

# Benefits and costs of social foraging in velvet worms

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## Abstract

Group living is ubiquitous in nature, and social foraging is among the common forms of cooperative behaviour in animals. Understanding the evolution and maintenance of social foraging requires knowledge of the underlying benefits and costs to group members, though these are only known for few model taxa, which often lie at the extremes of social organisation. Here, we experimentally examined hypothesised benefits and costs of social foraging in the velvet worm *Euperipatoides rowelli*; the only Onychophoran currently known to live and forage in groups. To explore benefits, we tested the effects of natural group size and controlled prey size on the latency to attack and begin consuming prey, the likelihood of complete prey consumption and the time taken to completely consume prey. Our focal cost was aggressive intraspecific interactions in the form of biting, kicking and striking, which may present a particular risk to soft-bodied velvet worms. As predicted, we found a positive scaling of most effects with the size of foraging groups. Larger groups were faster to attack and begin consuming prey, and more likely to completely consume prey, though they took longer to do so. This may be a consequence of the increasing representation of juveniles in larger aggregations. However, larger groups were also subject to heightened aggression among conspecifics, though it is unclear whether such a cost holds at the level of individual group members. Variation in prey size and, hence, resource availability had little effect across all outcomes, except for a slightly reduced likelihood of completely consuming larger prey. A time-course analysis of individual activity suggested the existence of feeding hierarchies with adults excluding juveniles, particularly when resources are scarce. Taken together, our results offer the first support for the existence of foraging benefits and costs to group membership in *E. rowelli*, which may contribute to the maintenance of group living in this evolutionary significant taxon.

## KEYWORDS

group hunting, group living, onychophora, social foraging, sociality

## 1 | INTRODUCTION

Animals often live and forage in groups, though the extent of social organisation varies dramatically among taxa (Ward & Webster,

2016). The key to understanding the form, diversity and maintenance of group living lies in enumerating the balance of benefits and costs across two broad ecological contexts; anti-predator defence and foraging (Krause et al., 2002). In the former case, individuals in

larger groups may benefit from turning “many eyes” to the detection of predators, along with the “dilution” that arises from being one possible target among many (Ale & Brown, 2007). With respect to foraging, members of larger groups must contend with the inherent costs of food competition, such as conspecific aggression and reduced per-capita resource share (Grand & Dill, 1999; Rubenstein, 1978). However, this can be counterbalanced if larger groups can secure a higher quantity or quality of prey, or process resources more efficiently (Giraldeau & Caraco, 2000; Krause et al., 2002). The pooling of information, effort or resources are among the general predicted benefits of group foraging, with the latter two holding particular significance for predatory species who must not only locate but subjugate their prey, with all the risks that entail (Mukherjee & Heithaus, 2013).

Empirical insight into group foraging has centred upon model vertebrate systems such as mammals (Creel & Creel, 1995; Fanshawe & Fitzgibbon, 1993; Funston et al., 2001; Holekamp et al., 1997), birds (Beauchamp, 2012; Cook et al., 2017; Harel et al., 2017; Krebs et al., 1972) and fish (Grand & Dill, 1999; Harpaz & Schneidman, 2020; Johnsson, 2003; Pitcher et al., 1982), or invertebrates at the extremes of social organisation (i.e. eusocial ants and bees; Balbuena et al., 2012; Bockoven et al., 2015). A notable exception among invertebrates is social spiders, which cooperate in a variety of tasks including the construction and maintenance of communal webs, foraging, colony defence and brood care (Avilés, 1997; Avilés et al., 2017; Grinsted & Lubin, 2019; Grinsted et al., 2020; Lubin & Bilde, 2007; Pruitt & Avilés, 2018; Whitehouse & Lubin, 2005; Wilson, 1971). Across spider groups, several theoretical benefits to collective foraging have been observed, including improved rates of feeding and prey capture, and access to a broader spectrum of prey sizes and types (Majer et al., 2018; Nentwig, 1985; Pasquet & Krafft, 1992; Rypstra & Tirey, 1991; Vanthournout et al., 2016; Ward, 1986; Yip et al., 2008). However, intraspecific competition for resources is a powerful counter to these benefits and has been forwarded as an explanation for the phylogenetic rarity of group living among spiders more generally (Amir et al., 2000; Avilés et al., 2017; Rubenstein, 1978). Outside of this relatively well-developed context, our knowledge of the evolutionary drivers of group foraging remains functionally and taxonomically constrained; a crucial limitation in light of the sheer diversity of strategies showcased among arthropods (Lihoreau et al., 2010; Nowak et al., 2010; Purcell et al., 2012; Wilson & Hölldobler, 2005). A richer causal understanding of collective foraging is of considerable theoretical interest as it bears important consequences for the fitness of individuals within groups (Clark & Mangel, 1986).

Velvet worms (phylum Onychophora) are soft-bodied carnivorous invertebrates patchily distributed throughout tropical and temperate forests (Mayer et al., 2015; de Sena Oliveira et al., 2012). They tend to occur in small, isolated populations and have an affinity for moist, humid microhabitats, such as the interior of decaying logs and leaf litter (Barclay et al., 2000a; Reid, 1996; Scott & Rowell, 1991). Dispersal outside of these saproxylic environments is restricted as velvet worms are vulnerable to desiccation due to their persistently



FIGURE 1 Aggregating behaviour of adult onychophoran *Euperipatoides rowelli*. (Photograph courtesy: T. Latty)

open spiracles and the absence of a waterproof integument (Clusella-Trullas & Chown, 2008; Periera et al., 1985; Woodman et al., 2007).

When hunting, velvet worms employ a unique mode of prey capture using a projectile non-toxic adhesive slime secretion to ensnare their prey (Baer et al., 2019). This glue-like slime secretion is produced and stored within dedicated glands, where it is ejected rapidly from a pair of specialised papillae (Baer & Mayer, 2012; Haritos et al., 2010). Once immobilised, the prey is injected with salivary enzymes to initiate extra-oral digestion prior to consumption (Mayer et al., 2015). Capturing prey poses a considerable energetic cost as shown in the velvet worm *Macroperipatus torquatus*, for whom the volume of stored slime comprises on average 11% of the organism's body mass and requires approximately 24 days to replenish after depletion (Read & Hughes, 1987). Further, the efficiency of extra-oral digestion may be linked to the volume of available enzymes, as is the case in comparable systems (Schneider & Bilde, 2008; Vanthournout et al., 2016). Indeed, the pooling of “expensive” resources for prey capture and sharing of costs for prey processing are among the key contributors to the maintenance of group living in social spiders (Avilés et al., 2017), which argues for a similar potential among velvet worms. However, limited evidence of group hunting and feeding within the Onychophora has been described (Read & Hughes, 1987; Reinhard & Rowell, 2005).

*Euperipatoides rowelli* (Reid, 1996) is a species of velvet worm endemic to the temperate forests of New South Wales, Australia (Bull et al., 2013; Reid, 1996; de Sena Oliveira et al., 2012; Figure 1). They live in aggregations within the decaying heartwood of *Eucalyptus/Corymbia* sp. logs and prey upon small invertebrates, such as termites and crickets (Barclay et al., 2000a, 2000b). Though our understanding of their natural history is nascent, evidence suggests individuals form close social groups and partake in collective hunting and feeding (Reinhard & Rowell, 2005). There is also evidence for hierarchical organisation within groups, which is characterised by dominant females establishing their rank through aggression (e.g.

biting, kicking and striking) and subsequently monopolising feeding opportunities (Reinhard & Rowell, 2005). The discovery of social behaviour in *E. rowelli* suggests the behavioural tendencies of Onychophorans may be more complex than previously documented (e.g. Barclay et al., 2000a, 2000b; Monge-Nájera & Aguilar, 1993; Read & Hughes, 1987; Sunnucks et al., 2000). More broadly, the existence of group living, combined with the placement of velvet worms as the sister group to the Arthropoda (Campbell et al., 2011; Giribet, 2016), presents *E. rowelli* as a promising model for examining the emergence and maintenance of less-extreme forms of social living, as well as the broader ecology of this cryptic and evolutionarily significant phylum.

Here, we used experimental assays to examine several hypothesised benefits and costs of social foraging in the velvet worm *E. rowelli*. Specifically, we tested the effects of variation in group size and prey size on four benefits: the latency to attack prey, the latency to begin consuming prey, the likelihood of complete prey consumption and the time to completely consume prey—and one potential cost—aggressive intraspecific interactions. In each case, theory predicts the positive scaling of effects with group size, such that larger groups should experience both improved foraging success and processing efficiency, as well as heightened intraspecific aggression relative to smaller aggregations.

## 2 | METHODS

### 2.1 | Specimen provenance and housing

We collected 122 individuals (85 adults, 37 juveniles) comprising 31 groups (ranging from 1–17 individuals in each; see table S1 for further detail) from decaying *Eucalyptus/Corymbia* sp. logs located within a single biogeographic region in the Tallaganda State Forest (New South Wales, Australia), between January and May of 2019. We sampled decomposing logs haphazardly within a 100 m radius of the study site (35°26'30.4"S, 149°35'56.6"E), and velvet worms were considered to belong to a "group" if they were collected within 0.5 m of one another in the same log, as consistent with previous literature (Reinhard & Rowell, 2005). We have no reason to believe our sample is biased or limited with respect to social background, trappability and self-selection, rearing history, natural changes in responsiveness or experience.

Once collected, we housed each group separately in enclosed plastic containers (17.2 × 12 × 5 cm), again consistent with previous literature (Reinhard & Rowell, 2005), and a temperature-controlled laboratory setting (18 ± 1°C) on a 12-h light:dark cycle. To mimic natural conditions, the housing containers comprised a moistened substrate layer of peat moss to a depth of 2–3 cm, moist sphagnum moss and decayed *Eucalyptus/Corymbia* sp. bark. Adults are morphologically distinguishable from juveniles by their size and the deep blue pigmentation characteristic of this species (Scott & Rowell, 1991; Figure 1). Smaller and less pigmented individuals were, therefore, classed as juveniles. Outside of trials, all containers were kept

closed and stored in a persistently dark box to imitate the natural temperature, humidity and lighting conditions within a log. Prior to this study, all groups were fed a controlled diet of field crickets (*Acheta domesticus*) every two weeks and enclosure contents were replaced every four weeks.

### 2.2 | Experimental procedures

We carried out the experiment at The University of Sydney, Australia, between January and March of 2020. To investigate foraging behaviour during prey hunting and feeding we used a repeated-measures design in which each *E. rowelli* group ( $n = 31$  groups, comprising  $n = 1$ –17 individuals; table S1) was offered a small ( $0.033 \pm 0.006$  g) and large ( $0.225 \pm 0.030$  g) field cricket (*Acheta domesticus*) across two separate trials, in a randomised order. Each trial was preceded by a 7–21 day starvation period to ensure velvet worms were motivated to feed. The variation in the starvation period was a consequence of COVID-19 restrictions and although initially included in our statistical models, was later removed owing to its lack of explanatory power. Before each trial, we removed all contents of the housing container except for the substrate layer for ease of observation. Contents were removed ca. 70 minutes before the commencement of a trial to allow groups to become accustomed to the slightly altered environment.

At the commencement of a given trial, we introduced a live cricket into a haphazard location in a group's housing container, which we both continuously observed and recorded (Sony Handycam HDR-CX405) until the termination of the trial. A trial was terminated when any of the following four criteria were met: the prey was not attacked after one hour from the time of prey drop (with an "attack" defined as the ejection of slime towards the prey), an initial bite was not taken after one hour from the time of the attack (or last attack, if multiple occurred), the prey was untouched by any velvet worm for 10 consecutive minutes after consumption had begun, or the prey was completely consumed (as defined below). All feeding trials were conducted with a transparent yellow sheet covering the open container to mimic nocturnal conditions and prevent photonegative behaviour, as velvet worms are insensitive to long-wavelength (i.e. yellow and red) light (Beckmann et al., 2015).

To quantify the consequences of group size and prey size on foraging, we derived four measures corresponding to each of the four hypothesised benefits (outlined above): the latency to attack prey, the latency to begin consuming prey, the likelihood of complete prey consumption and the time to completely consume prey. The latency to attack prey was defined as the total time (min) it took for a velvet worm to initiate its first attack on the prey. The latency to begin consuming prey was the total time (min) it took for a velvet worm to take an initial bite of the prey post attack. The likelihood of complete prey consumption was simply a binary measure of whether or not the prey's abdomen was entirely consumed, with no further feeding for 5 min. Finally, the time to completely consume prey denotes the total time (h) for complete consumption post initial bite.

To estimate the costs of group foraging, we continuously tallied the occurrence of aggressive behaviours directed towards conspecifics during each consumption period. We derived two measures of intraspecific competition corresponding to our focal hypothesised cost (outlined above): the number of aggressive interactions per minute, and the number of aggressive interactions per minute per-capita. The former reflects our group-level focus in quantifying the simple scaling of competition rates with the absolute size of a group, while the latter is an initial attempt at quantifying such costs at the level of individual group members. However, there is a crucial underlying assumption that such individual-level costs are borne equally among group members (see discussion for further detail). Aggressive behaviours displayed in interactions between conspecifics were defined as dominating behaviours, usually to restrict another individual's access to the prey, including biting, kicking and striking (Reinhard & Rowell, 2005). Finally, we also recorded the number and life stage (adult/juvenile) of velvet worms actively consuming the prey item at one-minute intervals for the entire duration of feeding.

## 2.3 | Statistical analyses

We used generalised linear-mixed models (GLMM) to test the effects of foraging group size and prey size on our four benefits and

one cost. Each of the five models included group size ( $n = 1-17$ ) and prey size (large/small crickets) as fixed effects. We initially specified an interaction term between group size and prey size, but as it was non-significant across all models, we maximised available power by only including main effects.

We modelled latency to attack prey (log-transformed) and aggressive intraspecific interactions (both absolute and per-capita rates) using a Gaussian error distribution and identity link function ( $n = 2$  trials excluded for non-attack and  $n = 31$  trials excluded due to group sizes of  $<2$ , respectively); latency to begin consuming prey using a Gamma distribution with log link ( $n = 10$  trials excluded for non-consumption of prey); likelihood of complete prey consumption as binomial with a logit link; and time to completely consume prey as Gaussian with a log link function ( $n = 29$  trials excluded owing to incomplete consumption of prey). We included colony ID as a random effect in all models to account for the repeated-measures experimental design. In all models, we mean-centred and standardised continuous predictors by dividing with their standard deviation, for ease of interpretation and comparison. See Table 1 for final sample sizes in all models.

Separate from the above, we also used a generalised additive-mixed model (GAMM) to explore the dynamics of juvenile and adult feeding over time. We specified the mean proportion of adults or juveniles actively feeding at every one-minute interval

**TABLE 1** Standardised and mean-centred parameter estimates and summary statistics from linear-mixed models examining the effects of foraging group size ( $n = 1-17$ ) and prey size (small/large) on four hypothesised benefits and one hypothesised cost of social foraging in the velvet worm *Euperipatoides rowelli*

Response	n	Parameter	Estimate	SE	t	P	R <sup>2</sup>
Latency to attack prey (m)	60	Intercept	0.264	0.340	0.776	.441	.116 (0.116)
		<b>Group size</b>	<b>-0.099</b>	<b>0.045</b>	<b>-2.181</b>	<b>.033</b>	
		Prey size	-0.064	0.370	-1.721	.090	
Latency to begin consuming prey (m)	52	<b>Intercept</b>	<b>0.800</b>	<b>0.210</b>	<b>3.803</b>	<b>&lt;.001</b>	<b>.270 (0.614)</b>
		<b>Group size</b>	<b>-1.360</b>	<b>0.396</b>	<b>-3.430</b>	<b>&lt;.001</b>	
		Prey size	0.417	0.294	1.416	.157	
Likelihood of complete prey consumption	62	<b>Intercept</b>	<b>2.765</b>	<b>1.134</b>	<b>2.437</b>	<b>.015</b>	<b>.615 (0.615)</b>
		<b>Group size</b>	<b>13.727</b>	<b>4.233</b>	<b>3.242</b>	<b>.001</b>	
		<b>Prey size</b>	<b>-2.428</b>	<b>0.940</b>	<b>-2.583</b>	<b>.010</b>	
Time to completely consume prey (h)	33	Intercept	0.213	0.119	1.787	.074	.258 (0.306)
		<b>Group size</b>	<b>0.585</b>	<b>0.158</b>	<b>3.704</b>	<b>&lt;.001</b>	
		Prey size	0.284	0.157	1.809	.070	
Aggressive intraspecific interactions (per minute)	31	<b>Intercept</b>	<b>0.425</b>	<b>0.090</b>	<b>21.531</b>	<b>&lt;.001</b>	<b>.247 (0.440)</b>
		<b>Group size</b>	<b>0.480</b>	<b>0.163</b>	<b>21.084</b>	<b>.008</b>	
		Prey size	-0.233	0.139	25.618	.106	
Aggressive intraspecific interactions (per minute per-capita)	31	<b>Intercept</b>	<b>0.305</b>	<b>0.058</b>	<b>5.202</b>	<b>&lt;.001</b>	<b>.068 (0.321)</b>
		Group size	0.003	0.007	0.355	.762	
		Prey size	-0.093	0.050	-1.876	.072	

Note: Latency to attack prey and aggressive intraspecific interactions (both absolute and per-capita rates) were modelled with Gaussian errors and an identity link function, latency to begin consuming prey as Gamma with a log link, likelihood of complete prey consumption as binomial with a logit link, and time to completely consume prey as Gaussian with a log link. Colony ID was included as a random effect in all models to account for the repeated-measures experimental design. Marginal R<sup>2</sup> values are reported, with conditional equivalents in parentheses. Bolding indicates parameters significant at  $\alpha = .05$ .

during the trial as the response, using a quasibinomial error distribution and logit link function. We again included group size ( $n = 1-17$ ) and prey size (large/small) as fixed effects, with the trial time (minutes) specified as a smooth term for each of the four-way combinations of adult/juvenile and large/small prey. As above, we included colony ID as a random effect to account for the repeated-measures design.

We performed all statistical analyses in R (v4.0.3; R Core Team, 2018) using the packages lme4 (v1.1-23; Bates et al., 2014) and lmerTest (v3.1-2; Kuznetsova et al., 2017) for mixed modelling. We visually confirmed model assumptions by examining residuals simulated from each model using the package DHARMA (v0.3.2.0; Hartig, 2020).

## 2.4 | Ethical statement

We collected all specimens under NSW Parks and Estates Scientific Investigation Licence No. SL102253 and Forest Permit No. RES100032.

## 3 | RESULTS

### 3.1 | Benefits and costs of group foraging

Our results identified significant effects of foraging group size variation on each of our measured outcomes in broad, but not complete, alignment with our predictions (see Table 1 for full numerical results). The effects of prey size were substantially weaker across all outcomes (Figure 2). Across all treatments, our foraging groups took an average of  $2.2 \pm 6.2$  (s.d.) min to capture the prey and  $3.8 \pm 5.5$  min to subsequently begin consumption. Prey items were completely consumed within  $1.55 \pm 0.93$  h. Aggressive interactions were frequent and averaged  $0.51 \pm 0.56$  conspecific encounters per minute across all groups.

With respect to benefits, we found larger groups of velvet worms were slightly faster to attack prey, and this effect held irrespective of the prey size (Figure 2a). Larger groups were also faster to begin consuming prey (Figure 2b), which again was independent of prey size. Once subjugated, prey items were far more likely to be completely consumed by larger groups of velvet worms (Figure 2c). However, we also identified a prey size effect, with larger prey less likely to be completely consumed. Finally, and in the only departure from our predictions, we found group size had a moderately positive effect on the time taken to completely consume prey (Figure 2d). Here, the influence of prey size was ultimately non-significant across all measures, though there was a very weak tendency for larger prey to be consumed over a longer period.

As anticipated, our focal cost scaled positively with group size, though only in absolute terms (Figure 2e). Larger aggregations of velvet worms were subject to a greater number of aggressive interactions with conspecifics, per unit time. However, we identified no

significant group size effect on per-capita rates of aggressive interactions (Figure 2f). Further, we did not find substantive evidence that the frequency of aggressive encounters varied with the size of prey.

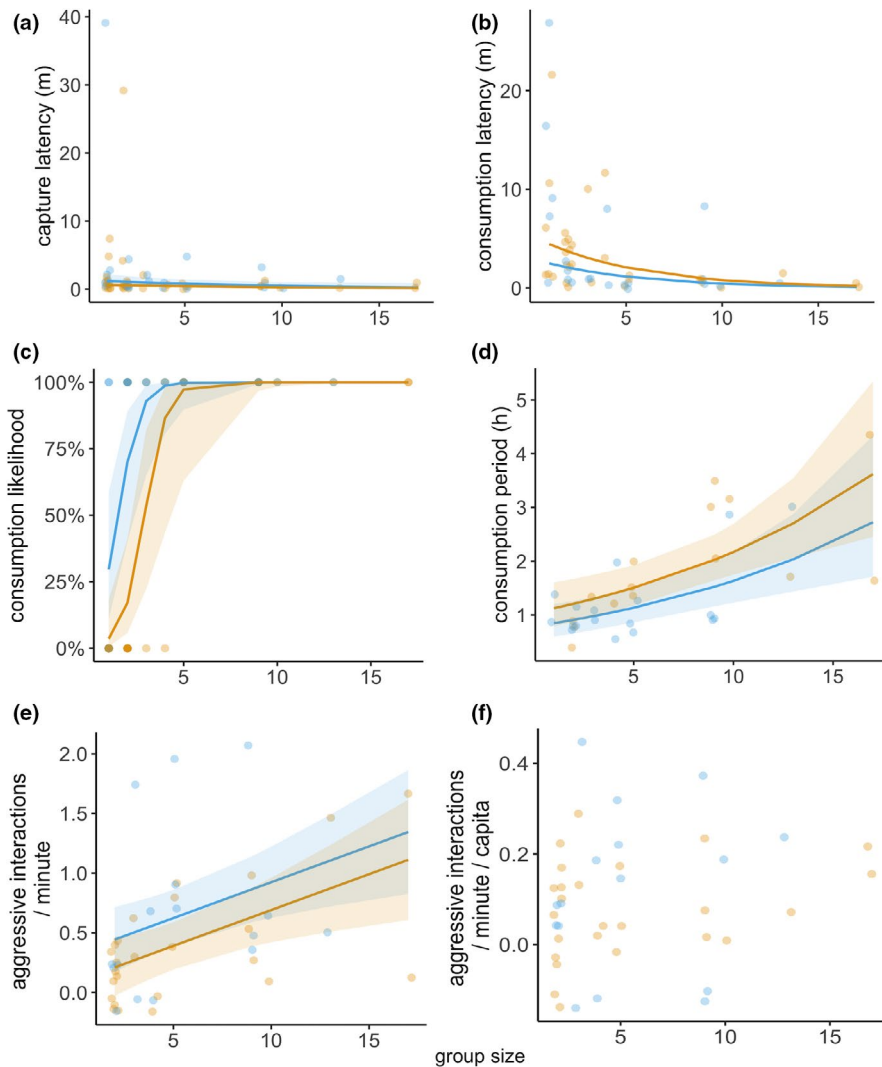
### 3.2 | Group feeding dynamics

Our GAMMs revealed the proportion of individuals feeding over time varied with life stage and prey size (see Table 2 for full numerical results). When facing large prey, both adult and juvenile velvet worms actively fed in approximately equal proportions and at similar times (Figure 3a). Feeding activity peaked ca. 30–60 min after prey capture and steadily decreased until the cricket was completely consumed. However, when facing small prey items, we found evidence for the partitioning of feeding activity among velvet worms across life stages (Figure 3b). Adult feeding activity peaked early at ca. 10 min post prey capture, before steadily declining over time. By contrast, most of the juvenile feeding activity was delayed until later in the trials, largely as a consequence of their active exclusion by adults (CAH pers. obs.). Peak activity occurred at ca. 110 min post-capture, with minor secondary spikes in feeding activity both earlier (ca. 10 min) and later (ca. 160 min) in the trials.

## 4 | DISCUSSION

Social living is a taxonomically widespread and functionally diverse behaviour dictating how animals meet basic challenges, such as foraging. Social foraging theory describes how group membership imparts benefits and costs to individual foragers, with evolutionary stability arising when the former outweigh the latter (Giraldeau & Caraco, 2000). Here, we experimentally examined hypothesised benefits and costs of social foraging in the Australian velvet worm *E. rowelli*; the only known Onychophoran to live and forage in groups. Our results reveal diverse effects of group size and prey size on resource acquisition among these unique social predators (Table 1; Figure 2).

As predicted, we found larger groups attacked prey more rapidly, though the effect was weak. Larger groups were also more likely to completely consume prey although, contrary to expectations, they took longer to do so (Figure 2d). Moreover, we identified an increase in the absolute rate of aggressive intraspecific interactions within larger foraging groups, with more frequent biting, kicking and striking of conspecifics (Figure 2e). The effects of prey size were statistically non-significant across all measures, with the exception that foraging groups were significantly less likely to completely consume larger prey. Taken together, our results offer the first evidence that group living confers foraging benefits and costs in *E. rowelli*. Further, this paper complements and expands on prior evidence in suggesting a role for social foraging in maintaining group living in this enigmatic species (Reinhard & Rowell, 2005). While our focus here was at the level of the group, we acknowledge such dynamics may not



**FIGURE 2** Effect of group and prey size on four hypothesised benefits (a-d), and one hypothesised cost (e-f), of social foraging in *Euperipatoides rowelli*. Depicted are (a) latency to attack prey, (b) latency to begin consuming prey, (c) likelihood of complete prey consumption, (d) time to completely consume prey, (e) aggressive intraspecific interactions per minute, and (f) aggressive intraspecific interactions per minute per-capita. Lines and shaded regions denote linear mixed-model fits  $\pm$  standard errors (see methods and Table 1 for full details), which are coloured to distinguish trials with large (blue) and small (orange) prey items

**TABLE 2** Parameter estimates and summary statistics from a generalised additive-mixed model examining the proportion of adult and juvenile *Euperipatoides rowelli* feeding over time ( $n = 52$  trials)

Parameter	Estimate	SE	$t$	$p$
Intercept	-0.313	0.103	-3.022	.003
Life stage	0.010	0.054	0.180	.857
Cricket size	-1.431	0.166	-8.614	<.001
Life stage $\times$ cricket size	0.495	0.192	2.581	.010
Smooth terms	edf		$F$	$p$
s(time) $\times$ adult w/ large prey	6.944		129.230	<.001
s(time) $\times$ adult w/ small prey	5.631		61.920	<.001
s(time) $\times$ juvenile w/ large prey	8.136		62.400	<.001
s(time) $\times$ juvenile w/ small prey	5.767		10.380	<.001

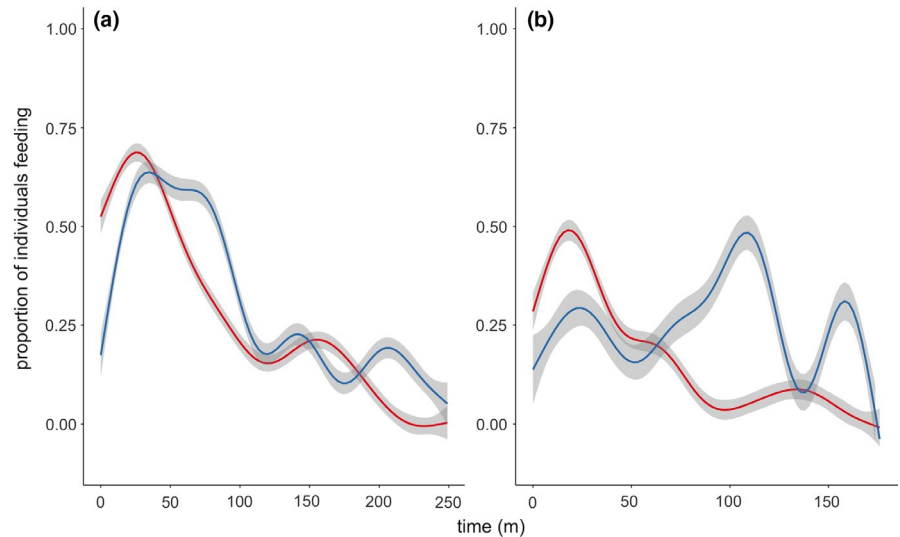
Note: Prey size (small/large) and the life stage of individuals (adult/juvenile) were included as main effects, time was specified as a smooth term, and colony ID was included as a random effect to account for the repeated-measures nature of the experimental assay. Adjusted  $R^2 = .312$ . Bolding indicates parameters significant at  $\alpha = .05$ .

map directly to all individuals therein, thus representing a pressing area for future study.

Our finding of a shorter latency to attack prey in larger groups (Figure 2a) suggests a direct relationship between the number of

velvet worms in a group and prey capture success. This is consistent with our knowledge that animals in larger groups tend to detect and encounter prey more frequently as a consequence of having the ability to cover a larger area when foraging, owing to a greater number

**FIGURE 3** Proportion of adult (red) and juvenile (blue) velvet worms feeding over time when foraging on (a) large and (b) small prey items. Lines denote generalised additive mixed-model fits  $\pm$  standard errors (see methods and Table 2 for full details)



of searchers (Cvikel et al., 2015; Pitcher et al., 1982). These effects may be amplified in environments where the immediate foraging space scales weakly (or not at all) with the size of foraging groups, as is the case in our experimental arenas and the log interiors inhabited by velvet worms (Barclay et al., 2000a). Such density effects are broadly aligned with previous findings in *E. rowelli* (Reinhard & Rowell, 2005), as well as studies of archetypal social foragers such as African wild dogs (Creel & Creel, 1995; Fanshawe & Fitzgibbon, 1993), lions (Funston et al., 2001) and spotted hyenas (Holekamp et al., 1997).

Once attacked, prey must be immobilised and subjugated before consumption can begin, although this process is not without risk for predators (Mukherjee & Heithaus, 2013). In velvet worms, this necessitates bringing prey under control with adhesive slime before puncturing their cuticle and injecting digestive saliva to begin emulsification, only then can feeding begin on the now-liquified remains (Baer & Mayer, 2012; Mayer et al., 2015). Therefore, our observation of a reduction in the latency to begin consuming prey with increasing group sizes, suggests larger groups are better able to surmount the initial challenges of subduing and handling prey.

We found a weak and non-significant effect of prey size on the latency to begin consumption, which contrasts the expectation larger prey may present a greater challenge or risk to foraging predators. Indeed, the direction of the prey size effect was as predicted, with slightly longer times taken to subdue larger prey (Table 1). However, across all measured outcomes the weak effect of prey size may be in part due to the limited variation in size and category of prey on offer in our experiment. Velvet worms are generalists who prey upon a suite of small invertebrates including termites, cockroaches, centipedes and spiders (Barclay et al., 2000b; Dias & Lo-Man-Hung, 2009; Read & Hughes, 1987; Scott & Rowell, 1991), which vary in the difficulty and intensity of threat posed to foragers. The literature in analogous systems such as social spiders has long shown how cooperation during foraging allows colonies to exploit larger and more dangerous prey than would be possible by individuals (Nentwig,

1985; Rypstra & Tirey, 1991; Ward, 1986). Our results suggest a similar potential exists among *E. rowelli*, though this awaits detailed study across a richer diversity of prey.

While larger groups were more likely to completely consume a given prey item, they took longer to do so. This latter point stands in contrast both to our initial prediction and to comparable work showing group membership can confer improved prey-processing efficiency, hence reducing an individual's exposure to threats such as predators and outgroup scavengers (Vanthournout et al., 2016). This result may, in part, be a consequence of group composition, since juveniles made up a larger proportion of groups as they increased in size (table S1). Our time-course data are consistent with the existence of a feeding hierarchy maintained by interference competition (Table 2; Figure 3), where dominant adults exclude subordinate juveniles from the feeding site in the early stages of prey consumption. This is akin to a producer-scrounger dynamic with adult producers contributing the majority of inputs to prey capture and reaping the initial rewards, before ceding access to juvenile scroungers who make use of residual resources (Barnard & Sibly, 1981; Giraldeau & Dubois, 2008). This subdivision of activity creates multiple feeding bouts on a given prey item (which is particularly acute when the prey item is small; Figure 3b) and may increase the total feeding time for larger groups disproportionately comprised of juveniles. Similar social hierarchies have been previously described in *E. rowelli* (Reinhard & Rowell, 2005) and are well-described in other systems (Edwards et al., 2003; Frank, 1986; Isbell, 1991; Whitehouse & Lubin, 1999; Wittig & Boesch, 2003), with a common consequence being intragroup competition and the unequal distribution of resources among group members.

Competition within groups, such as that suggested by our results (Figure 3), is a well-documented cost to group membership, which can take many forms (Chapman & Chapman, 2000; Wrangham et al., 1993). One is conspecific aggression, with larger groups expected to experience greater intragroup competition when foraging due to a rapid depletion of resources or increased likelihood of direct

interference by other group members (Beauchamp, 2012; Ward & Webster, 2016). Our results suggest a similar dynamic among *E. rowelli* (Figure 2e). In absolute terms, larger groups experienced markedly more incidents of biting, kicking and striking among individuals, which given the relatively fragile, soft-bodied anatomy of velvet worms, may inflict substantial injury. By contrast, this relationship did not hold when scaled by the number of group members, suggesting individuals may not face increased aggression within larger groups in per-capita terms (Figure 2f). This latter finding rests on the assumption that aggression is borne equally among group members, which we did not observe. Indeed, the vast majority of aggressive incidents were instigated by adults and directed towards juveniles or other adults, while little juvenile aggression was directed towards adults (unpublished data). Therefore, the positive scaling of absolute aggression with group size accords with the fact juveniles are over-represented within larger groups in our sample (table S1) and are actively and aggressively prevented from feeding before adults (as described above; Figure 3). Across both measures of aggression (i.e. absolute and per-capita rates), the weak and non-significant effect of prey size is again in the predicted direction (with increased aggression when facing smaller prey) and reflects the more active exclusion of juveniles by adults when resources are restricted (Figure 3b).

Here, we identify the accrual of several benefits and one cost of collective foraging in *E. rowelli*, which may contribute to the evolutionary maintenance of their group living. However, much remains to be learned. One pressing question is the extent to which group-level dynamics map to individual fitness, since the link is seldom direct. For example, a reduction in the latency to begin consuming prey at the group-level could indicate a scramble or contest to be first to feed. This may convey costs to subordinate individuals in the group who must compete with dominant members for a share of the resource. Thus, foraging benefits accrued at the level of the group are unlikely to be conferred to all at the individual-level, which can play an important role in shaping the trajectory of social evolution (M. Whitehouse & Lubin, 1999). Similarly, a richer understanding of individual-level costs, such as the expensive “slime” and extra-oral digestive enzymes required for prey processing (Read & Hughes, 1987), and their disproportionate contribution by adults, is vital. Further, previous work has documented differences in male and female foraging behaviour (Reinhard & Rowell, 2005), though we were unable to examine such effects in the present study owing to the impact of COVID-19 restrictions. Knowledge of the behavioural differences between sexes has clear relevance for better understanding the social dynamics in this species and is a valuable area for future study. More broadly, the presently unique status of *E. rowelli* as the only known velvet worm to exhibit social tendencies remains to be explained, as other species are yet to be studied in comparable detail. When taken alongside the position of the Onychophora as the sister group to arthropods, this system offers compelling opportunities for further probing the origins, maintenance and diversity of group living, which is a question of enduring biological fascination.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <https://dx.doi.org/10.5281/zenodo.5610337>.

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## REFERENCES

- Ale, S. B., & Brown, J. S. (2007). The contingencies of group size and vigilance. *Evolutionary Ecology Research*, 9(8), 1263–1276.
- Amir, N., Whitehouse, M. E., & Lubin, Y. (2000). Food consumption rates and competition in a communally feeding social spider, *Stegodyphus dumicola* (Eresidae). *The Journal of Arachnology*, 28(2), 195–200. [https://doi.org/10.1636/0161-8202\(2000\)028\[0195:FCRACI\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2000)028[0195:FCRACI]2.0.CO;2)
- Avilés, L. (1997). Causes and consequences of cooperation and permanent-sociality in spiders. *The evolution of social behavior in insects and arachnids* (p. 476498). Cambridge University Press.
- Avilés, L., Guevara, J., Rubenstein, D., & Abbot, P. (2017). Sociality in spiders. *Comparative Social Evolution*, 188–223.
- Baer, A., & Mayer, G. (2012). Comparative anatomy of slime glands in Onychophora (velvet worms). *Journal of Morphology*, 273(10), 1079–1088. <https://doi.org/10.1002/jmor.20044>
- Baer, A., Schmidt, S., Mayer, G., & Harrington, M. J. (2019). Fibers on the fly: multiscale mechanisms of fiber formation in the capture slime of velvet worms. *Integrative and Comparative Biology*, 59(6), 1690–1699. <https://doi.org/10.1093/icb/icz048>
- Balbuena, M. S., Molinas, J., & Farina, W. M. (2012). Honeybee recruitment to scented food sources: correlations between in-hive social interactions and foraging decisions. *Behavioral Ecology and Sociobiology*, 66(3), 445–452. <https://doi.org/10.1007/s00265-011-1290-3>
- Barclay, S. D., Ash, J. E., & Rowell, D. M. (2000a). Environmental factors influencing the presence and abundance of a log-dwelling invertebrate, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). *Journal of Zoology*, 250(4), 425–436.
- Barclay, S. D., Rowell, D. M., & Ash, J. E. (2000b). Pheromonally mediated colonization patterns in the velvet worm *Euperipatoides rowelli* (Onychophora). *Journal of Zoology*, 250(4), 437–446.
- Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29(2), 543–550. [https://doi.org/10.1016/S0003-3472\(81\)80117-0](https://doi.org/10.1016/S0003-3472(81)80117-0)
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). *Fitting linear mixed-effects models using lme4*. arXiv preprint arXiv:1406.5823.
- Beauchamp, G. (2012). Foraging speed in staging flocks of semipalmated sandpipers: Evidence for scramble competition. *Oecologia*, 169(4), 975–980. <https://doi.org/10.1007/s00442-012-2269-0>



- Beckmann, H., Hering, L., Henze, M. J., Kelber, A., Stevenson, P. A., & Mayer, G. (2015). Spectral sensitivity in Onychophora (velvet worms) revealed by electroretinograms, phototactic behaviour and opsin gene expression. *Journal of Experimental Biology*, 218(6), 915–922. <https://doi.org/10.1242/jeb.116780>
- Bockoven, A. A., Wilder, S. M., & Eubanks, M. D. (2015). Intraspecific variation among social insect colonies: Persistent regional and colony-level differences in fire ant foraging behavior. *PLoS One*, 10(7). <https://doi.org/10.1371/journal.pone.0133868>
- Bull, J. K., Sands, C. J., Garrick, R. C., Gardner, M. G., Tait, N. N., Briscoe, D. A., Rowell, D. M., & Sunnucks, P. (2013). Environmental complexity and biodiversity: the multi-layered evolutionary history of a log-dwelling velvet worm in montane temperate Australia. *PLoS One*, 8(12), e84559. <https://doi.org/10.1371/journal.pone.0084559>
- Campbell, L. I., Rota-Stabelli, O., Edgecombe, G. D., Marchioro, T., Longhorn, S. J., Telford, M. J., Philippe, H., Rebecchi, L., Peterson, K. J., & Pisani, D. (2011). MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. *Proceedings of the National Academy of Sciences USA*, 108(38), 15920–15924. <https://doi.org/10.1073/pnas.1105499108>
- Chapman, C. A., & Chapman, L. J. (2000). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology*, 21(4), 565–585.
- Clark, C. W., & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology*, 30(1), 45–75. [https://doi.org/10.1016/0040-5809\(86\)90024-9](https://doi.org/10.1016/0040-5809(86)90024-9)
- Clusella-Trullas, S., & Chown, S. L. (2008). Investigating onychophoran gas exchange and water balance as a means to inform current controversies in arthropod physiology. *Journal of Experimental Biology*, 211(19), 3139–3146. <https://doi.org/10.1242/jeb.021907>
- Cook, T. R., Gubiani, R., Ryan, P. G., & Muzaffar, S. B. (2017). Group foraging in Socotra cormorants: A biologging approach to the study of a complex behavior. *Ecology and Evolution*, 7(7), 2025–2038. <https://doi.org/10.1002/ece3.2750>
- Creel, S., & Creel, N. M. (1995). Communal hunting and pack size in African wild dogs. *Lycaon Pictus. Animal Behaviour*, 50(5), 1325–1339. [https://doi.org/10.1016/0003-3472\(95\)80048-4](https://doi.org/10.1016/0003-3472(95)80048-4)
- Cvikel, N., Egert Berg, K., Levin, E., Hurme, E., Borissov, I., Boonman, A., Amichai, E., & Yovel, Y. (2015). Bats aggregate to improve prey search but might be impaired when their density becomes too high. *Current Biology*, 25(2), 206–211. <https://doi.org/10.1016/j.cub.2014.11.010>
- de Sena Oliveira, I., Read, V. M. S. J., & Mayer, G. (2012). A world checklist of Onychophora (velvet worms), with notes on nomenclature and status of names. *ZooKeys*, 211, 1–70. <https://doi.org/10.3897/zookeys.211.3463>
- Dias, S. C., & Lo-Man-Hung, N. F. (2009). First record of an onychophoran (Onychophora, Peripatidae) feeding on a theraphosid spider (Araneae, Theraphosidae). *The Journal of Arachnology*, 37(1), 116–117. <https://doi.org/10.1636/ST08-20.1>
- Edwards, D. H., Issa, F. A., & Herberholz, J. (2003). The neural basis of dominance hierarchy formation in crayfish. *Microscopy Research and Technique*, 60(3), 369–376. <https://doi.org/10.1002/jemt.10275>
- Fanshawe, J. H., & Fitzgibbon, C. D. (1993). Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour*, 45(3), 479–490. <https://doi.org/10.1006/anbe.1993.1059>
- Frank, L. G. (1986). Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and Reproduction. *Animal Behaviour*, 34(5), 1510–1527.
- Funston, P., Mills, M., & Biggs, H. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology*, 253(4), 419–431. <https://doi.org/10.1017/S0952836901000395>
- Giraldeau, L.-A., & Caraco, T. (2000). *Social foraging theory*, Vol. 73. Princeton University Press.
- Giraldeau, L.-A., & Dubois, F. (2008). Social foraging and the study of exploitative behavior. *Advances in the Study of Behavior*, 38, 59–104.
- Giribet, G. (2016). Genomics and the animal tree of life: conflicts and future prospects. *Zoologica Scripta*, 45, 14–21. <https://doi.org/10.1111/zsc.12215>
- Grand, T. C., & Dill, L. M. (1999). The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition? *Animal Behaviour*, 58(2), 443–451. <https://doi.org/10.1006/anbe.1999.1174>
- Grinsted, L., & Lubin, Y. (2019). *Spiders: evolution of group living and social behaviour*. In *Encyclopedia of animal behavior* (pp. 632–640). Elsevier.
- Grinsted, L., Schou, M. F., Settepani, V., Holm, C., Bird, T. L., & Bilde, T. (2020). Prey to predator body size ratio in the evolution of cooperative hunting—a social spider test case. *Development Genes and Evolution*, 230(2), 173–184. <https://doi.org/10.1007/s00427-019-00640-w>
- Harel, R., Spiegel, O., Getz, W. M., & Nathan, R. (2017). Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. *Proceedings of the Royal Society B: Biological Sciences*, 284(1852), 20162654.
- Haritos, V. S., Niranjane, A., Weisman, S., Trueman, H. E., Sriskantha, A., & Sutherland, T. D. (2010). Harnessing disorder: onychophorans use highly unstructured proteins, not silks, for prey capture. *Proceedings of the Royal Society B: Biological Sciences*, 277(1698), 3255–3263.
- Harpaz, R., & Schneidman, E. (2020). Social interactions drive efficient foraging and income equality in groups of fish. *Elife*, 9, e56196.
- Hartig, F. (2020). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models* No Title.
- Holekamp, K. E., Smale, L., Berg, R., & Cooper, S. M. (1997). Hunting rates and hunting success in the spotted hyena (*Crocuta crocuta*). *Journal of Zoology*, 242(1), 1–15.
- Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2(2), 143–155. <https://doi.org/10.1093/beheco/2.2.143>
- Johnsson, J. (2003). Group size influences foraging effort independent of predation risk: An experimental study on rainbow trout. *Journal of Fish Biology*, 63(4), 863–870. <https://doi.org/10.1046/j.1095-8649.2003.00187.x>
- Krause, J., Ruxton, G. D., Ruxton, G. D., & Ruxton, I. G. (2002). *Living in groups*. Oxford University Press.
- Krebs, J. R., MacRoberts, M. H., & Cullen, J. (1972). Flocking and feeding in the great tit *Parus major*—an experimental study. *Ibis*, 114(4), 507–530. <https://doi.org/10.1111/j.1474-919X.1972.tb00852.x>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26.
- Lihoreau, M., Deneubourg, J.-L., & Rivault, C. (2010). Collective foraging decision in a gregarious insect. *Behavioral Ecology and Sociobiology*, 64(10), 1577–1587. <https://doi.org/10.1007/s00265-010-0971-7>
- Lubin, Y., & Bilde, T. (2007). The evolution of sociality in spiders. *Advances in the Study of Behavior*, 37, 83–145.
- Majer, M., Holm, C., Lubin, Y., & Bilde, T. (2018). Cooperative foraging expands dietary niche but does not offset intra-group competition for resources in social spiders. *Scientific Reports*, 8(1), 1–13. <https://doi.org/10.1038/s41598-018-30199-x>
- Mayer, G., Franke, F. A., Treffkorn, S., Gross, V., & de Sena Oliveira, I. (2015). *Onychophora evolutionary developmental biology of invertebrates 3* (pp. 53–98). Springer.
- Mayer, G., Oliveira, I. S., Baer, A., Hammel, J. U., Gallant, J., & Hochberg, R. (2015). Capture of prey, feeding, and functional anatomy of the jaws in velvet worms (Onychophora). *Integrative and Comparative Biology*, 55(2), 217–227. <https://doi.org/10.1093/icb/icv004>

- Monge-Nájera, J., & Aguilar, F. (1993). Behavior of *Epiperipatus biolleyi* (Onychophora: Peripatidae) under laboratory conditions. *Revista De Biología Tropical*, 689–696.
- Mukherjee, S., & Heithaus, M. R. (2013). Dangerous prey and daring predators: A review. *Biological Reviews*, 88(3), 550–563. <https://doi.org/10.1111/brv.12014>
- Nentwig, W. (1985). Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology*, 17(1), 79–85. <https://doi.org/10.1007/BF00299433>
- Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010). The evolution of eusociality. *Nature*, 466(7310), 1057–1062.
- Pasquet, A., & Krafft, B. (1992). Cooperation and prey capture efficiency in a social spider, *Anelosimus eximius* (Araneae, Theridiidae). *Ethology*, 90(2), 121–133. <https://doi.org/10.1111/j.1439-0310.1992.tb00826.x>
- Periera, J., Bicudo, W., & Campiglia, S. (1985). A morphometric study of the tracheal system of *Peripatus acacioi* Marcus and Marcus (Onychophora). *Respiration Physiology*, 60(1), 75–82. [https://doi.org/10.1016/0034-5687\(85\)90040-4](https://doi.org/10.1016/0034-5687(85)90040-4)
- Pitcher, T., Magurran, A., & Winfield, I. (1982). Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, 10(2), 149–151. <https://doi.org/10.1007/BF00300175>
- Pruitt, J. N., & Avilés, L. (2018). Social spiders: mildly successful social animals with much untapped research potential. *Animal Behaviour*, 143, 155–165. <https://doi.org/10.1016/j.anbehav.2017.08.015>
- Purcell, J., Vasconcellos-Neto, J., Gonzaga, M. O., Fletcher, J. A., & Avilés, L. (2012). Spatio-temporal differentiation and sociality in spiders. *PLoS One*, 7(4). <https://doi.org/10.1371/journal.pone.0034592>
- R Core Team. (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Read, V. S. J., & Hughes, R. (1987). Feeding behaviour and prey choice in *Macroperipatus torquatus* (Onychophora). *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 230(1261), 483–506.
- Reid, A. (1996). Review of the Peripatopsidae (Onychophora) in Australia, with comments on peripatopsid relationships. *Invertebrate Systematics*, 10(4), 663–936. <https://doi.org/10.1071/IT9960663>
- Reinhard, J., & Rowell, D. M. (2005). Social behaviour in an Australian velvet worm, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). *Journal of Zoology*, 267(1), 1–7.
- Rubenstein, D. I. (1978). *On predation, competition, and the advantages of group living* Social behavior (pp. 205–231). Springer.
- Rypstra, A. L., & Tirey, R. S. (1991). Prey size, prey perishability and group foraging in a social spider. *Oecologia*, 86(1), 25–30. <https://doi.org/10.1007/BF00317384>
- Schneider, J. M., & Bilde, T. (2008). Benefits of cooperation with genetic kin in a subsocial spider. *Proceedings of the National Academy of Sciences USA*, 105(31), 10843–10846. <https://doi.org/10.1073/pnas.0804126105>
- Scott, I., & Rowell, D. (1991). Population Biology of *Euperipatoides-Leuckartii* (Onychophora, Peripatopsidae). *Australian Journal of Zoology*, 39(5), 499–508. <https://doi.org/10.1071/ZO9910499>
- Sunnucks, P., Curach, N. C., Young, A., French, J., Cameron, R., Briscoe, D. A., & Tait, N. N. (2000). Reproductive biology of the onychophoran *Euperipatoides rowelli*. *Journal of Zoology*, 250(4), 447–460.
- 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. <https://doi.org/10.3389/fphys.2016.00018>
- Ward, A., & Webster, M. (2016). *Sociality: the behaviour of group-living animals*. Springer.
- Ward, P. I. (1986). Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. *Behaviour*, 97(3–4), 213–225. <https://doi.org/10.1163/156853986X00603>
- Whitehouse, M., & Lubin, Y. (1999). Competitive foraging in the social spider *Stegodyphus dumicola*. *Animal Behaviour*, 58(3), 677–688. <https://doi.org/10.1006/anbe.1999.1168>
- Whitehouse, M. E., & Lubin, Y. (2005). The functions of societies and the evolution of group living: Spider societies as a test case. *Biological Reviews*, 80(3), 347–361. <https://doi.org/10.1017/S1464793104006694>
- Wilson, E. O. (1971). *The insect societies*. The insect societies.
- Wilson, E. O., & Hölldobler, B. (2005). Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences USA*, 102(38), 13367–13371. <https://doi.org/10.1073/pnas.0505858102>
- Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, 24(4), 847–867.
- Woodman, J. D., Cooper, P. D., & Haritos, V. S. (2007). Effects of temperature and oxygen availability on water loss and carbon dioxide release in two sympatric saproxylic invertebrates. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 147(2), 514–520. <https://doi.org/10.1016/j.cbpa.2007.01.024>
- Wrangham, R. W., Gittleman, J. L., & Chapman, C. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, 32(3), 199–209. <https://doi.org/10.1007/BF00173778>
- Yip, E. C., Powers, K. S., & Avilés, L. (2008). Cooperative capture of large prey solves scaling challenge faced by spider societies. *Proceedings of the National Academy of Sciences USA*, 105(33), 11818–11822. <https://doi.org/10.1073/pnas.0710603105>

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