Local and global dynamics in social spider metapopulations

by

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Abstract

The relative costs and benefits of group living change with group size. In the social spider *Anelosimus eximius*, as colonies grow, the number of insects captured per capita decreases, but the size of insects increases, causing biomass captured per capita to peak at intermediate colony sizes. One aspect of group living that changes with group size is competition for resources. Whether intraspecific competition occurs via scramble vs. contest competition can affect the stability and survival of the group or population. By feeding large and small prey to artificial colonies of the social spider *Anelosimus eximius*, we investigated whether prey size could alter the type of competition that takes place and, thus, potentially, influence colony population dynamics. We found that large prey were shared more evenly, and that individuals in poor condition were more likely to feed when prey were large. Next, we investigated whether the condition of individuals vary as a function of colony size by measuring condition of individual spiders in a wide range of nest sizes. We found that, due to reducing per capita food supply as colonies grow, individuals have lower condition in larger colonies. We also found that condition variance decreases with colony size, further suggesting that scramble competition predominates in large colonies. Although dispersing females were larger and in better condition than philopatric ones, nests established by dispersing females had low survival rate, suggesting that dispersal is costly. Dispersers, therefore, likely face multiple constraints. They have to be large enough to stand a chance of survival following dispersal, but, due to dispersal costs and benefits of group living, should not disperse except from large colonies. Diminishing resources in large colonies, however, coupled with scramble competition, should make it hard for individuals to accumulate sufficient resources to disperse. This combination of factors may contribute to the observed sudden extinction of large colonies that fail to disperse representing a paradox of how social spider metapopulations persist. Using an individual-based simulation model, we demonstrate that rare increases in food supply due to environmental stochasticity may precipitate occasional mass dispersal from large colonies, allowing the metapopulation to persist.
Lay Summary

We use social spiders to investigate whether large colonies share food more evenly than small colonies and how this affects colony longevity. These spiders live together in colonies that can range in size from one individual to thousands. Large colonies do not have much food. We show that food may be shared too evenly in large colonies, which could result in no individuals getting enough food, so the colony goes extinct. We also show it is risky to leave the colony to start a new one. Therefore, for an individual to be able to disperse it has to be large and healthy, but at large colony sizes this may not be possible. This made us question how these spiders avoid extinction. Using computer simulations we found that rare random events that increase food available to large colonies can allow individuals to get enough food to disperse, allowing re-colonization and persistence.
Preface

This dissertation is original, unpublished, independent work by the author, R.V. Sharpe with guidance from Leticia Avilés.

Chapter 2 is modified from a publication in the Journal of Animal Ecology, authored by myself, and Leticia Avilés. I led the following stages of the research: developing the methods, collecting the data, analyzing the results, and writing the manuscript. Leticia Avilés contributed with the development of methods, interpreting the results, and writing and editing the manuscript.

Publications related to thesis chapters:

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Dedication

To Gerd and Fran from your funny little forest!
1 Introduction

In essence, ecology is the study of the relationships between organisms and the biotic and abiotic factors in their environments that affect their distribution and abundance. It is not sufficiently appreciated, however, that, in order to have a robust understanding of these systems, it is necessary to take into account the three levels of organization that impact this interaction, namely the individual, the population, and the community of populations across the landscape. Crucial to ecological research is the study of the dynamics of both populations and metapopulations within ecosystems, as well as the biotic and abiotic factors that affect their growth rates, fluctuations and extinctions and hence how populations regulate or fail to regulate their size. Understanding these dynamics is important not only because these processes may have profound effects on species survival and evolution, but also because biological diversity faces new and unprecedented threats from habitat destruction and global climate change (Ranta et al. 2006).

1.1 Population dynamics

It has been established that there are many potential factors affecting population dynamics, both in a density-dependent and density-independent fashion. To have a stabilizing effect on population dynamics, these factors, at a minimum, need to be negatively density-dependent, acting to reduce population size when large and increasing population size when small. These negative density-dependent factors could be caused by crowding, predators, and competition.

One example of density dependence in populations is intraspecific competition. Competition occurs when the use of a resource by one individual reduces availability of that resource to other individuals. Such resources can include food, space or water. Interspecific competition occurs when the competing individuals are of different species whereas intraspecific competition is between individuals of the same species. A lot of work has been done on potential effects of intraspecific competition on population and metapopulation dynamics, but little work has focused on the form of intraspecific competition i.e. how resources are distributed among individuals. This is unfortunate as the form intraspecific competition takes could significantly affect the outcome. In general, it has been accepted that the form of intraspecific competition lies on a spectrum between the two extremes of contest competition and scramble competition. The concept of contest and scramble competition was originally proposed by Nicholson (1954). He defined scramble competition as prevailing when shared resources are shared approximately evenly among individuals and contest competition when a limited number of individuals monopolize resources to survive and reproduce, with others losing out.
In any population that shares resources, the form of intraspecific competition can have profound consequences on its dynamics, especially when resources are scarce (Lomnicki 1999; Lomnicki 1978; Lomnicki 2009). If group members share resources via scramble competition, and resources are limited, no individual may get enough to reproduce, causing the population dynamics to be unstable, which would result in large population fluctuations, cycles and an increased risk of population extinction (Hassell 1976; Lomnicki 1988). In contrast, if resources are shared via contest competition, some individuals are able to access sufficient resources to reproduce, whereas others do not. This would result in the population shrinking, but persisting.

Another density dependent mechanism that has the potential to stabilize population dynamics is dispersal. There have been plenty of studies demonstrating density-dependent dispersal, where overcrowding or deteriorating conditions within the population promote dispersal (for review see Clobert 2001 and Lambin, Aars, and Piertney 2001). How effective dispersal is in regulating population sizes is dependent on when individuals disperse and the ability of all individuals within the population to disperse. For example, dispersers might need a threshold size or condition to disperse, if dispersal entails costs (Bowler and Benton 2005; Gyllenberg et al. 2008).

1.2 Metapopulation dynamics

To gain a better understanding of what affects population dynamics it must be remembered that populations may exist across a landscape with both habitable and uninhabitable areas, with populations going extinct and new populations arising due to the dispersal of individuals (Hanski and Gilpin 1997). This is considered a metapopulation, with these areas, or patches, being linked with each other by dispersal. The term metapopulation was introduced by Levins (1969). He defined a metapopulation to be a population of populations, in which he considered each population in a similar way to how he considered individuals within populations, where the local populations within a metapopulation are subject to ‘births’ and ‘deaths’. The local populations ‘die’ by going extinct and are ‘born’ by immigration of individuals from surrounding subpopulations. The factors that contribute to metapopulation dynamics and persistence are of vital importance in today’s increasingly fragmented and variable world.

1.3 What affects metapopulation dynamics?

Obviously, the behaviour of local populations affects the dynamics and persistence of the metapopulation as a whole. For example, many studies have confirmed that dispersal characteristics, such as propensity, frequency, and density-dependence have profound effects on metapopulation stability (Gonzalez et al. 1998; Hanski 1999; Loreau et al. 2003). Another factor shown to have the potential to affect
metapopulation persistence is environmental variation. It is well known that population dynamics are affected by environmental stochasticity (May 1974b; Roughgarden 1975; Lande 1993; Ludwig 1996), with theory suggesting that many systems are prone to extinction in fluctuating environments (Benton et al. 2002; Drake and Lodge 2004; Sæther et al. 2002; Bull et al. 2007). However, even though many studies address the effect of noise on local populations, the role of environmental stochasticity on metapopulation dynamics is much less understood (Bonsall and Hastings 2004). In addition, potential interactions between density-dependent and density-independent processes have not been fully explored. Indeed, there is growing awareness that the numerous factors that affect both population and metapopulation dynamics are likely to interact in complex and counterintuitive ways (Aiken and Navarrete 2011; Bull et al. 2007; Chase and Ryberg 2004; Childs et al. 2004; Sæther et al. 2002). For example, these density-dependent processes have the potential to change how a population responds to noise, sometimes damping or amplifying its effect (Greenman and Benton 2003; Turchin and Ellner 2000). Experimentally it has been demonstrated that observed fluctuations in population sizes are affected by non-linear interactions between environmental noise and density-dependent life-history characteristics (Sæther et al. 2002). More attention needs to be paid to how interactions between density-dependent and density-independent stochastic factors affect dynamical systems.

1.4 Anelosimus eximius – model species

In order to investigate how population size, the form of intraspecific competition and density-dependent processes interact to effect population and metapopulation dynamics, I used colonies of a Neotropical social spider Anelosimus eximius as models for populations. In addition to being social groups, these colonies are also self-contained populations that grow through internal recruitment, generating dispersal events and going extinct (Avilés 1997). Colonies of this species are ideal to study local population dynamics as they have a short generation time and a high rate of colony extinction and establishment, with one study suggesting that 21% of well-established colonies go extinct per generation (Avilés 1992). Such extinction events may involve the sudden crash of large and apparently healthy colonies, often with no individuals dispersing before the colony dies (Vollrath 1982; Venticinque et al. 1993; Thomas and Wardlaw 1992; Avilés 1997). A. eximius are highly cooperative social spiders that engage in communal prey capture, shared brood care and joint web maintenance (Avilés 1997). Colonies range in size from a single individual to tens of thousands (D’Andrea 1987; Avilés 1997). Parental and offspring generations tend to be relatively discrete with the females usually dying as the offspring generation are maturing (Aviles & Tufino 1998). Most individuals spend their entire lives within their natal nest, mating only with nest mates, generation after generation. This results in extremely inbred colonies with a highly female-biased sex ratio. New colonies appear to be founded by single females dispersing from their natal nest
and establishing a solitary nest (Vollrath 1986). However, the processes that influence the growth and extinction of social spider species are poorly understood (Crouch and Lubin 2001).

1.5 Research aims

Chapter 2

Using a simple mathematical model we predicted that scramble competition would predominate if prey is large, as large prey cannot be monopolized. Using artificial colonies on A. eximius we tested this experimentally, by measuring whether large prey is shared more evenly compared to small prey. As the size of prey captured by A. eximius nests increases with colony size (Yip et al. 2008), we suggest that this could cause an increase in the degree of scramble competition as colonies grow.

Chapter 3

(a) By measuring the size and condition of individual spiders in a wide range of colony sizes, we investigated whether the size and condition of individuals of the Neotropical social spider Anelosimus eximius vary as a function of colony size in ways that could help clarify this species’ unstable colony population dynamics and the sudden extinction of its large colonies. The observation that food per capita peaks at intermediate colony sizes (Yip et al. 2008) suggests that individuals will be larger and in better condition in intermediate-sized colonies. We suggest that intraspecific competition will move towards scramble competition as colony size increases, due to the increase in the size of the prey captured. Hence, we predicted that this will result in lower variance in size and condition of individuals as colonies increase in size.

(b) We also studied whether size and condition of individuals differed between dispersers and non-dispersers. To assess the potential cost of dispersal, we measured how long newly founded propagules survived, predicting that, potentially due to the high cost of dispersal, dispersers should be larger compared to philopatric individuals and that propagules would have low survival rate.

Chapter 4

To investigate what affects the metapopulation dynamics of systems similar to that of A. eximius, we created an individual-based simulation model. We examined how density-dependent dispersal, size-dependent dispersal, the form of intraspecific competition, and environmental noise combine to affect dispersal rates and metapopulation persistence.
2 Prey size and scramble vs. contest competition in a social spider: implications for population dynamics

2.1 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 (West-Eberhard 1983; Isbell 1991; Pfennig et al. 2007). Less well studied is 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 (Zhang et al. 1992; Reeve et al. 1998) and in frugivorous primates (Chapman 1990; Koenig 2002). Contest competition, on the other hand, can be seen in species whose individuals defend a territory or in those with dominance hierarchies (Sterck and Steenbeek 1997; Pruetz and Isbell 2000), such as in social primates where individuals at the top of the social hierarchy get preferential access to resources (Isbell 1991; Wittig and 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 et al. 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 and 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 and 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 and 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; Lomnicki 1999; Lomnicki 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 (Zhang et al. 1992; Reeve et al. 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 and Avilés 2014) and high rates of extinction (Vollrath 1982; Venticinque et al. 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 are is not economically defensible by single individuals, and are therefore 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 and 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 et al. 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 et al. 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 et al. 1993; Avilés 1997;
Crouch and Lubin 2001). In our study species, for example, it has been estimated that 21% of well-
established colonies in the forest understory go extinct per generation (Avilés 1997). Hart & Avilés
(2014) reconstructed the parameters governing the growth of A. eximius colonies in the lowland tropical
rain forest and obtained results consistent with dynamics of these colonies 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 1974a; May and Oster 1976; Lomnicki and Sedziwy
1989; Lomnicki 2009). A. eximius colonies appear to fulfil these conditions because 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.

In this chapter, we use a simple mathematical model to show that prey above a certain size may not be
economically defensible by single individuals if benefits, which are expected to be proportional to prey
volume, exhibit diminishing returns due to satiation or other factors, but the costs of defending the prey,
which should be proportional to the prey surface area, continue to increase as prey size increases. 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 are large, as individual spiders would not be able to prevent others from joining at either the prey capture or feeding stage. Here, we test this prediction using artificial colonies of *A. eximius*. We provided prey to these test colonies that were either small (approximately 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 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; Avilés 1999; Hart and Avilés 2014).

### 2.2 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

\[
b = \frac{GP_v e}{E + P_v}
\]

(eqn 2.1),

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

\[
c = A P_v^{2/3} + C_0
\]

(eqn 2.2),

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, which is the cost of defending a prey of size zero.
2.3 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 and Avilés 2007). The colonies have highly female-biased sex ratios, with colonies containing only about 10% males (Avilés and Maddison 1991).

Experimental Set-Up

To test the predictions made by the model, we fed small and large prey to artificial A. eximius colonies to investigate whether large prey is shared more evenly compared to small prey. 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 because this is the age that determines how soon and at what size spiders will reach maturity and therefore their reproductive success (Spence et al. 1996; Uhl et al. 2004; Salomon and Lubin 2007; Salomon et al. 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 x 11 x 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 at least one very large and one 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 and Avilés 2007). 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 approximately equalize total biomass. Small prey boxes received one prey item 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 all 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,

\[ I = \frac{-\sum_{i=1}^{s} t_i \ln t_i}{\ln s} \]  

(eqn 2.3)

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 square root 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 et al. 1996), which we estimated for spiders of each instar for all colonies combined. Within spiders, condition is expected to correlate inversely with hunger level (Jakob et al. 1996; Andrade 1998). 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. With the residual index, the individual body conditions of the two instars were not significantly different from each other (see Appendix A), 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 and with artificial colony ID as a random effect. 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 (glm) 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. Again, artificial colony was included as a random effect. In order to ascertain the best model for each test, we successively removed non-significant fixed effects from each model until each of the remaining fixed effects was significant.

2.4 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 (Figure 2.1). 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 diminishing returns from feeding on larger prey, but linear or accelerating costs of defending prey as its size increases, large prey may also not be worth defending. The model can be solved numerically, but as the equations are nonlinear, there
are no exact algebraic solutions. Therefore, we predicted that our experiment would show that large prey is shared more evenly compared to small prey.

![Graphical representation of the energetic costs and benefits to a single individual of defending a prey against competitors as a function of prey volume. 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, which are the prey sizes that are economically defendable. This model suggests that tiny 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.](image)

**Figure 2.1:** Graphical representation of the energetic costs and benefits to a single individual of defending a prey against competitors as a function of prey volume. 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, which are the prey sizes that are economically defendable. This model suggests that tiny 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.

**Experiment**

We found that the best model for how evenly prey was shared contained both instar and prey size, but not the interaction between the two. Large prey were shared more evenly than small prey (lmer: $\chi^2_{4.5} = 4.09$, $p = 0.043^*$, Figure 2.2) 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: $\chi^2_{5.6} = 0.16$, $p = 0.68$).
Figure 2.2: Intragroup evenness for small and large prey. This was calculated using a modified Pielou’s J measure of species evenness (eqn 2.3), 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.

Figure 2.3: 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.
Given artificial colonies of homogeneous instar, the final model to explain individual participation in prey capture included individual condition, prey size, and the interaction between the two, but not an individual’s instar. 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 most pronounced for large prey (interaction between condition and prey size: glmer: $\chi^2_{6,6} = 3.84, p = 0.0499^{*}$, Figure 2.3a). The mean difference in condition between individuals that participated in prey capture and those that did not was $0.070 \pm 0.014$ for large prey (glmer: $\chi^2_{3,4} = 17.35, p < 0.0001^{***}$), but only $0.015 \pm 0.014$, 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: $\chi^2_{5,6} = 0.14, p = 0.71$).

The probability that an individual fed, on the other hand, did depend on instar, in addition to these other factors, and so was included in the best model. There was also a significant difference in condition between individuals that fed and those that did not (glmer: $\chi^2_{5,7} = 29.22, p < 0.001^{***}$), with those of poorer condition being more likely to feed (Figure 2.3b). The magnitude of this difference also depended on prey size, as the interaction between prey size and condition was significant. Thus, when prey was large, the difference in condition between individuals that fed and those that did not was $0.096 \pm 0.017$ (glmer: $\chi^2_{4,5} = 30.61, p < 0.0001^{***}$), whereas for small prey this difference was smaller, at $0.022 \pm 0.013$ and non-significant (glmer: $\chi^2_{4,5} = 2.35, p = 0.12$, Figure 2.3). Significantly, more spiders of the younger than older instar fed (57.9 vs. 33.0%; glmer: $\chi^2_{6,7} = 19.04, p \leq 0.001^{***}$).

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 was the best model. 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 (Figure 2.4). This difference was significant (glmer: $\chi^2_{4,5} = 71.08, p < 0.0001^{***}$), but it did not depend on prey size (individual fed 9 prey size interaction, glmer: $\chi^2_{5,6} = 0.04, p = 0.85$), nor instar (individual fed 9 instar interaction glmer: $\chi^2_{5,6} = 0.07, p = 0.80$).
Figure 2.4: The percentage of individuals that fed as a function of whether they participated in prey capture or not. 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 by capture interaction: $p > 0.05$) ($n$ trials large = 19, small = 24).

2.5 Discussion

We constructed a simple mathematical model showing that prey above a certain size may not be economically defensible by single individuals when, as prey size increases, the costs of defending the prey item increase at a faster rate than the energy the prey item provides. This suggested that large prey items would have a higher probability of being more evenly shared among colony members (Figure 2.1). 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 (Figure 2.2), with individuals in poorer condition getting preferential access to food items (Figure 2.3). The degree of scramble competition, however, depended on prey size, as large prey were shared more evenly than small prey (Figure 2.2), 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 greater access to large prey (Figure 2.3b). Likewise, individuals in poorer condition were more likely to participate in prey capture when prey were large than when prey were small (Figure 2.3a). 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 (Figure 2.4). 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 and 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 (Grant 1993; Brown 1964). 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 decays (Rypstra and Tirey 1991). Our model extrapolates from these simple concepts to propose that only intermediate prey or patch sizes would be economically defendable (Figure 2.1). 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. Likewise, prey above a certain size should not be defended if the cost of defending an item increases faster than the energy contained in it or prey items above a certain size cannot be physically defended. 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 ‘economically defendable’.

Our experiment showed that large prey are shared more evenly than small prey (Figure 2.2) and that individuals in poorer condition have greater access to large prey compared to small prey (Figure 2.3b). This suggests that smaller prey, as long as not too small (i.e. tiny prey), 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 (Figure 2.2 and Figure 2.3). Exclusion of other individuals from a prey item may take the form of direct behavioural contests or of less competitive individuals not attempting to feed on prey that is already in the possession of more competitive or larger individuals. In addition, very 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. Unlike Rypstra’s study, however, here 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 and Grant 1995). In social spider colonies in the wild, prey arrive intermittently (Yip et al. 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. Sharpe and L. Aviles, 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 (Krafft et al. 1986; 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 (Figure 2.4), as the cost of participating in prey capture could 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, food-deprived spiders participate in prey capture more frequently than satiated spiders (Beleyur et al. 2015). In contrast however, in Stegodyphus dumicola, larger spiders were more likely to engage in prey capture (Wright et al. 2015).

In addition, we found that the younger subadult instar 1 individuals shared food more evenly compared to subadult instar 2s. As we only used two instars in our experimental design, and did not combine instars within each experimental nest, conclusions on how intraspecific competition might change with individual age are only tentative. There are, nonetheless, 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
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 Maculinea 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 and Wardlaw 1992). However, in the related Maculinea 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 et al. 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 (Figure 2.2), suggests 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 and Creel 1995). Likewise, in social spiders, Yip et al. (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 and 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 et al. 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 and 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 and Avilés 2007; Guevara and Avilés 2009; Powers and 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.
3 Group size, individual size and dispersal in a social spider

3.1 Introduction

Population stability and persistence is an important aspect of ecology, especially in a world experiencing increasing levels of human disturbance. Dynamical instability may occur when populations exhibit fast rates of growth which, in combination with discrete generations or time delays in population control feedback mechanisms, may result in populations overshooting their local carrying capacity (May 1974a; Hassell et al. 1976; May and Oster 1976; Guckenheimer et al. 1977). These effects may be exacerbated in social groups (Avilés 1999), especially if the method of intraspecific competition is scramble competition (Lomnicki 1988; Lomnicki 1999). While dispersal is an individual adaptation to escape locally deteriorating conditions, it may also allow groups or populations to regulate their size. The occurrence of dispersal, however, may depend on the balance between cost and benefits of dispersal vs. philopatry (for review see Clobert 2012). Thus, although costs and benefits of group living change with group size, such that there is an optimum group size where individual fitness is maximized, this optimum group size may not be stable. Sibly (1983), for instance, used a mathematical model to show that if there are no mechanisms for forced dispersal, an individual will only leave a group if its fitness within the group would be lower than if it dispersed (see also Giraldeau and Caraco 1993; Highashi and Yamamura 1993; Avilés 1999). Assuming there is no Allee effect, this would result in the stable group size being one where group members have the same fitness as lone individuals (Sibly 1983; Giraldeau and Caraco 1993; Highashi and Yamamura 1993; Avilés 1999). Indeed, there have been many studies that have demonstrated that although individual fitness may peak at intermediate group sizes, groups typically exceed their optimum size (Cash et al. 1993; Booth 1995; Avilés and Tufino 1998; Wilson 2000; Yip et al. 2008; Rubenstein and Wrangham 1986).

Intraspecific competition and group size

In the Neotropical social spider *Anelosimus eximius*, for instance, it has been shown that the amount of food obtained per capita peaks at intermediate colony sizes and decreases as colonies grow beyond this size (Yip et al. 2008). Therefore, one might expect that body size and condition of individuals may peak at intermediate colony sizes. By changing the size distribution of individuals within groups, how resources are distributed among conspecifics may, in turn, have a profound influence on group size and individual behaviour. It may affect, for instance, the tendency of individuals to join or remain in groups. Indeed, several papers extended Sibly’s (1983) model (above) by including individual variation and competitive asymmetries, showing that the cost benefit trade-off of group living will be different for group members depending on their internal state, such as hunger level, and phenotype (Vehrencamp
1983; Keller and Reeve 1994; Hamilton and Sih 2000). For example, whether food resources are distributed via contest or scramble competition will influence the variance in body size and condition of individuals within groups. Contest competition occurs when each successful individual gets sufficient access to a limited resource to survive and reproduce, whereas other individuals fail to do so (Nicholson 1954). Scramble competition occurs when resources are shared more or less evenly among all individuals in a population. If food resources are distributed evenly, i.e. via scramble competition, then there will be little difference among group members in their size and condition. If food can be monopolized on the other hand, variation in size and condition among individuals will depend on the amount of available resources and the number of competitors (Altmann and Alberts 2005), with more dominant or larger individuals being less affected by increasing competition or lower per capita food availability (Uchmanski 1985; Lomnicki 1988). It is not often considered, however, that the mode of intraspecific competition may change with group size. Sharpe & Avilés (2016) showed that in social spider colonies larger prey are shared more evenly. As prey size increases with colony size (Yip et al. 2008), this may result in larger colonies having a more even size distribution of individuals. Another example of this effect was demonstrated in a recent paper by Holdridge et al. (2016). They showed that as densities of protozoa populations increase, intraspecific competition changes from contest to scramble.

**Dispersal Constraints**

Dispersal is a critical behaviour that allow individuals to escape deteriorating conditions within a population or group (for review see Clobert 2012). There is plenty of evidence for density dependent dispersal, with many empirical examples demonstrating that increasing competition for limited resources promotes dispersal (for review see Lambin et al. 2001)). However, only recently has it been recognised that individuals that disperse are not likely to be a random subset of the population, but in fact differ from non-dispersers in behavioural tendencies, internal state, size, or other aspects of their phenotype (Clobert 2001a; Bowler and Benton 2005; Clobert et al. 2009). Depending on the species, the size and condition of dispersers can be both larger (Barbraud et al. 2003; Bowler and Benton 2005) or smaller (Hanski et al. 1991; Lawrence 1987) compared to philopatric individuals. Dispersing individuals may be smaller if within the group they would lose out in terms of food or space to larger and more competitive individuals and the costs of dispersing are not too high. On the other hand, more competitive group members with greater access to food resources or better location within the group would have higher fitness if they remained in the group (Lawrence 1987; Léna et al. 1998). In other systems, dispersal may entail large energetic costs or high risk of death (Clobert 2001; Stamps 2001a; Bonte et al. 2012). In such cases, individuals with greater amount of body fat or larger body size would have more energy reserves to bear the costs of dispersal (Bowler and Benton 2005; Gyllenberg et al. 2008). For example, root voles with a
greater propensity to disperse were heavier compared to philopatric conspecifics and heavier individuals were more likely to survive when forced to disperse (Gundersen et al. 2002). In addition, an individual’s age, sex, developmental stage or fertilization status may influence dispersal, as individuals may be too young to survive on their own or unable to find a mate outside their group (Bowler and Benton 2005). In the social spider A. eximius, for instance, only gravid females disperse since, due to limited male dispersal, those leaving their group prior to mating are unlikely to find a mate (Vollrath 1982).

**Consequences to population dynamics**

If a population distributes food resources via contest competition and there is a sudden reduction in resource abundance, then certain individuals may still get enough food to survive and reproduce, whereas less competitive individuals may not. The population will then shrink, but persist. However, if resources are distributed via scramble competition, then no individual may get enough resources when resources are scarce, resulting in the population crashing and potentially going extinct (Kendall and Fox 2002; Vindenes et al. 2008; Lomnicki 2009; Caswell 2009). A potential example of this can be seen in the social spider A. eximius, where large colonies may suddenly go extinct. In this species, large colonies are expected to experience reduced food availability and greater scramble competition, as they capture fewer, but larger prey, which cannot be monopolized (Yip et al. 2008; Sharpe and Avilés 2016). Given dispersal limitations, which require that only adult inseminated females disperse, the combination of scramble competition and low food availability could then result in individuals failing to secure sufficient resources to grow and reproduce (Avilés 1999). The mode of intraspecific competition, coupled with a species’ dispersal constraints, may thus have profound consequences on a population’s ability to regulate its size, and therefore its dynamical stability (Andreassen et al. 2002; Hanski 2001). If a population is not able to reduce its size when it is too large, unstable population dynamics and a higher risk of population extinction would follow (Ims and Hjermann 2001).

Here we study whether the size and body-condition of individuals of the Neotropical social spider Anelosimus eximius vary as a function of colony size in ways that could explain this species’ unstable colony population dynamics and the sudden extinction of large and apparently healthy colonies, often with no individuals dispersing before the colony dies (Vollrath 1982; Venticinque et al. 1993; Thomas and Wardlaw 1992; Avilés 1997). Hart and Avilés (2014) reconstructed the parameters governing the growth of A. eximius colonies in the lowland tropical rainforest and obtained parameter values consistent with colony dynamics being intrinsically unstable. Unstable colony dynamics are expected if, in addition to rates of growth being high, generations discrete, and dispersal limited, scramble competition predominates, in particular at large colony sizes.
Several predictions can be made about the expected size and condition of *A. eximius* individuals as a function of colony size. The observation that food per capita peaks at intermediate colony sizes (Yip et al. 2008) suggests that individuals will be larger and in better condition in intermediate-sized colonies, noting that individual size may reflect the colony size in which individuals developed, rather than the current colony size. Furthermore, since the size of the prey captured increases with colony size (Yip et al. 2008) and that larger prey are shared more evenly (Sharpe and Avilés 2016), we expect an increase in scramble competition, relative to contest competition, as colony size increases and thus a more even distribution of individual body size and condition in larger colonies. We also studied whether size and condition differed between dispersing and philopatric individuals, expecting that, due to potentially high cost of dispersal, dispersers should be larger compared to philopatric individuals as they will have greater energy stores (Jakob et al. 1991) and be more likely to survive. As an indication of costs of dispersal, we recorded how long newly founded nests (i.e. propagules) survived.

### 3.2 Methods

**Study organism**

We used the social spider *Anelosimus eximius* Keyserling (Araneae: Theridiidae) to address these questions. *A. eximius* occurs in lowland wet tropical areas from Panama to southern Brazil (Levi 1963; Agnarsson 2006). Its colonies, which range in size from one adult female to tens of thousands of individuals, represent not only social groups, but also self-sustaining populations as individuals remain together throughout their lives and mate with other colony members to produce successive generations (Avilés 1997). Colonies exhibit high rates of population growth due to their cooperative behaviours and highly female biased sex ratios (Avilés and Maddison 1991; Hart and Avilés 2014). They also suffer relatively high rates of extinction, which may involve the sudden death of large and apparently healthy colonies (Avilés 1999). Due to limited male dispersal, only gravid females disperse, alone or in small groups, to set up new colonies (Vollrath 1982). After emerging from the egg sac, females undergo six moults and males five moults to attain maturity (Avilés 1986). This results in adult females being larger, and of a chronologically older instar, compared with adult males. Secondary sexual characters allow the sexes to be readily distinguished starting in the fifth instar. In Ecuador *A. eximius* ranges from lowland tropical rainforest up to approximately 1200 m above sea level in lower montane rainforest (Purcell and Avilés 2007). Our study area was located along the road to Loreto, Napo Province, Ecuador (0°703’S, 77°736° W, 1000 m elevation).
Data collection

With the goal of estimating how the mean and variance (disparity) of body size and condition changed with colony size, we collected 1306 specimens from 19 natural A. eximius colonies observed from the road side between May and August 2013. Colonies ranged in size from a single individual to 5500 individuals, with only five colonies larger than 2000 individuals (see Appendix B), which, based on an earlier study from this area (Purcell and Avilés 2007), corresponds to just above ‘intermediate’ size (~700-1000 individuals). Lack of colonies near at the upper end of the colony size range was likely due in recent human disturbance to the area. We estimated the size of colonies from the cross sectional area of their nests (areas estimated from drawings taken in the field using Inkscape, version 0.91), which has been shown to be highly correlated with the number of adult females they contain (Purcell and Avilés 2007). Using the regression equation from Purcell & Avilés (2007), we inferred the number of adult female spiders present in the colonies, except in colonies with fewer than 30 individuals, which could be counted directly.

From each colony we aimed to collect 20 individuals from each of the following instar categories: juvenile instar 4, subadult instar 1 females (instar 5), subadult instar 2 females (instar 6), adult females (instar 7), subadult males (instar 5) and adults males (instar 6), although, depending on the size and age composition of the colony, this was not always possible. We weighed each individual using a XS105DU Analytical Balance (Mettler Toledo, Ohio, USA) and measured the leg length of the first pair of legs (tibia plus patella). The leg is a fixed body part that can be used as a measure of body size (Uhl et al. 2004) that is independent of current feeding state. The condition of the spiders was calculated using the residual index, which corresponds to the residuals of the regression of body mass on cephalothorax length (Ulbrich et al. 1996), with separate regressions calculated for each instar and sex (but across all colonies) to remove differences in body shape across instars and the two sexes that would affect the calculation of condition.

Data collection to estimate the survival of newly established nests (i.e., propagules) took place between May and August 2012 in the same location. Newly established nests, which typically appeared in the immediate vicinity of large colonies and contained single females, were marked and checked every three days to record the number of spiders and egg sacs they contained. At these times, any additional newly-established colonies were searched for and recorded. If a colony had no spiders in it for two consecutive censuses it was considered extinct. When comparing the condition of disperses to their philopatric nest mates, all dispersed females who did not have an egg sac or juveniles present in her newly-established nest were excluded from the analyses due to the high chance they were gravid, which would skew the condition measurement.
**Statistical analysis**

All statistical analyses were carried out with R statistical software version 3.1.1 (R Core Team 2014).

To test whether individual condition and leg length varied with colony size we constructed a linear mixed effect model (lmer) using the lme4 package in R (Bates *et al.* 2015). The initial model had the following fixed effects (1) colony size, (2) instar age, (3) instar sex nested in instar age, (4) colony size by instar age interaction, and (5) the three-way interaction colony size by instar age by instar sex, and (7) the square of nest size. Individual colony ID was included as a random factor and instar age was coded as an integer. Instar sex was nested within instar age to ensure that when testing differences between the two sexes, comparisons were only done within the age classes (instars 5 and 6) for which the two sexes could be distinguished. Instar 4 juveniles, where the sexes could not be distinguished, were coded as female, as the sex ratio in this species if heavily female biased (~10 females per male; Avilés and Maddison 1981). The final model used for statistical analysis was calculated by successively removing non-significant fixed effects until all remaining effects were significant. To test the significance of individual variables in the ‘full model’, we used a likelihood ratio test to compare the ‘full model’ to that of a reduced model lacking the term of interest (Pinheiro and Bates 2009).

To determine how uniformly individual size (leg length) and body condition were distributed within colonies as a function of colony size, we developed a “disparity” index using a bootstrap algorithm (Appendix C). We developed this index, rather than using the variance of the traits, given that both the sample size and the mean of condition and leg length were correlated with colony size. When estimating the variance of a measure that can only take limited values, standard measures of variance, including the coefficient of variation, are correlated with sample size, in particular when sample is size small and covaries with the mean (Einum *et al.* 2012 and Appendix C). We, therefore, devised a new method of calculating the spread of body condition and leg length, which we refer to as a ‘bootstrap disparity index’. This was calculated using the following steps: (1) we calculated the mean and standard deviation of the measurement for each instar sample from each colony; (2) for each of these samples, we obtained 10,000 randomly generated samples of the measurements, ensuring that each randomly generated sample had the same size and same mean as the experimental sample. The values in the random sample could take any value between the minimum and maximum observed for each instar across all nests, as we assumed this would reflect the minimum and maximum possible in this environment. (3) The standard deviation was calculated for all randomly generated samples. (4) We obtained a relative cumulative frequency distribution of the standard deviations of the randomly generated samples. (5) The standard deviation of each experimental sample was cross-referenced with its corresponding cumulative frequency distribution of standard deviations calculated from the randomly generated samples. (6) Where the experimental
standard deviation fell along the cumulative frequency distribution of randomly generated samples gave us our ‘*bootstrapped disparity index*’ (see Appendix C). Therefore, the bootstrapped disparity index could take any value between 0 and 1, with a value of 0 indicating complete uniformity and a value of 1 indicating maximum disparity among individuals within a colony.

Statistical tests on within-colony disparity of leg length and condition were conducted using generalized linear mixed effects models with penalised quasi-likelihood estimation (glmmPQL) from the MASS R package (Venables and Ripley 2002; Zuur *et al.* 2009). As the disparity index values were limited to range between 0.0 and 1.0 and were right skewed, we arcsine square root transformed them and then used a Gaussian error distribution with a log link function for the analyses. The initial model contained the same fixed effects as the body size and condition measures (see above), with colony ID included as a random factor. We used the Wald test to simplify the initial model by sequentially removing all non-significant terms to achieve the minimal adequate model. The final model was the model where all the remaining fixed effects had a significance value below $p = 0.05$. The survival function for single female nests was estimated using R’s survival package (Therneau and Grambsch 2000).

### 3.3 Results

**Leg length against colony size**

The final model included the two-way interaction instar age by instar sex and colony size by instar age. After confirming, not surprisingly, that leg length was highly correlated with instar age ($\text{lmer; } \chi^2_{4,7} = 4339.88, p = < 0.001***$), we found that leg length increased as colony size increased ($\text{lmer; } \chi^2_{5,7} = 32.68, p = < 0.001***$, Figure 3.1), but, with a significant interaction with instar age ($\text{lmer; } \chi^2_{6,7} = 22.83, p = < 0.001***$) and a significant interaction between instar age and instar sex ($\text{lmer; } \chi^2_{6,7} = 27.35, p<0.00***$).

Due to the significant interaction between instar age and colony size we performed tests on each instar individually. We found that leg length increased with colony size in the older instars, but not significantly so in the younger ones (Table 3.1) and (Figure 3.1).
Table 3.1: Results of separate analyses of leg length against colony size for each instar age. Leg length increases with colony size in the overall model ($\chi^2_{5.7}= 32.68$, $p<0.001$***). When tested individually the relationship is only significant for the older instars.

<table>
<thead>
<tr>
<th>Instar Age</th>
<th>Instar Name</th>
<th>$\chi^2$</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Juvenile</td>
<td>1.48</td>
<td>0.224</td>
</tr>
<tr>
<td>5</td>
<td>Subadult 1 (females and males)</td>
<td>0.79</td>
<td>0.374</td>
</tr>
<tr>
<td>6</td>
<td>Subadult 2 (females and males)</td>
<td>13.64</td>
<td>&lt; 0.001 ***</td>
</tr>
<tr>
<td>7</td>
<td>Adult</td>
<td>8.54</td>
<td>0.003 **</td>
</tr>
</tbody>
</table>

Figure 3.1: Leg length (tibia plus patella) as a function of colony size. The points represent each individual’s measurement and the superimposed lines are the predicted values of the full linear model for each random factor, i.e. nest ID. Overall, leg length increased with colony size ($\chi^2_{5.7}= 32.68$, $p = < 0.001$***), but with a significant interaction between colony size and instar age ($\chi^2_{6.7}= 22.83$, $p = < 0.001$***). When tested individually, only the older instars exhibited a significant relationship. n= 19 colonies.

**Individual condition against colony size**

The final linear model for individual condition did not include any interaction effects. The effect of colony size (lmer; $\chi^2_{4.5} = 4.66$, $p = 0.031$ *) and instar age (lmer; $\chi^2_{4.5} = 5.81$, $p = 0.016$ *) were significant, with individual condition decreasing as colony size increased and decreasing slightly as instar age increased (figure 3.2).
Figure 3.2: Individual condition against colony size. The points represent each individual’s measurement and the superimposed lines are the predicted values of the full linear model for each random factor, i.e. Nest ID. Overall condition decreases with colony size ($\chi^2_{4.5} = 4.66, p = 0.031^*$)

**Within-colony individual disparity against colony size**

*Leg length size disparity*

There was no significant effect of nest size on within-colony disparity in leg length. However, the average within-colony disparity in leg length was 0.09 ± 0.02, which is small given that the range of possible values is between 0.0 and 1.0, where 0.0 means complete uniformity in leg length.

*Body condition disparity*

The average within-colony condition disparity was also small at 0.07 ± 0.02. However, there were significant fixed effects. The final model included the square of instar age and the two way the interaction instar age by instar. Colony size had a significant effect (glmmPQR; $\chi^2_1 = 4.333, p = 0.037^*$) as within-colony body condition disparity decreased with increasing colony size (figure 3.3). The interaction instar age by sex was significant (glmmPQR; $\chi^2_1 = 35.468, p <0.001^{***}$), as was instar age squared (glmmPQR; $\chi^2_1 = 9.015, p= 0.003^{**}$ figure 3.3). Within-colony condition disparity peaked at intermediate instar ages and was higher for males (figure 3.4).
Figure 3.3: Within-colony condition disparity (arcsine transformed) against colony size with the results of the generalized linear model for individual instars superimposed. Colony size had a significant effect on condition variance ($p = 0.037^*$).

Figure 3.4: Within-colony condition disparity (arcsine transformed) as a function of instar age and sex. Overlaid is the generalized linear model, which has the square of instar age as a significant term ($\chi^2_1 = 9.015, p = 0.003^{**}$).
**Size and condition of dispersers**

Adult female leg length was larger (lmer; \( \chi^2_{4,5} = 3.9, \ p = 0.048^* \)), and their individual condition greater (lmer; \( \chi^2_{4,5} = 9.45, \ p = 0.002^{**} \)), when dispersed in propagules compared to adult females remaining in their natal colonies (figure 3.5).

![Figure 3.5: Leg length and individual condition of adult females in propagules compared to adult females in their natal colony following dispersal. There was a significant difference between the two for both variables (leg length: lmer; \( \chi^2_{4,5} = 3.9, \ p = 0.048^* \), condition: \( \chi^2_{4,5} = 9.45, \ p = 0.002^{**} \)), n source colonies = 2, n propagules = 39](image)

**Single female colony survival**

We found that propagules established by single females had a very low survival rate, with a mid-life of 37 days and only ~15% surviving to 50 days following establishment (Figure 3.6).
Figure 3.6: The survival function of 40 propagules from 10 source colonies. Grey shading represents the 95% confidence interval.

3.4 Discussion

Understanding the factors that contribute to population stability and persistence is an important aspect of ecology. Here, we investigated how body size and condition of individuals within colonies of the Neotropical social spider *Anelosimus eximius* change with colony size and whether individuals that disperse differ from those that remain. As a way of assessing costs of dispersal, we also estimated the survival rate of dispersers establishing new nests. We further assessed the degree of uniformity within colonies of body size and condition to investigate whether the form of intraspecific competition — scramble vs. contest— changes with group size. As larger colonies capture larger prey (Yip *et al*. 2008) and large prey is harder to monopolize compared to small prey (Sharpe and Avilés 2016), we predicted that the spread of leg length and body-condition would decline with colony size. Given expected costs of dispersal we further expected that dispersers would be larger and in better condition compared to non-dispersers and that the survival rate of new nests would be low.

Changing cost and benefits with group size

The finding that body size increased (Figure 3.1), whereas individual condition decreased (Figure 3.2), as colony size increased is at odds with our prediction that both would peak at intermediate colony sizes. This prediction was based on Yip *et al*. (2008)’s observation that food intake in *A. eximius* colonies in the lowland tropical rainforest peaks in colonies of intermediate size (~400-900 individuals), with spiders in
smaller and larger colonies expected to receive less food per capita. We suggest that the discrepancy may be due to body size reflecting the colony size in which individuals grew, whereas body condition would reflect the colony size at the time measurements were taken. In spiders, body size, including leg and cephalothorax length, can only change when an individual moults (Foelix 2011), contrasted with condition, which is an approximate measure of food intake (Jakob et al. 1996). According to a reconstruction of the growth function of A. eximius colonies in the tropical rainforest (Hart and Avilés 2014), individuals in colonies of ~1000 individuals are likely to have developed in colonies containing ~400 maternal spiders. Thus, it is likely that spiders in our sampled colonies, especially those in the older instars, would have developed in smaller colonies, introducing a feedback delay. This would result in the body size of individuals reflecting the circumstances in colonies that were smaller than those sampled. Thus, taking into account the feedback delay on body size, we might postulate that individual condition and leg length would peak at different colony sizes: individual condition should peak at the colony size that corresponds to the greatest per capita food availability, whereas leg length would peak in colonies whose size in the previous generation was within this range. If the difference in the peak between condition and leg length is large enough, and with sufficient noise in the data to preclude fitting a squared term in the linear model, condition would then appear to decrease linearly with colony size, whereas leg length would increase. We further conjecture that, had our sample included even larger colonies that those available, we might find that body size peaks and then decreases among the largest colonies, in line with other studies showing that adults in other social spider species are smaller in larger colonies (Riechert et al. 1986; Ward and Enders 1985).

A feedback delay in body size could affect instar ages differently. On the one hand, younger instars would have had less time to grow, so their size may more accurately reflect present colony conditions. Larger individuals, on the other hand, would not only have had a longer time to develop, but may also be more affected by low per capita resources due to their greater resource requirements, especially if there is a feedback delay in body size response to prevailing conditions so individuals are too large for the current colony size (Latto 1992; Persson et al. 1998; Pfister and Peacor 2003). In addition, younger instars may be better able to compensate for decreases in food availability by moultng at a smaller size or by increasing the length of time between moults, something adults are unable to do. The humped function of within-colony individual condition disparity against instar age (Figure 3.4) could reflect this. Within-colony condition variance might peak at intermediate age instars if they delay moulting when conditions are bad. Indeed, it has been shown that females that have greater access to food resources mature earlier (Vollrath and Rohde-Arndt 1983; Rypstra 1993; Salomon et al. 2008). The small observed within-colony
condition disparity in juveniles could be due to the smaller feedback delay they experience because they are younger, so their body size more accurately reflects current colony conditions.

**Colony size and intraspecific competition**

Our data on within colony disparity in individual size and condition are consistent with scramble competition predominating in *A. eximius* colonies. Thus, bootstrap measures of within-colony disparity were small, with the mean disparity for both leg length and condition being in the lowest 95 percentile of possible disparity values each colony could take. In addition, we found that condition disparity decreased with colony size (Figure 3.3), consistent with the prediction of Sharpe and Aviles (2016) that scramble competition should increase with colony size, as larger colonies capture increasingly large prey (Yip et al. 2008), which single individuals cannot monopolize (Yip et al. 2008; Sharpe and Avilés 2016). We did not detect, however, any pattern of leg length disparity and colony size. This may result from spiders having greater control over their body size by, for example, delaying moulting until they grow larger (Foelix 2011).

**Dispersal**

It has been well studied in multiple taxa that individuals disperse to escape deteriorating local conditions (for review see Clobert 2012). Here we show that individual dispersal in *A. eximius* results in low survival of the newly founded propagules (Figure 3.5). Indeed, it has been shown that there are significant risks of predation for dispersing spiders (Vollrath 1985; Riechert et al. 1986; Sundström 1995) and costs associated with the production and maintenance of nests by single females, in particular in rainy environments (Riechert et al. 1986; Tanaka 1989; Salomon et al. 2008; Hoffman and Avilés 2017). For example, a widow spider of the Negev desert had a 40% chance of death during dispersal compared to 2% for non-dispersers (Lubin 1995).

High dispersal cost may be the reason behind dispersers being larger and in better condition compared to philopatric conspecifics (Figure 3.5). Thus, Bodasing et al. (2001) found that in the social spider *Stegodyphus mimosarum*, low food availability discouraged dispersal despite increased mortality within colonies. They further found that more spiders dispersed when colonies were better fed, but that, even then, smaller spiders remained philopatric, suggesting that dispersal risk is too high, or the benefits comparatively low for individuals in poor condition. Likewise, Berger-Tal et al. (2016) demonstrated that *Stegodyphys dumicola* individuals from food augmented webs dispersed sooner and had greater survival compared to dispersers from food restricted webs.

Dispersal decisions may depend on an assessment of expected fitness inside vs. outside the groups, termed ‘fitness-dependent dispersal’ by (Ruxton and Rohani 1999). In social spiders, costs of inbreeding
depression, which often drive dispersal in many species, appear to be vastly lower than potential costs of avoiding inbreeding by dispersing in the environments in which they live (Avilés and Purcell 2012). Thus, dispersing spiders would not only face high rates of predation, but also, given that colonies are often few and far between, the risks of failing to find a mate if they dispersed prior to mating. Dispersing spiders would also lose significant advantages of remaining in the natal nests. Reanalyzing the Avilés and Tufiño (1998) data, Avilés and Purcell (2012), for instance, found that adult *A. eximius* females living in groups had an average of 2.0 offspring per capita surviving to maturity, compared to 0.75 for females living solitarily or in pairs. Thus, spiders that stay benefit from allomaternal care (Samuk and Avilés 2013), access to a larger range of prey items (Yip et al. 2008), both active predator protection and passive protection due to the large three-dimensional web (Uetz and Hieber 1994; Henschel 1998), and the protection that large webs afford against abiotic conditions such as heavy rain and heat (Seibt and Wickler 1988; Lubin and Crouch 2003). Finally, individuals that counter the effect of reduced food by delaying moulting (Vollrath 1985) may not be able to disperse if conditions within the colony deteriorate rapidly, as individuals need to be inseminated adults in order to disperse (Vollrath 1982). Therefore, using Sibly’s model and Avilés and Purcell (2012), we argue that individuals would not disperse until colony sizes are very large, as only in large colony sizes would the fitness benefits of dispersing outweigh the costs.

**Population Dynamical Consequences**

Given costs and constraints on dispersal, and in particular dispersal being limited to adult inseminated females, as noted above, colonies reaching large sizes be unable to disperse if of the wrong age structure (i.e. individuals not having yet reached reproductive maturity). Even if the colony is in the ‘correct’ age structure when it reaches colony sizes that trigger dispersal, the high cost of dispersal means that dispersing females need to be large in size and in good condition to be able to survive dispersing. But, at these large colony sizes, food per capita is low and prey size is large. As inividuals may be unable to monopolize these large prey items, these would result in scramble competition predominating in large colonies. Compounded by the fast rate of growth of *A. eximius* colonies (Hart and Avilés 2014), declining resources would be spread too thinly among potentially too many colony members, making it difficult for potential disperses to obtain sufficient size and condition to disperse. This reduction in food intake as colonies grow could also result in juveniles and subadults delaying their moulting, which would result in the offspring generation not moulting in time to replace a dying adult generation, further weakening the colony. Potential disperses therefore face a triple bind, they have to be large enough to disperse to offset the cost of dispersal, but, as those costs are high, it is only worthwhile dispersing from very large colonies. However, in these large colonies food per capita is low and scramble competition predominates, making it difficult for adult females to obtain sufficient resources to disperse. The
decreasing food per capita as colonies grow, along with increasing scramble competition and dispersal constraints, could be the reasons for the observed sudden extinction of large colonies without dispersal. We thus suggest that we must take into consideration potential interactions between population size, strength and type of intraspecific competition, and constraints on dispersal when investigating stability and extinction risk of animal populations, in general.
4 Environmental variation, dispersal, intraspecific competition and metapopulation persistence

4.1 Introduction

Understanding the factors that affect metapopulation persistence is of vital importance. Many species occupy habitats that are divided into patches, either naturally or due to anthropogenic land use. With increasing habitat fragmentation, studies of metapopulation dynamics are more important than ever. Much theoretical and empirical work has been done on this topic, but few studies have investigated how realistic life-history choices and other individual level processes interact with biotic and abiotic factors to influence metapopulation persistence. For example, many studies show that dispersal characteristics, such as propensity, frequency, and density-dependence, are key processes driving metapopulation dynamics (Gonzalez et al. 1998; Hanski 1999; Loreau et al. 2003). When modeling metapopulations, however, few studies take these processes into account. For instance, many studies assume dispersal to be density independent (Ruxton & Rohani 1999; Travis, Murrell & Dytham 1999; Law, Murrell & Dieckmann 2003; Fowler 2009; Bocedi, Heinonen & Travis 2012; Bocedi et al. 2014). However, this does not reflect reality as dispersal is often triggered by population density or the availability of resources (Watson et al. 1984; Rhainds, Gries & Saleh 1998; Hanski, Saastamoinen & Ovaskainen 2006; De Bie et al. 2012). For example, if we assume that the fitness of individuals within populations changes with population size, being low under crowded conditions (Krause & Ruxton 2002), we could surmise that individuals would not disperse until their potential fitness following dispersal exceeded that if they remained. This would result in high population densities being a trigger for dispersal as the net benefit of dispersal should rise with density (Poethke & Hovestadt 2002). When modelling population or metapopulation processes ignoring density-dependent dispersal is potentially problematic as it is likely to have a large effect on population and metapopulation dynamics (Bowler & Benton 2005).

Of those studies that do model density-dependent dispersal, most assume that all individuals have the potential to disperse when density-dependent conditions are met (Hovestadt & Poethke 2006; Münkemüller & Johst 2006; Fowler 2009). However, dispersal propensity could differ among individuals, either as a function of their size or condition. Indeed, it has been shown empirically across a wide range of taxa that dispersing individuals are a non-random subset of population members, often with larger individuals being more likely to disperse (Lawrence 1987; Anholt 1990; O’Riain, Jarvis & Faulkes 1996; Léna et al. 1998; Barbraud et al. 2003). If dispersal is costly or risky and survival is more likely if the individual is of better condition or has a certain amount of stored resources, then fitter individuals would be expected to disperse (Bowler & Benton 2005). Such effects could reduce the number of dispersers and
therefore the colonization rate of empty patches, which in turn could increase a metapopulation’s extinction risk, especially if local patches have a relatively low survival rate (Parvinen et al. 2003; Münkemüller & Johst 2006). Indeed, empirical studies have shown that dispersal rate can affect metapopulation persistence (see Hanski & Gilpin 1997 for a review).

**Intraspecific competition**

Another important factor affecting metapopulation persistence is intraspecific competition. Some work has been done on the strength of intraspecific competition in relation to population and metapopulation dynamics, but not much on the mode of intraspecific competition. The mode of intraspecific competition can be thought of as a spectrum, ranging from contest competition (or compensatory regulation) to scramble competition (or over-compensatory regulation). Contest competition occurs when successful individuals within a population get sufficient access to resources to survive and reproduce, whereas other individuals fail to do so. In this case the population may shrink, but remain viable. In contrast, in scramble competition resources are assumed to be shared more or less equally among all individuals, which may result in no individual being able to obtain sufficient resources (Lomnicki 1978, 1999, 2009), causing the population to go extinct (Hassell 1976; Lomnicki 1988). The form of intraspecific competition is therefore likely to affect not only patch turnover but also patch size, growth rate and stability, which in turn will affect metapopulation dynamics.

**Environmental variation**

It is well known that population dynamics are influenced by stochasticity (May 1974a; Roughgarden 1975; Lande 1993; Ludwig 1996), with theory suggesting that single species systems are more vulnerable to extinction in fluctuating environments (Benton et al. 2002; Sæther et al. 2002; Drake & Lodge 2004; Bull et al. 2007). However, despite significant work on the effect of noise on populations (Earn, Levin & Rohani 2000; Hanski & Gaggiotti 2004), there remain many potential unexplored consequences of environmental stochasticity on metapopulation dynamics (Bonsall & Hastings 2004).

**Interactions**

There is growing realization that the many factors that influence both population and metapopulation dynamics are likely to interact in complex, and often, unpredictable and counterintuitive ways (Sæther et al. 2002; Childs et al. 2004; Chase & Ryberg 2004; Bull et al. 2007; Aiken & Navarrete 2011). For example, the term ‘paradox of enrichment’ was coined to describe the effect where increasing food availability can cause population dynamics to become unstable (Rosenzweig 1971; May 1972, 1974b; Bull & Bonsall 2008). Likewise, ‘sustainable’ fishing could increase the nonlinear effect of environmental noise interacting with intrinsic demographic factors and life-history traits to increase the
instability of populations (Anderson et al. 2008). How density-dependent population processes interact with density-independent factors to influence population and metapopulation persistence is another understudied research area (Grenfell et al. 1998; Turchin & Ellner 2000; Finkenstädt & Grenfell 2000; Bjørnstad 2000; Greenman & Benton 2003). For example, density-dependent processes can alter a population’s response to noise, sometimes dampening or amplifying its effect (Turchin & Ellner 2000; Greenman & Benton 2003). Sæther et al. (2002) showed experimentally that fluctuations in the sizes of populations were affected by complex interactions between a species’ density dependent life-history characteristics and environmental noise. Therefore, more study of how density-dependent, density-independent, and stochastic factors and their interactions affect dynamical systems is needed.

In order to get a realistic understanding of dynamical systems it is vital that all these things are taken into account. Social spiders, such as the Neotropical Anelosimus eximius, appear to be an ideal system in which these factors and their interactions can be explored (Avilés 1997, 1999). A. eximius live in social colonies that range in size from one individual to tens of thousands. Colonies grow through internal recruitment, much as self-sustaining populations. As in many group-living species, fitness of group members varies with group size, peaking at intermediate group sizes (Avilés & Tufino 1998). Dispersal appears to be density dependent, with dispersal of single individuals only taking place at large colony sizes (Vollrath 1982), presumably when disperser’s potential fitness would be greater upon dispersing, compared to not dispersing. In addition, mortality of dispersers appears high and, being costly, appears to preferentially involve large and high condition individuals (Sharpe and Avilés in prep). Food per capita peaks at intermediate colony sizes (Yip et al. 2008) and appears to be allocated predominantly via scramble, rather than contest competition (i.e. approximately evenly) (Sharpe & Avilés 2016). This combination of patterns appear to lead to a double bind: When colonies are large enough for dispersal to be a viable option, the majority of individuals within the colonies may be too small to have any chance of successful dispersal (Sharpe and Avilés in prep). With scare resources being distributed too evenly, no individuals would likely get sufficient food to disperse, which could result in the sudden extinction of many large colonies without dispersers being produced (personal observation). This presents us with an apparent paradox, making it hard to explain the continued persistence of A. eximius metapopulations.

By considering each social spider colony as a patch, we can use metapopulation theory to attempt to understand the dynamics of this and similar systems. In fact, A. eximius colonies fit all the four criteria set out by Hanski et al. (1995) to constitute a true metapopulation: (1) All habitat patches i.e. colonies, must have the ability to support a breeding population; (2) all populations are prone to extinction (unlike mainland – island systems); (3) recolonization of all patches is possible; and (4), local patch dynamics are asynchronous. The main difference between the A. eximius metapopulation and the classic Levins
metapopulation (Levins 1966) is that individuals do not disperse to occupied patches, but to empty ones, creating a new population. By investigating the dynamics of metapopulations such as those of social spiders, we are shining light on an understudied, but common metapopulation structure.

To investigate how density-dependence, size-dependent dispersal, environmental variation, and the form of intraspecific competition combine to affect metapopulation persistence, we constructed an individual based model based on the metapopulation structure of social spiders. As in social spiders (Avilés and Guevara 2007), we modeled individual fitness as a peaked function of group size, rather than a decreasing function of population size, as is typical of traditional population models. A peaked fitness function is a common feature of many group living and social species (Krause & Ruxton 2002). We further modeled dispersal as single individuals dispersing to unoccupied patches when their local populations had grown above a certain size, which mirrors the life-cycle of many social insects i.e. ants, wasps, termites and even potentially the naked mole rat (Braude 2000). We decided to use an individual based model in order to analyse the influence of individual variability and stochastic events on local population and metapopulation dynamics. In reality all process arise out of individual behaviour and their traits, such that the majority of factors that affect local population and metapopulation dynamics in single species systems are bottom-up processes, except for environmental variation. We examined how density-dependent dispersal, condition-dependent dispersal, the form of intraspecific competition, and environmental noise combine to affect metapopulation persistence.

4.2 Methods

Model structure

We considered a metapopulation system that was not spatially explicit (i.e. the location of a patch did not affect dispersal probability or patch dynamics). Each local population was age-structured, consisting of two age classes with adults reproducing asexually. Local populations grew by internal recruitment. Adults were able to disperse to only to empty patches. Individuals dispersed singly from local populations that had reached or exceed a certain size. Local populations went extinct if all the individuals died or dispersed. The global metapopulation consisted of 200 patches, starting with 70 patches of 35 different sizes. Each time step represented one generation (Figure 4.1). Simulations were run for 500 generations or until the metapopulation went extinct.
Figure 4.1: A graphical representation of one time step of the local population model
Table 4.1: Table of mathematical symbols and parameter values uses

<table>
<thead>
<tr>
<th>Input parameters varied between simulation runs</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbol</td>
<td>Definition</td>
</tr>
<tr>
<td>$F_D$</td>
<td>Food required to disperse</td>
</tr>
<tr>
<td>$C$</td>
<td>Degree of contest competition</td>
</tr>
<tr>
<td>$V$</td>
<td>Environmental variation (the variance of the normal distribution that affects food assigned to each colony)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Constants i.e fixed values</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbol</td>
<td>Definition</td>
</tr>
<tr>
<td>$F_L$</td>
<td>Expected Food population consisting of a single adult gets</td>
</tr>
<tr>
<td>$\Omega$</td>
<td>Disperser’s survival probability</td>
</tr>
<tr>
<td>$O_{min}$</td>
<td>minimum number of offspring possible</td>
</tr>
<tr>
<td>$O_{max}$</td>
<td>maximum number of offspring possible</td>
</tr>
<tr>
<td>$S_{min}$</td>
<td>minimum adult size possible (i.e. size needed to survive to adulthood)</td>
</tr>
<tr>
<td>$S_{max}$</td>
<td>Maximum possible adult size (here 1, as size varies between 0 and 1)</td>
</tr>
<tr>
<td>$K$</td>
<td>Local population carrying capacity</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variables computed within simulations</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbol</td>
<td>Definition</td>
</tr>
<tr>
<td>$F_S$</td>
<td>mean food allocation per individual</td>
</tr>
<tr>
<td>$F_{col}$</td>
<td>Total food colony receives</td>
</tr>
<tr>
<td>$R_i$</td>
<td>Individual rank</td>
</tr>
<tr>
<td>$F_i$</td>
<td>Amount of food to individual</td>
</tr>
<tr>
<td>$O_i$</td>
<td>Number of offspring an individual adult produces</td>
</tr>
<tr>
<td>$S_i$</td>
<td>Size of an individual</td>
</tr>
<tr>
<td>$A_f$</td>
<td>Adults size i.e. amount of food adult received as a juvenile</td>
</tr>
<tr>
<td>$D_f$</td>
<td>Expected per juvenile food if adult dispersed</td>
</tr>
<tr>
<td>$P_f$</td>
<td>Expected per juvenile food if adult stayed</td>
</tr>
</tbody>
</table>

**Competition and resource availability**

We assume that the amount of resources acquired by individuals in a population is a humped function of population size, reflecting either an Allee effect (Avilés, 1999) or, in a group living organism, the interplay between costs and benefits of group living. To model this we use the following function, modified from Courchamp, Clutton-Brock & Grenfell (1999):
\[
F_{\text{col}} = N e^{(1 - \frac{N}{K})(\frac{N}{K} - 1) \ln(\frac{1}{FL})}
\]

(eqn 4.1),

where \( N \) is the number of adults in the population; \( K \) is the local population carrying capacity, where the amount of food captured per capita is at a maximum; \( F_L \) is the amount of food a population consisting of one adult receives.

Food is distributed competitively within a population only to juveniles, as we assume that the ‘final’ size of adults will be directly proportional to the amount of food they received as juveniles. An adult’s size is directly proportional to her juvenile size. If the mode of competition is pure scramble then the total food a population gets is divided equally among all juveniles, otherwise food is allocated according to the equation

\[
F_i = F_S \left( 1 + \frac{cF_{\text{col}}(F_S - \frac{FR_l}{F_{\text{col}}})}{F_S^2} \right)
\]

(eqn 4.2),

where \( C \), is the degree of contest competition assumed to range between 0 and 1, where 0 is full scramble and 1 is full contest competition; \( F_i \) is the average amount of food individuals receive (i.e. the total food for the populations divided by the number of juveniles in the population); and \( R_l \) is the competitive rank of an individual within its population. Individual ranks are assigned at random, simulating demographic factors that could result in juveniles having differing competitive abilities. We assume that individuals can reach satiation, i.e. there is a maximum amount of food an individual can consume. We tested six different competition regimes ranging from full contest to full scramble competition (Figure 4.2).

Figure 4.2: The different food distribution equations used. Here, demonstrated when average food to an individual is half of the maximum possible.
Individual size is directly proportional to the amount of food received and an individual’s fitness is directly proportional to its size. Only juveniles who receive a threshold amount of food grow into adults. Juveniles who fall below this threshold die. All juveniles that moult into adults reproduce. The number of offspring an adult produces is a log linear function of her size, adapted from (Marshall & Gittleman 1994):

\[
\log(O_i) = \frac{S_i(O_{\text{min}} + O_{\text{max}} - O_{\text{min}}S_{\text{max}} - O_{\text{max}}S_{\text{min}})}{S_{\text{min}} - S_{\text{max}}}
\]  

(4.3),

where \(O_i\) is the number of offspring an individual has, \(S_i\) is the size of the individual, \(S_{\text{min}}\) is the minimum size an adult needs to mature to adulthood, and \(S_{\text{max}}\) is the maximum size an adult can reach when allocated the maximum amount of food possible. \(O_{\text{min}}\) and \(O_{\text{max}}\) are the minimum and maximum number of offspring possible.

**Dispersal**

Dispersal is by single adult individuals colonizing an empty patch. To reflect risks associated with dispersal, the probability that an individual survives dispersal is initially set to 0.3, but could be lower if there are more surviving dispersers than empty patches. Surviving individuals are chosen at random, whereas the rest die. Before asexual reproduction takes place, an adult has to decide whether to disperse and set up a new population or stay in the current population. An adult will disperse if the following two conditions are met.

(1) **Density-dependent dispersal**

As in Ruxton & Rohani (1999), an individual will disperse if its expected future fitness is greater if dispersing than staying in her natal population. Expected fitness within the natal nest is calculated as

\[
\frac{N \bar{O}}{E[F_{\text{col}}]}
\]

where \(N\) is the number of adults in the current population, \(\bar{O}\) is the average number of offspring per adult and \(E[F_{\text{col}}]\) is the expected amount of food the population will receive. Expected fitness upon dispersal is \(\Omega \frac{O_i}{F_L}\), where \(\Omega\) is the dispersal risk, \(O_i\) is the number of offspring the adult will have and \(F_L\) is the amount of food lone adults receive.

(2) **Condition-dependent dispersal**

Successful dispersal will only occur if an individual exceeds a certain body size \((F_D)\), regardless of population size.
Environmental Variation

We introduced environmental stochasticity in the amount of food a local population will receive by varying its carrying capacity and the amount of food to lone individuals, with the values being pulled from a Gaussian distribution with mean K and standardized variances ranging from 0.0 to 0.8 (see Table 4.1) for each individual local population and generation. Carrying capacities will thus varied across different local populations within the same metapopulation.

The combination of parameter values explored in the simulations is shown in Table 4.1. We were particularly interested in how the degree of contest vs. scramble competition interacted with required individual size at dispersal and different degrees of environmental noise to determine dispersal rates and metapopulation persistence. All simulations were run in Python 2.7.1. Graphs and statistics were produced using R 3.3.2 (R Core Team 2014).

4.3 Results

Whether or not dispersal took place within the metapopulation depended on the interaction between minimum individual dispersal size and competition (Figure 4.3). When competition was more contest-like, dispersal always took place, except when dispersal was completely prohibited when the minimum dispersal size was set above 1.0. When competition was more scramble-like, dispersal could not take place if the minimum dispersal size was too large. Environmental variation increased the number of parameter combinations under which dispersal took place (Figure 4.3b). Metapopulation survival exhibited similar patterns as those of dispersal, with metapopulation persistence increasing with increasing contest competition and decreasing with minimum individual dispersal size (Figure 4.4). However, from Figure 4.4, it can be seen that with increasing environmental variation metapopulation persistence to 500 generations became possible under conditions when previously it wasn’t, namely under a combination of scramble competition and high condition-dependent dispersal size. Figure 4.5 shows that in simulations where dispersal increased with environmental variation, metapopulation survival increased as well.
Figure 4.3: How competition type and minimum adult dispersal size interact to determine whether any dispersal takes place with (a) no environmental variance (b) environmental variance greater than 0.6. Competition type ranged from 0.0 to 1.0, with 0.0 being full scramble competition and 1.0 being full contest competition. Individual size varies from 0.0 to 1.0. Black squares indicate no dispersal took place, light grey squares indicate dispersal occurred, with darker gray squares indicating dispersal occurring in a greater proportion of metapopulations. The square with the black outline is the one combination of competition and minimum dispersal size where dispersal did take place, but the metapopulation did not survive to 500 generations.
Figure 4.4: Metapopulation survival time in generations as a function of competition type and minimum dispersal size, for (a) no environmental variation, and (b) environmental variation greater than 0.6. Metapopulation persistence measured as log transformed generations. If a metapopulation did not go extinct its survival time was set to 500 generations.

Figure 4.5: Average of number of colonies (log transformed) that produce dispersers per time step against environmental variation.
Apart from three anomalies, when there was no environmental variation, if any dispersal took place within the metapopulation, then the metapopulation survived to 500 generations (Figure 4.6). The parameter combination where the metapopulation survived to 500 generations despite no dispersal taking place was when dispersal size was set so that no individuals could disperse and the degree of contest competition was high. This resulted in all local populations surviving to 500 generations. The anomaly where dispersal does take place, but the metapopulation survives only to 12 generations occurred when minimum dispersal size was 0.8 and the degree of contest competition was 0.4. Dispersal only took place until the fifth generation and all the initial local populations died. The new local populations, initiated by this dispersal, grew too fast, such that, either populations were below the size where dispersal would improve the fitness, or too large for there to be sufficient food available for individuals to grow above the minimum dispersal size.

![Figure 4.6: Comparing metapopulation survival (log transformed generations) to a binary measure of whether any populations within the metapopulation produced dispersers at any time. There was no environmental variation, but all competition regimes are included. Metapopulation survival is log transformed and the line is a polynomial linear model.](image)

When comparing metapopulation survival to local population survival, we see that, even though local population survival either remained the same or decreased as environmental variation increased (Figure 4.7), metapopulation survival either remained the same or increased as environmental variation increased, except where dispersal was prohibited (Figure 4.8). When the size needed to disperse was small, the
metapopulation survived to 500 generations, regardless of local population longevity. The larger individual dispersal size, the more local population survival time affected metapopulation survival time.

Figure 4.7: Local population survival against environmental variation by competition type (0.0 = pure scramble, 1.0 = pure contest competition), looking only at minimum adult dispersal size 0.6 and 0.8. Population survival is log transformed and fitted lines are squared linear models.
Figure 4.8: Maximum metapopulation age as a function of environmental variation by competition type (0.0 = pure scramble, 1.0 = pure contest competition). Graph only shows minimum adult dispersal size 0.6 and 0.8. Metapopulation survival log transformed

4.4 Discussion

Although the factors that affect metapopulation survival have received much attention, it is increasingly acknowledged that potentially important interactions are yet to be considered. Interactions between density-dependent processes, life history traits, and density-independent factors, for instance, could affect metapopulation dynamics in complex and counterintuitive ways. We thus constructed an individual based model to examine how density-dependent dispersal, condition-dependent dispersal, mode of intraspecific competition, and environmental stochasticity combine to affect metapopulation persistence.

Intraspecific Competition

We demonstrate that the mode of intraspecific competition interacts with condition-dependent dispersal to affect metapopulation survival, even without environmental variation (Figure 4.3a). Local population persistence had little effect on metapopulation longevity, unless dispersal was severely constrained by a high minimum individual dispersal size coupled with scramble competition.

Within our model, the main factor that influenced metapopulation survival was dispersal (Figure 4.6). When dispersal could occur, then the metapopulation survived. Mode of intraspecific competition interacting with condition-dependent dispersal determined whether populations were able to produce
dispersers. Scramble competition resulted in individuals not being able to gain enough food to disperse when dispersal would have been favourable in large populations, i.e. when individuals remaining would have had lower fitness than those dispersing. With contest competition, in contrast, some individuals were able to gain sufficient food when population were large, dispersing to create new populations in unoccupied patches, thereby allowing the metapopulation to persist.

**Environmental Noise**

We found that the effect of competition mode on dispersal probability and metapopulation persistence decreased or was reversed when environmental variation increased. Thus, as environmental variation increased, metapopulation survival increased, except when dispersal was completely restricted (Figure 4.8). The effect was not caused by an increase in the survival of local populations (Figure 4.8), but by dispersal probability increasing in populations with scramble competition and high maximum dispersal size when environmental noise increased (Figure 4.5). The apparent reason is that, at large population sizes, unpredictable increases in food occasionally allowed individuals to obtain sufficient food to disperse. Even when such events were rare, when they did occur, they resulted in a large number of dispersers being produced given the even distribution of resources among individuals in the local population. This occasional surge of dispersers populated empty patches, allowing metapopulations to persist, a result that may appear surprising and counterintuitive. Such an effect may not have been previously appreciated as, when investigating environmental variance, many studies only account for negative disturbances such as catastrophes or habitat destruction (e.g., Kareiva & Wennergren 1995; Bascompte & Sole 1996; Gyllenberg & Hanski 1997; Hanski & Ovaskainen 2000; Casagrandi & Gatto 2002; Reigada *et al.* 2015). However, here we demonstrate that it is possible for positive stochastic events to profoundly affect metapopulation dynamics. Scramble competition reduces variance in food distributed to individuals within a generation, increasing the probability that no dispersal takes place. Here we show that environmental variation, on the other hand, increases variance in food resources between generations, thus, increasing the chances that, within the metapopulation, some individuals can disperse. As Hovestadt & Poethke (2006) we believe that modelling environmental noise as both negative and positive, rather than only as random catastrophes or negative forcing, is a more realistic representation of the natural environment. Indeed, climate change is producing not only unidirectional environment change, but also causing environments to exhibit more stochastic variability. There have been several studies that have shown that under certain conditions environmental variance can indeed promote the persistence of metapopulations, both theoretically (Jansen & Yoshimura 1998; Gonzalez & Holt 2002; Roy, Holt & Barfield 2005) and experimentally (Matthews & Gonzalez 2007). These studies demonstrate that
environmental variability allows populations that otherwise would have consistently negative growth to have short periods of positive growth.

**Interactions**

Our study demonstrates that this counterintuitive effect of environmental noise can also be caused by interactions between density-dependent dispersal, the form of intraspecific competition, and condition-dependent dispersal, factors that are lacking from many models. Indeed, Münkemüller & Johst (2006) show that combing factors such as intraspecific competition type and density-dependent dispersal may increase patch connectivity and metapopulation persistence. One theoretical study investigating how density-dependent dispersal could interact with intraspecific competition type found that, if dispersal were density dependent, species that engaged in scramble competition would be better able to track climate change by producing more dispersers (Best et al. 2007). This study, however, did not account for condition-dependent dispersal and only included negative environmental change.

Our results also help explain the persistence of social spider metapopulations, as well as provide insights on metapopulation dynamics of species with similar metapopulation structures. The colonies of our focal species, *A. eximius*, appear to exhibit scramble competition, especially at large colony sizes (Sharpe & Avilés 2016). Dispersal seems to only take place at large colony sizes when food availability per capita is low (Yip et al. 2008), but with only high-condition individuals dispersing (Sharpe and Avilés in prep). This, coupled with high colony growth rates and dispersal being restricted to adult females, results in large colonies frequently going extinct, often without producing dispersers (personal observation). Thus, the factors that allow the persistence of *A. eximius* metapopulations has remained an open question. Our study provides a potential answer to this paradox by demonstrating that rare events, which cause temporary increases in resources, could be sufficient to allow these metapopulations to persist.

We demonstrate that density-dependent processes, life history traits, and density-independent factors have the potential to interact in complex and perhaps counterintuitive ways to influence metapopulation persistence. This highlights the need to take into account interactions between factors when modelling population and, especially, metapopulation dynamics.
5 Concluding chapter

Understanding how interactions among individuals in a population and with biotic and abiotic factors in their environment influence population and metapopulation dynamics is vital. However, how these factors interact and the potential of non-linear and unpredictable interactions is an often overlooked, but potentially important element that affects population dynamics. Here we used the neotropical social spider species *Anelosimus eximius* as a model system to address these questions. *A. eximius* colonies are self-sustaining populations that grow through internal recruitment, with colonies having the potential to survive for many generations, with individuals remaining together throughout their lives. Once a colony has reached a large size, individuals may disperse to start new colonies. Colonies frequently go extinct, which occasionally takes the form of large colonies suddenly crashing (Vollrath 1982; Venticinque *et al.* 1993; Avilés 1997; Crouch and Lubin 2001).

In chapter 2, we investigated whether prey size could affect the degree of contest competition exhibited by *A. eximius* by constructing a mathematical model and experimentally manipulating the size of prey fed to artificial *A. eximius* colonies. We demonstrated that large prey is shared more evenly compared to small prey.

In chapter 3 we investigated how condition and body size of *A. eximius* individuals changes with colony size and how the trade-offs of group living and the form of intraspecific competition could affect dispersal. We found that body size increased with colony size, reflecting increasing food per capita as colonies grow from small to intermediate size. Body condition, however, decreased with colony size, potentially because as colonies grow above intermediate sizes, body sizes are too large for the prevailing circumstances. In addition, within-colony variance for body condition decreased with colony size, suggesting that the degree of scramble competition increases as colony size increases.

In chapter 3 we also investigated survival of nests constructed by newly dispersed females, finding that these propagules had a very low survival rate, despite dispersing females being larger and in better condition than philopatric ones. These finding suggest that dispersal is costly, potentially explaining absence of dispersal except at large colony sizes.

In chapter 4 we used an individual based model to investigate how density-dependence, size-dependent dispersal, environmental variation, and the form of intraspecific competition combine to affect metapopulation persistence. We show that in the absence of environmental variation the form of intraspecific competition interacts with size-dependent dispersal to affect metapopulation survival. If food is distributed via contest competition or the minimum dispersal size is low, sufficient individuals are able to disperse for the metapopulation to persist. In contrast, when individuals have to be large in order to
disperse and metapopulations distribute food via scramble competition, individuals may not get sufficient food to disperse, resulting in low metapopulation persistence. In contrast, when environmental variation is present, it results in metapopulations surviving longer because occasional increases in resources can result in mass dispersal events that allow quick recolonization and thus, metapopulation persistence.

5.1 *Interspecific competition*

One factor that has the potential to have profound effects on the dynamics of both population and metapopulations, but is frequently overlooked, is the form of competition between group members. The method by which individuals share limited resources falls on a scale between two extremes, scramble and contest competition. Contest competition occurs when only successful individuals obtain sufficient access to a limited resource, allowing them to survive and reproduce. Alternatively, scramble competition arises when resources are shared approximately evenly among individuals. How resources are shared could have severe consequences on population stability, with contest competition promoting more stable population dynamics, whereas, scramble competition could subject populations to unstable dynamics when resources essential for survival and/or reproduction are limited.

In chapter 2 we hypothesised that in *A. eximius* colony size may alter the degree of scramble vs. contest competition due to changes in the characteristics of resources, as prey size increases with colony size (Yip *et al.* 2008). It is thought that one of the principal elements determining the method of intraspecific competition is the degree to which common resources can be monopolised (Ward *et al.* 2006). We argued that large prey will not be able to be monopolized by single individuals compared to small prey. It has been shown that, compared to scattered resources, contest competition dominates if resources are aggregated, either in space or time. As long as the resource patches are not too large, solitary individuals can dominate, preventing others access (Rubenstein 1981; Bryant and Grant 1995). If resources are scattered, or the patches too large, scramble competition will dominate. All this can be considered under the umbrella of ‘economic defendability’ (Brown 1964), which seeks to address the conditions under which benefits of defending a resource outweigh the costs. We constructed a model to investigate when three-dimensional resource items should be defended and when it is not worthwhile to do so. We demonstrated mathematically that it is only intermediate sized prey that are economically defendable when the costs of defending prey items increase linearly with prey size, but benefits increase with diminishing returns. Furthermore, as there should be an upper limit to the amount of resource an individual can consume before the resource spoils, we suggest that only intermediate sized resources are worth defending (Figure 2.1). By feeding both large and intermediate sized prey to artificial colonies of *A. eximius* we show that, as predicted, larger prey are shared more equitably than small prey (Figure 2.2).
The results that, within *A. eximius*, larger prey is divided among individuals more uniformly compared to smaller prey is especially interesting because large *A. eximius* colonies capture larger prey items compared to small ones (Yip *et al.* 2008). Even though there have been some studies looking at how the form of intraspecific competition changes with biotic or abiotic factors, few studies have investigated the consequences this could have on whether these populations have stable or unstable dynamics. Therefore, we suggest that as *A. eximius* colonies grow in size, the way by which food is distributed tends towards scramble competition. Indeed, in Chapter 3 we show that, in *A. eximius*, condition variance within colonies decreases as colony size increases (Figure 3.3), which indicates that resources are shared more evenly as colonies grow. As scramble competition should destabilize population dynamics (Lomnicki 1988; Lomnicki 2009), this implies that as *A. eximius* colonies grow, their population dynamics should become more unstable, therefore making colonies more prone to extinction. Indeed, a few empirical studies have indicated that scramble competition promotes unstable dynamics in contrast to contest competition (Thomas and Wardlaw 1992; Thomas *et al.* 1993; Bender *et al.* 1998; Gawlik 2002).

### 5.2 Group size, intraspecific competition and life-history trade-offs

Even though, by itself, intraspecific competition type has the ability to affect the stability of populations, little attention has been paid to the potential interactions between intraspecific competition and other elements that affect population dynamics. This is important, because the relative costs and benefits of group living change with group size, with there being a group size that corresponds to when individual fitness is at a maximum, i.e. the optimum group size. However, Sibly (1983) pointed out that the optimum group size is not likely to be stable, as lone individuals, with lower fitness outside a group, will likely still seek to join groups. Likewise, group members should avoid dispersal even if this results in group size increasing beyond the optimum, as the fitness of being alone will be lower compared to being in the group. Consequently, the stable group size will be where the fitness of group members is the same as that of lone individuals. In *A. eximius*, it has been show that although individual fitness peaks at intermediate group sizes, colonies commonly exceed this size (Avilés and Tufiño 1998; Yip *et al.* 2008). It has also been found that the amount of food individuals acquire per capita peaks at intermediate colony sizes in this social spider (Yip *et al.* 2008). We thus expected that individual body size and condition would show a similar pattern. However, contrary to this prediction, we found that body size increased with colony size, whereas condition decreased. We suggest that our prediction did not hold because there is a feedback delay with regards to body size, as individuals are only able to change their size during moulting. Therefore, body size is likely to depend on the size of the colony in which individuals grew, which, once intermediate group size is surpassed, would result in individuals having body sizes larger than current conditions would imply. In contrast, body-condition is a more instantaneous measure of prevailing colony
conditions. However, if an individual’s body size is too large for the current colony size, they would need greater food resources to maintain adequate body-condition, potentially resulting in a sharp decline in body-conditions as colonies grow.

5.3 Dispersal

Dispersal is a behaviour permitting individuals to leave groups or populations when conditions deteriorate (for review see Clobert 2012). Density-dependent dispersal also has the potential to serve as a way to regulate population size. Many empirical studies demonstrate that multiple species engage in density-dependent dispersal triggered by increasing intraspecific competition (for review see Lambin et al. 2001). However, little attention has been paid to the possibility that not all individuals in a population have the same propensity to disperse. For example, dispersers could differ from philopatric individuals in a multitude of characteristics including internal state, condition, behavioural tendencies, as well as other aspects of their phenotype (Clobert 2001b; Bowler and Benton 2005; Clobert et al. 2009). Indeed, empirical studies have demonstrated that, in many species, dispersers are large or in better condition compared to non-dispersers (e.g Barbraud, Johnson & Bertault 2003; Bowler & Benton 2005). It is suggested that this could be due to dispersal involving large energetic costs or danger (Clobert 2001; Stamps 2001a; Bonte et al. 2012), such that an individual with phenotypic traits that allow it to better cope with dispersal costs, such as larger size or better condition, would be more likely to disperse.

In chapter 3 we proposed that dispersal of single female *A. eximius* is extremely costly, as only around 15% of propagules established by single females survive over 50 days (Figure 3.7). As dispersal is costly, individuals would only disperse from very large colonies, since only at this point would the potential fitness of dispersers be greater than that of non-dispersers. In addition, we also found that dispersers were larger and had higher body condition compared to philopatric individuals within their natal nest (Error! Reference source not found.), possibly as only high condition individuals would stand a chance of surviving dispersal. However, at these large colony sizes, food per capita is low and prey are large. Hence, individuals may be unable to monopolize prey items, potentially resulting in scramble competition predominating in large colonies. Therefore, as large colonies grow, the diminishing prey capture biomass would be spread too evenly among colony members to allow potential dispersers to gain high enough size and condition to disperse, which may explain why large *A. eximius* colonies sometimes suddenly go extinct without dispersing (Vollrath 1982 and personal observation).
5.4 Metapopulation persistence

The predominance of scramble competition at large colony sizes, with its potential to lead to unstable local dynamics and extinction in our target social spider leaves us with a potential paradox. How do its metapopulations persist? In chapter 4 we used an individual based model to show that density-dependent processes, life history traits, and density-independent factors interact in complex and counterintuitive ways to affect metapopulation dynamics, a topic that is not widely investigated.

Within our model, when conditions allowed dispersal to occur, the metapopulation survived (Figure 4.6). The mode of intraspecific competition interacted with body size-dependent dispersal to determine whether individuals could disperse and therefore whether the metapopulation persisted. When the degree of contest competition was high, some individuals were allowed access to sufficient food when populations were large, which resulted in these individuals being able to disperse when populations grew large. Even if a fraction of the populations produced dispersers, these were sufficient to establish new local populations in unoccupied patches, which allowed the persistence of the metapopulation. Conversely, when there was a low degree of contest competition (i.e. scramble competition), individuals were unable to access sufficient food when populations were large, so no dispersal took place, resulting in the extinction of the local populations and thus the metapopulation. However, as the degree of environmental variation increased, the persistence of the metapopulations increased. This was due to environmental variation occasionally leading to sufficient large stochastic increases in food supply to allow individuals access to enough food to disperse, even when the threshold body size for dispersal was large and the model of competition was primarily scramble. Even if these events were rare, the large number of dispersers produced allowed sufficient recolonization for the metapopulation to persist (Figure 4.5).

5.5 Complex interactions

Here, we demonstrate that metapopulation and population dynamics can be dramatically changed due to the interactions between density-dependent dispersal, the form of intraspecific competition, and condition-dependent dispersal. It has been previously shown that, by combining different factors, complex interactions result. For example, Münkemüller and Johst (2006) demonstrate that interactions between the form of intraspecific competition, landscape dynamics and density-dependent dispersal affect metapopulation persistence in ways that could not have been predicted by considering these factors independently. Best et al. (2007) theoretically showed that species that engaged in scramble competition may be better able to track climate change by producing more dispersers compared to species where contest competition prevails.
Overall we show that the degree of contest competition can change with biotic variables such as prey and group size, potentially resulting in large colonies of the social spider *A. eximius* suddenly crashing. This effect could be exacerbated by interactions with dispersal costs, as may be difficult to get sufficient resources for a high enough condition to disperse successfully. As dispersal is costly, it is expected to be worthwhile only at large colony sizes. This created a paradox, how do *A. eximius* metapopulations persist. However, we show that this could be due to environmental noise occasional increasing available resources to allow large number of individuals to disperse and, through recolonization, maintain a viable metapopulation.
Bibliography


Appendices

Appendix A: Chapter 2 - Counts of spiders measured

(a)

(b)
Figure A.1: *Anelosimus eximius* individuals used during the experimental trials of the effect of prey size on how evenly prey are shared. Shown are (a) the raw individual weights, (b) the ratio index weight/cephalothorax length, and (c) the residual condition index (see Jakob *et al.* 1996), which was the measure of condition used for the statistics and graphs in chapter 2. With the residual method, there was no difference in the condition between the two instars (lmer; $F_{80}, p = 1$), whereas with the ratio index, older (subadult 2) spiders had higher “condition” compared to younger ones ($n = 470$ $n = 340$ sub1 and 470 sub2 spiders)
Appendix B: Chapter 3 - Spider counts and linear models

Figure B.1: *Histogram of the size of colonies used in chapter 3’s observational study.*
Table B.1: The full models used for each test after non-significant factors were removed using a stepwise method. Variables printed as (1|variable name) indicate random factors. ColonyID represents the colony from which each individual spider was collected.

<table>
<thead>
<tr>
<th>Test</th>
<th>Full Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leg length vs. colony size</td>
<td>ColonySize + InstarAge + ColonySize:InstarAge + InstarAge:InstarSex + (1</td>
</tr>
<tr>
<td>Condition vs. colony size</td>
<td>ColonySize + InstarAge + (1</td>
</tr>
<tr>
<td>Condition Variance vs. colony size</td>
<td>ColonySize + InstarAge:InstarSex + InstarAge² + (1</td>
</tr>
<tr>
<td>Leg length dispersed female vs. source colony</td>
<td>ColonyType + (1</td>
</tr>
<tr>
<td>Condition dispersed female vs. source colony</td>
<td>ColonyType + (1</td>
</tr>
</tbody>
</table>
Appendix C: Chapter 3 – Disparity measures

In order to determine whether the coefficient of variation changes with sample size or sample mean, I created 2500 randomly generated samples containing numbers that vary between 0.88 and 1.33, which is the log of the minimum and maximum length of adult female *A. eximius*. The sample sizes of these randomly generated samples varied between 2 and 26, which were the sizes of actual samples in the study. All statistical tests were linear models.

For the randomly generated samples, the coefficient of variation increased with sample size (Figure C.1, lmer; $F_{2498} = 18.16$, $p < 0.001$). In addition, the spread of the values of the coefficient of variation was larger when sample sizes were small (Figure C.1).

![Coefficient of variation of the randomly generated samples against their sample size.](image)

Figure C.1: Coefficient of variation of the randomly generated samples against their sample size.

In addition, the coefficient of variation of the randomly generated samples was a humped function of the mean of the quantity measured, in this case leg length (lmer; $F_{2498} = 264.46$, $p < 0.001$, Figure C.2).
Figure C.2: Coefficient of variation of the randomly generated samples against the mean value of the measurement being analysed.

Calculating Bootstrap disparity index

Our ‘bootstrap disparity index’ was calculated using the following steps:

1. For each randomly generated sample used for the analysis above, I obtained 10,000 new randomly generated samples, ensuring that each new sample had the same size and same mean as the original sample (i.e. $2.5 \times 10^7$ new samples in total). The values in the new random samples could take any value between the minimum and maximum indicated above.

2. Using the newly generated samples, I obtained a relative cumulative frequency distribution of the standard deviations of the new samples (Figure C.3).

3. The standard deviation of each original sample was cross-referenced with its corresponding cumulative frequency distribution of standard deviations calculated from the new randomly generated samples (Figure C.3).

4. The place where the experimental standard deviation fell along the cumulative frequency distribution of randomly generated samples gave us our ‘boot strapped’ variance.
Figure C.3: The ‘bootstrap disparity index’ was calculated by comparing the standard deviation of the original sample to all standard deviations of its corresponding 10,000 new random samples.

In contrast, the bootstrap disparity measure does not change with sample size ($F_{2498} = 0.117$, $p = 0.732$, Figure C.4) and does not change with sample mean ($F_{2498} = 0.037$, $p = 0.85$, Figure C.5)
Figure C.4: Bootstrap disparity of the original randomly generated samples against their corresponding sample size.

Figure C.5: Bootstrap disparity index of the original randomly generated samples against their corresponding sample mean.