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Prey size and scramble vs. contest competition in a social spider: implications for population dynamics

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Summary

1. There are many benefits of group living, but also substantial costs, one of which is competition for resources. How scarce food resources are distributed among different members of a population or social group – whether via scramble or contest competition – can influence not only the variance in individual fitness, but also the stability and therefore survival of the group or population.
2. Attributes of the food resources themselves, such as their size, may influence the type of intraspecific competition that occurs and therefore the intrinsic stability of a group or population.
3. By experimentally manipulating the size of prey fed to artificial colonies of the social spider *Anelosimus eximius,* we investigated whether prey size could alter the degree of scramble vs. contest competition that takes place and, thus, potentially influence colony population dynamics.
4. We found that large prey were shared more evenly than small prey and that individuals in poor condition were more likely to feed when prey were large than when prey were small. Additionally, we show that individuals participating in prey capture are also more likely to feed on the captured prey.
5. We developed a simple mathematical model to explore the prey sizes that would be energetically worth defending, i.e. prey that are 'economically defendable'. The model shows that neither very small prey, nor prey above a certain size is worth monopolizing, with only intermediate size prey being 'economically defendable'. We therefore suggest the small and large prey in our experiment corresponds to our model's intermediate and large prey categories, respectively.
6. As the size of prey captured by social spider colonies increases with colony size, our findings suggest that scramble competition may predominate in large colonies. Scramble competition, combined with the fact that prey biomass per capita declines as colonies grow beyond a certain size, would then explain why extremely large colonies of this social spider may suddenly go extinct. Our project thus illustrates the potential triple link between characteristics of the resources, individual behaviour and population dynamics, a link rarely considered in an empirical setting.

Key-words: environment, extinction, patch size, persistence, resource distribution, sociality, survival

Introduction

The method by which individuals in a population compete for limited resources such as food, mating opportunities or nesting space is known to have a powerful selective influence on individuals (e.g. West-Eberhard 1983; Isbell 1991; Pfennig, Rice & Martin 2007). Less well studied is

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how intraspecific competition can affect the stability and long-term persistence of a population, as well as potential links between properties of the resources, individual behaviour and population dynamics. In general, it has been accepted that there are two extreme forms of intraspecific competition – contest and scramble. These were originally proposed by Nicholson (1954) who defined contest competition as occurring when each successful individual gets sufficient access to a limited resource to survive and

reproduce, whereas unsuccessful individuals fail to do so. Scramble competition, in contrast, occurs when resources are shared more or less evenly among all individuals in a population or allocated to those in most immediate need. In the latter case, when resources are limited, no individual may get sufficient resources to reproduce or even survive. Scramble competition has been demonstrated in species such as the southern pine beetle when attacking trees (e.g. Zhang, Byers & Schlyter 1992; Reeve, Rhodes & Turchin 1998) or in frugivorous primates (e.g. Chapman 1990; Koenig 2002). Contest competition, on the other hand, can be seen in species that defend a territory or in those with dominance hierarchies (e.g. Sterck & Steenbeek 1997; Pruetz & Isbell 2000), such as in social primates where individuals at the top of the hierarchy get preferential access to resources (e.g. Isbell 1991; Wittig & Boesch 2003). The majority of species are likely to lie somewhere between the extremes of these two forms of competition, with a variety of factors, both biotic and abiotic, potentially affecting how resources are allocated. Such factors, which may change with season, population size, or geographic location, include the density of conspecific competitors and the prevailing size and spatial distribution of resource patches or prey.

One of the main factors thought to determine intraspecific competition type is the extent to which resources can be monopolized (Ward, Webster & Hart 2006). When resources are clumped either in space or time, single individuals can monopolize them so that contest competition prevails. Dispersed resources, on the other hand, are not defendable, causing scramble competition to predominate (Rubenstein 1981; Bryant & Grant 1995). Vahl (2005), for example, showed that in a wading bird spatially clumped food increased the difference in food intake between dominant and subordinate individuals. Likewise, Weir & Grant (2004) showed that in cichlids food that arrives asynchronously is more likely to be monopolized when compared to synchronously arriving food. Resource size may also determine the extent to which monopolization by individuals is possible. If prey are small, individuals can exclude conspecific competitors, so that contest competition prevails. In contrast, scramble competition is more likely when resources are too large for single individuals to capture and defend solitarily. In the latter case, group-hunting strategies may evolve (Packer & Ruttan 1988), but this does not preclude intraspecific competition and uneven distribution of captured resources.

In any population that shares resources, the method of resource allocation may, in turn, have profound consequences for population stability, especially when resources are limited (Lomnicki 1978, 1999, 2009). Under scramble competition, no individual may get enough of the limited resource to reproduce and the population is thus at greater risk of extinction (Hassell 1976; Lomnicki 1988). In contrast, under contest competition, the most competitive individuals can get sufficient resources to reproduce, which may result in the population shrinking, but persisting. In

an early empirical demonstration of the effect that scramble competition may have on the health of individuals, Bakker (1962) fed low food levels to groups of *Drosophila melanogaster* larvae. This resulted in the majority of flies pupating but emerging half starved, rather than a few individuals emerging fully fed. In a more recent study, Camphuysen *et al.* (2002) showed that an observed mass mortality of eiders in the Dutch Wadden Sea was due to a reduction in available food resources. The fact that all individuals measured had reduced body condition suggested that scramble competition predominated and contributed to the population's collapse. In bark beetles, it has been shown that an increase in tree attack density above an optimum level results in a dramatic decline in the number of mature beetles emerging (e.g. Zhang, Byers & Schlyter 1992; Reeve, Rhodes & Turchin 1998). A deeper understanding of the conditions that lead to the preponderance of one form of competition over the other could therefore be vital in predicting a population's stability and potential persistence in a given environment.

Here, we study the mode of competition in a social spider whose colonies are known to have boom and bust dynamics (Hart & Avilés 2014) and high rates of extinction (Vollrath 1982; Venticinque, Fowler & Silva 1993; Avilés 1997), which is consistent with scramble competition predominating in this system (Rypstra 1993). In particular, using a simple mathematical model, we show that large prey is not economically defensible and thus more likely to be shared. We then test this prediction experimentally by feeding small and large prey to artificial colonies of the neotropical social spider *Anelosimus eximius*. Social spiders typically feed on prey items that can range in size from smaller than an individual spider to many times larger (Rypstra & Tirey 1991). Therefore, prey size is an important factor to consider, particularly as the size of the prey captured has been shown to increase with colony size (Yip, Powers & Avilés 2008). Consequently, social spiders, and *A. eximius* especially, provide an ideal opportunity to investigate the potential triple link between properties of the resources, individual behaviour and population dynamics. There have been a few studies investigating how different species' behavioural response to differing food patch characteristics can influence the severity of those species' population declines when resources are scarce (e.g. Bender, Contreras & Fahrig 1998; Gawlik 2002), suggesting this is an important factor to consider when investigating a species' response to resource scarcity and habitat change. However, there have been surprisingly few studies that have considered this triple link despite the several examples of scramble and contest competition in the literature and the underlying conditions that may be responsible for them.

Social spiders are unusual among social organisms in that their colonies represent not only social groups, but also self-sustaining populations (Avilés 1997). Colony members, typically multiple females and their offspring, remain together throughout their lives and mate with each

other to produce successive generations. Through this process of intracolony mating, colonies may grow to contain hundreds to tens of thousands of individuals, depending on the species. Once a colony has reached a large size, dispersal to produce daughter colonies may take place. Colonies, however, may also suffer relatively high rates of extinction, which may involve the sudden crash of large and apparently healthy colonies, often with no individuals dispersing before the colony dies (Vollrath 1982; Venticinque, Fowler & Silva 1993; Avilés 1997; Crouch & Lubin 2001). In our study species, for example, it has been estimated that 21% of well-established colonies in the forest understorey go extinct per generation (Avilés 1992). Hart & Avilés (2014) reconstructed the parameters governing the growth of *A. eximius* colonies in the lowland tropical rain forest and obtained results consistent with their dynamics being intrinsically unstable. Boom and bust dynamics may arise when rates of growth are high, generations discrete, and scramble the predominant form of intraspecific competition (May 1974; May & Oster 1976; Lomnicki & Sedziwy 1989; Lomnicki 2009). *A. eximius* colonies appear to fulfil these conditions as parents usually die before their offspring reach maturity (Avilés 1986) and large rates of growth may result from the spiders' cooperative behaviours and highly female-biased sex ratios (Avilés 1999). Moreover, Grinsted & Bilde (2013) found that increasing competition within artificial colonies of the social spider *Stegodyphus dumicola* did not increase size asymmetry among the spiders, further suggesting a predominant role of scramble competition in these systems.

We use a simple mathematical model to show that prey above a certain size may not be economically defensible as prey surface area, which needs to be defended, increases at a faster rate than prey volume, which is proportional to the energy a prey item provides. Our model thus suggests that larger prey items would have a higher probability of being evenly shared among colony members. Therefore, we predicted that scramble competition would be more pronounced when prey were large, as individual spiders would not be able to prevent others from joining at either the prey capture or feeding stage. We test this prediction using artificial colonies of *A. eximius*. We provided prey to these colonies that were either small (approximatively the same size as a single spider) or large (two to three times larger). We also investigated the effect of an individual's body condition and participation in prey capture on the likelihood that it fed on captured prey. In spiders, growth rate and body size are highly correlated with mating success and fecundity, making foraging success an important factor determining an individual's fitness (Petersen 1950; Kessler 1971; Schneider & Bilde 2008; Pruitt & Riechert 2009). Consequently, we expected that individuals in poorer condition (i.e. hungrier individuals) would have greater access to larger prey. A finding that prey sharing and scramble competition are more pronounced when prey are large would help explain why large colonies of this social spider, which capture larger prey, tend to be subject to boom and bust

dynamics and high rates of colony extinction (Avilés 1997, 1999; Hart & Avilés 2014).

Model construction

We constructed a simple mathematical model to determine how prey size could influence the likelihood that a prey item will be monopolized. The model is based on an optimal foraging function proposed by Sih (1980). We assumed that an individual's only consideration when deciding whether to defend a prey item is its net energy gain and that the energy gained by consuming a prey item is proportional to its volume, up to the point at which the individual is satiated (i.e. gut capacity). We assumed that any remaining prey will not 'keep' for repeat feedings by a single individual and that prey arrives sufficiently intermittently so that the individual is only making decisions about one prey item at a time. Therefore, we propose that the energy gain per unit volume of the prey would be

$$b = \frac{GP_V}{E + P_v}, \qquad \text{eqn 1}$$

where P_V is the prey volume, G is a constant representing individual gut capacity, that is the maximum amount of food an individual can consume, and E is a constant that determines the initial rate of food intake for a lone individual.

We assumed that the cost to an individual defending a prey item is directly proportional to the surface area of the prey as this is the area that has to be defended. The energetic cost of defending the prey to an individual will then be

$$c = AP_V^{3/2} + C_0, \qquad \text{eqn 2}$$

where A is a constant that depends on the degree of competition in the population, which in our specific case could be the density of competitors. C_0 assumes that there is always a cost to defending any sized prey and is therefore the *y*-intercept of the function, that is the cost of defending a prey of size zero.

Experimental methods

STUDY ORGANISMS

Anelosimus eximius Keyserling (Araneae: Theridiidae) occurs in lowland wet tropical areas from Panama to southern Brazil (Levi 1963; Agnarsson 2006). In Ecuador, it ranges from lowland tropical rain forest up to approximately 1200 m above sea level in the lower montane rain forest. Our study area was located along the road to Loreto, Ecuador (0·703°S, 77·736°W, 1000 m elevation, Napo Province, Ecuador), where *A. eximius* colonies are often found along the road edge. At this site, colony sizes range from a single female plus her progeny to nests over 6 metres in length, containing thousands of spiders (Purcell & Avilés 2007). The colonies have highly female-biased sex ratios, with colonies containing only about 10% males (Avilés & Maddison 1991).

SET-UP

Collections and experiments took place between May and August 2013. Subadult instar 1 (antepenultimate instar) and subadult instar 2 (penultimate) females were collected from four wild nests located along a road side. We used subadults as this is the age that determines how soon and at what size spiders will reach maturity and therefore their reproductive success (Spence, Zimmermann & Wojcicki 1996; Uhl *et al.* 2004; Bilde *et al.* 2007; Salomon, Mayntz & Lubin 2008). Within 24 h of being collected, the spiders were weighed (XS105DU Analytical Balance, Mettler Toledo, OH, USA). Ten spiders of the same instar and from the same nest were placed in each box to form artificial colonies. Boxes were made of clear plastic and measured 13 × 11 × 11 cm. To distinguish individuals, a dot of *Luminous* insect paint was applied to the spiders' abdomen (BioQuip Products, Rancho Dominguez, CA, USA). The spiders were left in the box for two days before the start of the experiment to allow them time to build a web. The spiders were not fed during these two days. We assigned spiders to boxes after they were weighed. For each box, we chose spiders of the same instar, but attempted to include a very large and a very small spider in an effort to maximize competition within groups. At the same time, we tried to maintain a similar spread of weights across all boxes. Thus, we attempted to maximize variance within boxes, but standardize within-box variance across them. In total, we had 19 boxes in the large prey treatment and 18 in the small prey treatment.

EXPERIMENT

Boxes were randomly assigned to receive either large or small prey (flying Hymenoptera and Diptera). Large prey weighted between 6·5 and 9·5 mg, which is approximately 2–3 times heavier than a subadult female, whereas small prey weighed between 1·1 and 3·5 mg, which is approximately the same weight as a subadult female. In wild nests in the lowland rain forest, *A. eximius* colonies captured prey, on average, six times larger than the spiders themselves (Powers & Avilés 2007). Since our colonies and prey were not as large as under natural field conditions, any effects of prey size we detect are thus expected to be conservative relative to what might be obtained in the field (i.e. if we conducted the experiment with even larger prey, we would expect more significant differences between small and large treatment groups than observed with our set-up).

Boxes assigned to receive large prey were allowed to consume one prey item in total, whereas small prey boxes were provided a total of four small prey in order to equalize total biomass. Small prey boxes received prey in the morning and evening for two consecutive days. The evening prey was introduced approximately 10 h after the morning prey. In every case, the old prey had been fully consumed and removed before a new prey was introduced. We collected data on prey introduced during the day only in order to match the time period when large prey were tested.

The first 2 h after the prey was introduced, the boxes were monitored more or less continually. If prey capture was observed, the identities of all individuals that participated were recorded. An individual was classified as having participated in prey capture if the attack was successful (i.e. the prey was killed) and the individual was seen touching or biting the prey while it was still alive. For the first 2 h after the prey was captured, the identity of every individual consuming the prey was recorded at 15-min

intervals. A spider was said to be consuming the prey if its mouth parts were touching the prey and the spider was immobile. From 3 to 8 h after the prey was captured, the identity of each individual feeding was recorded every 30 min. If the prey was not captured after 2 h, the old prey was removed and a new prey introduced. We assumed that all individuals detected the presence of prey as boxes were relatively small and there was enough webbing built within them for all spiders to sense the vibration of the prey.

STATISTICAL ANALYSIS

To measure how evenly prey were shared among individuals within a group, we used a modified version of Pielou's J measure of species evenness (Pielou 1966). We refer to this index as intragroup evenness,

$$I = \frac{-\sum_{i=1}^{s} t_i \ln t_i}{\ln s} \qquad \text{eqn 3}$$

where t_i is the fraction of time each spider spent feeding on the prey, as a proportion of the total time all spiders spent feeding, and s is the total number of spiders in each group. The intragroup evenness index ranges from 0 to 1, where 0 indicates that only one individual fed and 1 is when all individuals fed for the same length of time. For all analyses, intragroup evenness was arcsine-transformed.

To test whether intragroup evenness was affected by prey size, we used a linear mixed-effect model (lmer) with intergroup evenness as the response variable, treatment and instar as fixed effects and the artificial colony ID as a random effect.

We calculated the condition of individual spiders using the residual index, which corresponds to the residuals of the regression of body mass on cephalothorax length (Jakob, Marshall & Uetz 1996). Condition is expected to correlate inversely with hunger level. Much as leg length, which has been used in other studies (e.g. Uhl *et al.* 2004), the cephalothorax is a fixed body part that can be used as a measure of body size independent of current feeding state. The conditions of the two instars were not significantly different from each other (see the Supporting Information), which allowed us to graph the two instars together. We also calculated spider condition using the ratio index, which was obtained by dividing the weight of each spider by the length of its cephalothorax. As there was no difference in the results obtained with the two methods, we report results obtained with the first method only.

To test whether condition (or hunger level) influenced an individual's likelihood to (a) participate in prey capture, or (b) feed, and (c) whether these tendencies differed with prey size and individual instar, we constructed generalized linear mixed models (glmer) with binomial error distributions. Fixed effects were spider condition, instar and prey size. To further investigate how the patterns differed at different prey sizes, we analysed the data separately for the two prey sizes with condition and instar in the model.

To investigate whether an individual that fed on prey was more likely to have participated in its capture, we used a generalized linear model (glmer) with a binomial error distribution. Whether an individual fed was the response variable, with instar, prey size, and whether the spider participated in prey capture as fixed effects.

All statistical analyses were carried out with R statistical software version 3.1.1 (R Core Team 2014) using either linear models or generalized linear models with a binomial error distribution, both in the lme4 package (Bates *et al.* 2014). For all models using measurements on individual spiders, individual spider ID and the artificial colony ID were included as random factors. We used the Akaike Information Criterion (corrected for finite sample sizes, AICc) to select the combination of factors and their interactions that most parsimoniously explained the data (smallest AICc). We then used this model to test the significance of individual factors using a likelihood ratio test which compares the ratio of the likelihood of the best model to that of a reduced model lacking the term of interest (Pinheiro & Bates 2009).

All means are quoted ± the standard error.

Results

MODEL

Solving the model graphically shows that only at intermediate prey sizes do the energetic gains of defending a prey item outweigh the costs of defending it (Fig. 1). As we assume there is always some cost of defending any sized prey, the energetic gains from defending prey below a certain size may be lower than the benefits of consuming it. For large prey, due to the increasing surface area to volume ratio as prey size increases, large prey may also not be worth defending, as defence costs are proportional to prey surface area which needs to be defended, but energetic gains are proportional to prey volume. The model can be solved numerically, but as the equations are nonlinear, there are no exact algebraic solutions. In our experimental set-up, the small prey treatment corresponds to the intermediate category of our model.

EXPERIMENT

The model that best explained how evenly prey were shared among spiders in a group contained both prey size and spider instar, but not the interaction between the two [lmer: ΔAIC(full−reduced) = 1.83; interaction: $\chi^2_{5,6}$ = 0.16, P = 0.68]. Given groups of homogeneous instar, the probability that an individual participated in prey capture was best explained by an individual's condition, prey size, and the interaction between the two, but not an individual's instar [glmer: ΔAIC(model with − without instar) = 1.86]. The probability that an individual fed, on the other hand, did depend on instar, in addition to these other factors [glmer: ΔAIC(model with − without instar) = −17.04]. Looking at whether those individuals that fed also participated in capturing that prey item, the model with capture, instar, and prey size, but without interactions of instar and prey with capture, had the lowest AIC value [glmer: ΔAIC(full−reduced) = 3.92].

Within artificial colonies, large prey were shared more evenly than small prey (lmer: $\chi^2_{4,5}$ = 4.09, P = 0.043*) (Fig. 2), with younger, and therefore smaller, instar individuals (subadult instar 1) sharing prey more evenly than larger ones (subadult instar 2) (lmer: $\chi^2_{4,5}$ = 12.28, $P \leq 0.001$***). There was no significant interaction between prey size and instar (lmer: $\chi^2_{5,6}$ = 0.16 P = 0.68).

Fig. 1. Graphical representation of the energetic costs and benefits of defending a prey against competitors (eqns 1 and 2). The shaded area indicates the prey sizes at which the benefits of monopolizing a prey item are greater than the cost of defending that item, that is the prey sizes that are economically defendable. This model suggests that small prey would not be worth defending, but also that it would not pay off for single individuals to defend and monopolize prey above a certain size. The intermediate category of the model corresponds to the 'small prey' in our experimental set-up.

Fig. 2. Intragroup evenness for small and large prey, calculated using a modified Pielou's J measure of species evenness (eqn 3), where a score of 1 corresponds to completely egalitarian sharing and 0 when only one individual feeds (*n* boxes with large prey = 19, small prey = 18). The difference was significant ($P < 0.043$*), with large prey being shared more evenly compared to small prey.

(a)

(b)
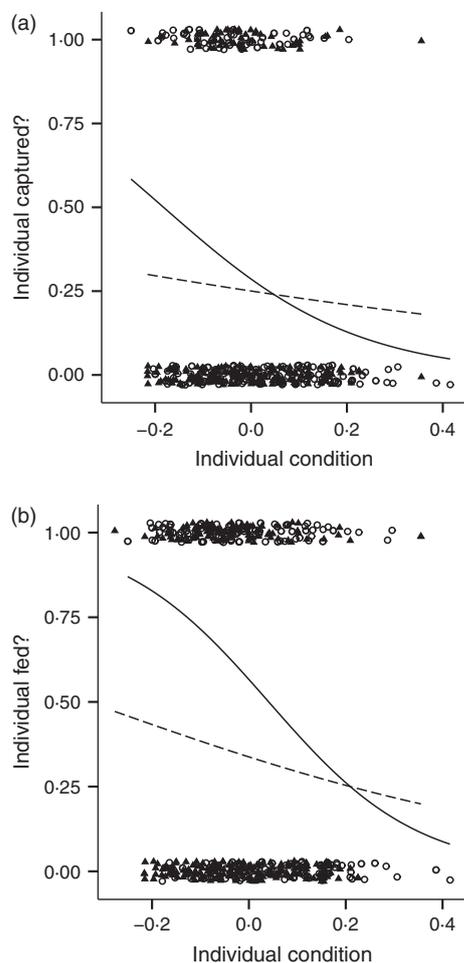
Fig. 3. A logistic regression of the condition of individuals that either did or did not participate in (a) prey capture, or (b) feeding. The dotted line and triangles represent small prey, while the solid line and circles are large prey. Prey capture and feeding are both binary measures, with 1 indicating 'did participate' and 0 'did not participate' (n trials with observed prey capture, large = 25, small = 27, n trials with observed feeding large = 19, small = 30). There was a significant interaction with prey size, with the difference between those that captured and fed and those that did not being greater for large than small prey.

There was a significant difference in condition between individuals that participated in prey capture and those that did not (glmer: $\chi^2_{4,6} = 18.20$, $P < 0.001***$), with those in poorer condition being more likely to participate. This effect was more pronounced for large prey (interaction between condition and prey size: glmer: $\chi^2_{5,6} = 3.84$, $P = 0.0499*$) (Fig. 3a). The mean difference in condition between individuals that participated in prey capture and those that did not was 0.070 ± 0.014 for large prey (glmer: $\chi^2_{3,4} = 17.35$, $P < 0.0001***$), but only 0.015 ± 0.014, and non-significant, for small prey (glmer: $\chi^2_{3,4} = 0.87$, $P = 0.35$). There was no difference in the number of individuals participating in prey capture between instars (glmer: $\chi^2_{5,6} = 0.14$, $P = 0.71$).

There was also a significant difference in condition between individuals that fed and those that did not
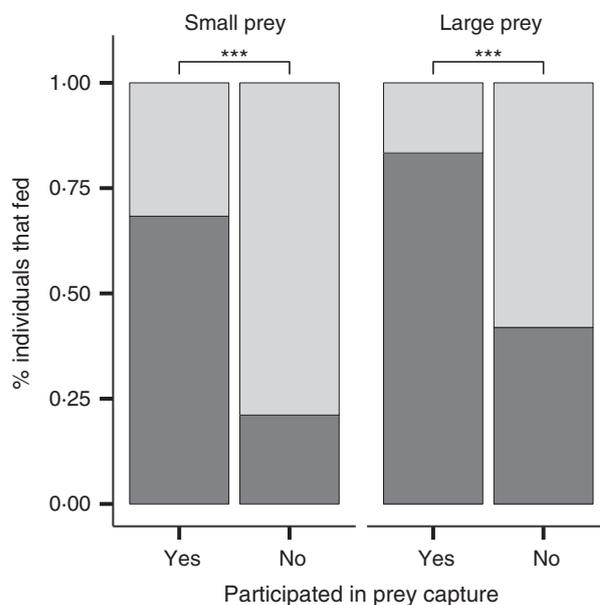
Fig. 4. The percentage of individuals that fed as a function of whether they participated in prey capture or not, combining spiders in all boxes. Dark grey bars are those that fed on the captured prey, and light grey, those that did not. If an individual participated in prey capture, she was significantly more likely to feed on that prey item ($P < 0.0001***$), with a comparable effect for both prey sizes (treatment × capture interaction: $P > 0.05$) (n trials large = 19, small = 24).

(glmer: $\chi^2_{5,7} = 29.22$, $P < 0.001***$), with those of poorer condition being more likely to feed (Fig. 3b). The magnitude of this difference also depended on prey size, as the interaction between prey size and condition was significant (glmer: $\chi^2_{6,7} = 7.59$, $P = 0.006**$). Thus, when prey was large, the difference in condition between individuals that fed and those that did not was 0.096 ± 0.017 (glmer: $\chi^2_{4,5} = 30.61$, $P < 0.001***$), whereas for small prey this difference was smaller, at 0.022 ± 0.013 and non-significant (glmer: $\chi^2_{4,5} = 2.35$, $P = 0.12$) (Fig. 3). Significantly, more spiders of the younger than older instar fed (57.9 vs. 33.0%; glmer: $\chi^2_{6,7} = 19.04$, $P \leq 0.001***$).

Overall, 75.4% of those that participated in prey capture also fed on that prey item, whereas of those that did not participate in prey capture only 30.3% fed (Fig. 4). This difference was significant (glmer: $\chi^2_{4,5} = 71.08$, $P < 0.0001***$), but it did not depend on prey size (individual fed × prey size interaction, glmer: $\chi^2_{5,6} = 0.04$, $P = 0.85$), nor instar (individual fed × instar interaction glmer: $\chi^2_{5,6} = 0.07$, $P = 0.80$).

Discussion

Mediated through individual behaviour, the form of intraspecific competition – scramble vs. contest – is an important property of populations that can potentially link attributes of the resources to population dynamics. We constructed a simple mathematical model showing that prey above a certain size may not be economically

defensible by single individuals as prey surface area, which needs to be defended, increases at a faster rate than prey volume, which is proportional to the energy a prey item provides. This suggested that large prey items would have a higher probability of being more evenly shared among colony members (Fig. 1). We investigated this further by using colonies of the social spider *Anelosimus eximius* experimentally set up in the laboratory. We show that the competition regime within colonies tends towards scramble rather than contest competition, as prey were relatively evenly shared (Fig. 2), with individuals in greater need (i.e. in poorer condition) getting preferential access to food items (Fig. 3). The degree of scramble competition, however, depended on prey size, as large prey were shared more evenly than small prey (Fig. 2), in particular when individuals were of a smaller instar. Additionally, the difference in condition between spiders that fed and those that did not was greater for large than small prey, with individuals in poorer condition getting preferential access to large prey (Fig. 3b). Likewise, individuals in poorer condition were more likely to participate in prey capture when prey were large than when prey were small (Fig. 3a). We also investigated when and how individuals gained access to prey, finding that individuals that participated in prey capture were more likely to feed on a given prey item than those that did not (Fig. 4). The finding that scramble competition predominates in these spiders is consistent with the observation that their colonies are prone to boom and bust dynamics and high rates of extinction (Avilés 1997; Hart & Avilés 2014).

The term 'economic defendability' was coined by Brown (1964) who used it to explain under what circumstances it is economically worthwhile for an individual to defend a resource, such as a food patch or mate and when it is not. Whether a prey item or patch is 'economically defendable' appears to be one of the main factors determining whether a population engages in scramble or contest competition. In the simplest case, a more competitive individual will be more likely to defend a small prey item or patch than a large one, as large patches may either not be defendable or the energy needed to defend them may be greater than the benefits gained given the potential for diminishing returns with increasing patch size (Brown 1964; Grant 1993). Additionally, the amount of food contained in a large patch or prey item could attract scavengers (personal observation) or may be too large for an individual to consume before the food either decays or is taken by scavengers (Rypstra & Tirey 1991). Our model extrapolates from these simple concepts to propose that only intermediate prey or patch sizes would be economically defendable (Fig. 1). If we accept that there is always a non-zero cost to defending any food item, prey that are too small to provide sufficient energy to outweigh the costs of defence should not be defended. However, as we assumed that the cost to defend a prey item is proportional to its surface area, which is what needs to be defended, the cost of defending an item increases faster than the energy contained in the prey. Consequently, there is an upper limit to prey size above which the costs of defence outweigh energetic gains of monopolization. Therefore, only 'intermediate' prey should be 'ecologically defendable'.

Our experimental result that large prey are shared more evenly than small prey (Fig. 2), and that individuals in poorer condition have greater access to large prey compared to small prey (Fig. 3b), suggests that our experimental small prey actually falls into our model's 'intermediate' prey category, with our experimental large prey corresponding with our model's 'large' prey section (Fig. 1). This suggests that smaller prey, as long as it is not too small, are indeed more economically defendable by single individuals compared to large prey, with more competitive individuals (i.e. individuals of high condition) being more able to exclude less competitive ones from small than large prey (Figs 2 and 3). In addition, small prey may be more likely to remain undetected by others in large nests, resulting in there being fewer individuals from whom to defend the prey. These results differ from those of Rypstra (1993), in which it was found that large prey increased size asymmetry within artificial colonies of *A. eximius*. Our study differed from Rypstra's, however, in that we introduced one prey item at a time, whereas in Rypstra's study, multiple prey items were introduced simultaneously. As the total biomass in Rypstra's study was equalized between treatments, this would have resulted in many more small than large prey being available at any one time, thus allowing more individuals to feed simultaneously in the small prey treatment. The simultaneous availability of many small food items has been shown empirically in other systems to preclude resource monopolization (Rubenstein 1981; Bryant & Grant 1995). In social spider colonies in the wild, prey arrive intermittently (Yip, Powers & Avilés 2008; personal observation), suggesting that simultaneously arriving prey is a less realistic scenario. Consistent with the suggestion that small, but not large prey can be monopolized, we have observed that in wild *A. eximius* colonies small prey tend to be moved under a leaf or other sheltered location within the nest by the individual(s) that capture them. In contrast, large prey are often seen exposed, with upwards of 20 individuals feeding simultaneously on them (R.V. Sharpe and L. Avilés, unpublished data). Indeed, previous studies have found that once a single individual has captured and started to feed on a small prey item, she is seldom joined by others (Pasquet & Krafft 1992; Ebert 1998). A cost/benefit analysis can also help explain our result that individuals were more likely to feed on a prey item if they participated in its capture (Fig. 4), as the cost of participating in prey capture would be offset by the benefits of gaining preferential access to the item. Indeed, it has been shown, in another social spider, *Stegodyphus sarasinorum*, that when food is scarce, hungry spiders participate in prey capture more frequently than satiated spiders (Beleyur, Bellur & Somanathan 2015). In contrast

however, in *Stegodyphus dumicola*, larger spiders were more likely to engage in prey capture (Wright, Keiser & Pruitt 2015).

In addition, we found that the younger subadult instar 1 individuals shared food more evenly compared to subadult instar 2's. As we only used two instars in our experimental design, and did not combine instars within each experimental nest, it is not possible to draw any firm conclusions about how intraspecific competition might change with individual age. There are, however, some plausible reasons for this trend. First, since we used the same size prey for both instars, the smaller instar individuals would have been smaller relative to the size of prey, thus explaining why they shared it more evenly. Another potential explanation is that the larger-instar individuals would be more competitive than the younger ones, as the amount of food they obtain just prior to moulting to maturity could have a large effect on their size and therefore their reproductive success as adults.

COMPETITION AND POPULATION STABILITY

Through its effect on the form of intraspecific competition, it follows that the economic defendability of a patch or prey item could also affect the intrinsic stability of that population when food is scarce. There have been several theoretical studies demonstrating that populations that engage in scramble competition should be more intrinsically unstable compared to those that engage primarily in contest competition (Lomnicki 1978, 1999, 2009; Ulbrich *et al*. 1996). The link between internal dynamics and intraspecific competition can be explained by assuming there is a relatively closed, self-sustaining population, such as *A. eximius* colonies. Due to external or internal causes, there is a sudden reduction in food available or an increase in the number of individuals with no corresponding increase in food. If this population distributes food via contest competition, then the more competitive individuals will get enough food to survive and reproduce, whereas the less competitive ones will not. The population will then shrink in size but persist. However, if food is distributed via scramble competition, none of the individuals will get enough food, resulting in the population possibly going extinct.

A mismatch between the number of individuals in a population and available food can occur for a number of reasons, such as large environmental fluctuations coupled with high population growth rate and delays in the feedback mechanisms to control population size, which would result in too many offspring being produced. Two studies on predacious caterpillars from the genus *Maculiana* showed that scramble competition, coupled with scarce food resources, can indeed result in almost total mortality. When too many individual caterpillars of the species *Maculinea arion L* fed in one ant colony, and food was distributed by scramble competition, none of the caterpillars survived (Thomas & Wardlaw 1992). However, in the related *Maculina rebeli*, worker ants actively selected particular caterpillars to feed, thus distributing food by contest competition, resulting in a fixed number of individuals surviving and excess individuals dying from starvation (Thomas, Elmes & Wardlaw 1993). In the case of *A. eximius*, insufficient resources coupled with scramble competition may result in delayed growth of individuals so that offspring fail to grow to maturity in time to replace a dying maternal generation. This would result in the nests being occupied by individuals that are too young to efficiently maintain them and could result in colony collapse.

STABILITY AND ENVIRONMENTAL CONDITIONS

That large prey may be less economically defendable than small prey, and therefore more evenly shared (Fig. 2), implies there is a triple link between properties of the environment (i.e. resources), individual behaviour and population dynamics. Thus, any biotic or abiotic conditions that affect the size of prey or food patches available to a population could also affect its dynamics. The possibility that changes in food item or patch size may change over time, thus affecting the degree of scramble vs. contest competition, is seldom considered, with the majority of studies assuming that patch size distribution remains constant or any changes are unimportant (Vahl 2005). For example, within social carnivore groups, the size of prey available to them has been shown to increase as group size increases (Creel & Creel 1995). Likewise, in social spiders, Yip, Powers & Avilés (2008) showed that as colonies increase in size, the actual number of prey captured per capita decreases, but the size of individual prey items increases. As an increase in prey size appears to shift competition towards scramble competition, this implies that as group size increases, the group's population dynamics could become more unstable. Although dispersal could relieve population density and prevent a crash, in the lowland tropical rain forest *A. eximius* can only disperse as adult inseminated females (Vollrath 1982). The reason is that colonies are few and far between, which, combined with high costs of dispersal, make it unlikely that mates could be found outside the natal nest (Avilés & Purcell 2012). With colonies having discrete generations, they may not be at the correct age structure to disperse when a crash appears to be imminent. Such dispersal constraints, coupled with the observed decrease in the amount of food per capita and the size of the prey captured in larger colonies (Yip, Powers & Avilés 2008), could explain why *A. eximius* colonies appear to exhibit intrinsically unstable dynamics, with the extinction of large colonies occurring suddenly and swiftly (Vollrath 1982; Hart & Avilés 2014).

Finally, as environmental conditions may change over a species range or over time, the stability of its populations could correspondingly change. In the case of *A. eximius*, for example, the size of insects, and thus available prey, varies with elevation, with prey being larger at low

elevation tropical rain forest sites compared to higher elevations (Guevara & Avilés 2007, 2009; Powers & Avilés 2007). This implies that colonies at low elevations may have more intrinsically unstable population dynamics compared to their higher elevation counterparts. As with elevation, the size of resources available for other species could change with a multitude of environmental factors, such as time of year, latitude, the age of the ecosystem and human disturbance, such as habitat fragmentation. Therefore, if the environment can affect the degree of scramble vs. contest competition, it follows that the environment could affect the stability and therefore persistence of populations. We suggest that this potential triple link between environment, individual behaviour and population dynamics is important and warrants further study and that prior studies that investigate populations, resource patches and competition may need to be revisited.

Acknowledgements

Data accessibility

Data available from the figshare repository: 10.6084/m9.figshare.3365335 (Sharpe 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Histograms *Anelosiums eximius* individuals used during the experimental trails calculated showing (a) the raw individual weights (b) the ratio index weight/cephalothorax length (c) the residual condition index (see Jakob *et al.*, 1996) which was the measure of condition that was used for the statistics and graphs in the paper. There was no difference in residual condition between the two instars ($P = 1$).