td>
</tr>
<tr>
<td>Attack latency</td>
<td>Time in minutes until attack (per group and trial)</td>
</tr>
<tr>
<td>Attack latency of spiderlings</td>
<td>Time in minutes until attack (per group and trial) being performed by one or more spiderlings</td>
</tr>
<tr>
<td>Scrounger percentage</td>
<td>Maximal number of simultaneously scrounging spiderlings in relation to the theoretically possible maximum number (per group and attack)</td>
</tr>
<tr>
<td>Scrounger percentage for spiderling attacks</td>
<td>Maximal number of simultaneously scrounging spiderlings in relation to the theoretically possible maximum number (per group and attack) for attacks being performed by spiderlings</td>
</tr>
</tbody>
</table>
a maximum of 33 spiderlings, resulting in a mean of $11.27 \pm 0.72$ 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 $<1.5 \text{ mm}$: $N_{\text{nests}} = 19$; Size Class 2, with $1.5–2.5 \text{ mm}$: $N_{\text{nests}} = 25$; Size Class 3, with $2.5–3.5 \text{ mm}$: $N_{\text{nests}} = 19$), with the exception of one nest group assigned to Size Class 4 ($3.5–4.5 \text{ mm}$). 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 (Fig. 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; Fig. 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; Fig. 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; Fig. 1c). The scrounger percentage for spiderling attacks, however, did not differ between treatments (Table 2; Fig. 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 spiderlings fed alone) did not differ between treatments. A reanalysis 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 GLMM (binomial) $\chi^2 = 11.94$, $P = 0.0005$

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

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

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.
Maternal care and offspring interactions in a crab spider

The maternal weight change values showed that all mothers (except one) lost weight over the course of the experiment, even though they had attacked the prey in most cases (Fig. 1a). Specifically, maternal weight at the end of the trials was lowered by $6.45 \pm 3.28\%$ compared with the initial weight, which translated into an absolute maternal weight change of $-0.72 \pm 0.38$ 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 canonical trend for maternal weight loss (one-sided sign test: paired: $s = 1, P = 0.0625$, $N_{\text{mothers}} = 7$).

**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. Regarding 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 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 and 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 and 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 (Yip and Rayor 2014, data from 35 species). 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

![Fig. 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 for attacks performed by spiderlings in the ‘mother present’ treatment $\left(N_{\text{attacks}} = 42\right)$ 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 $\left(N_{\text{attacks}} = 12\right)$. The asterisk marks a significant treatment difference.](image-url)
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 and 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. Coleotes terrestris: Gundermann et al. 1991; Amaurobius ferox: Kim and 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 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 and 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,
higher numbers of hungry spiderlings in orphaned groups, tended to exhibit extremes—however, this 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 and 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 and Rayor 2014). Maternal signalling 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 Anelesimus crassipes spiderlings correlates with a certain walking behaviour of the mother (Ito and 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 and Nentwig 2001). It remains to be studied whether maternal signalling 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. By scrounging, they repeatedly leave the costs associated with attacking—such as energy and venom use and the risk of injury (Kim et al. 2005)—to their ‘producer’-siblings while gaining the benefits of feeding (Barnard and 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 and Li 2009), producer–scrounger dynamics have been investigated only in the subsocial crab spider A. ergandros. Experimental evidence indicated that A. ergandros spiderlings specialise 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 specialisation 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. 2014; 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.

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