

Allee effects in social species

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Abstract

1. Allee effects have important implications for many aspects of basic and applied ecology. The benefits of aggregation of conspecific individuals are central to Allee effects, which have led to the widely held assumption that social species are more prone to Allee effects. Robust evidence for this assumption, however, remains rare. Furthermore, previous research on Allee effects has failed to adequately address the consequences of the different levels of organisation within social species' populations.
2. Here, we review available evidence of Allee effects and model the role of demographic and behavioural factors that may combine to dampen or strengthen Allee effects in social species. We use examples across various species with contrasting social structure, including carnivores, bats, primates and eusocial insects. Building on this, we provide a conceptual framework that allows for the integration of different Allee effects in social species.
3. Social species are characterised by nested levels of organisation. The benefits of cooperation, measured by mean individual fitness, can be observed at both the population and group levels, giving rise to "population level" and "group level" Allee effects respectively. We also speculate on the possibility of a third level, reporting per capita benefits for different individuals within a group (e.g. castes in social insects).
4. We show that group size heterogeneity and intergroup interactions affect the strength of population-level demographic Allee effects. Populations with higher group size heterogeneity and in which individual social groups cooperate demonstrate the weakest Allee effects and may thus provide an explanation for why extinctions due to Allee effects are rare in social species.
5. More adequately accounting for Allee effects in social species will improve our understanding of the ecological and evolutionary implications of cooperation in social species.

KEYWORDS

demography, metapopulation, population dynamics, social group, task specialisation

[†]Both authors contributed equally to this work.

1 | INTRODUCTION

Allee effects have been documented for a wide variety of taxa and have influenced many aspects of basic and applied ecology during the past decades (Courchamp, Berec, & Gascoigne, 2008; Kramer, Dennis, Liebhol, & Drake, 2009). In general, an Allee effect can be defined as a positive relationship between mean individual fitness and population size or density (hereafter population size), generally occurring in small populations (Stephens, Sutherland, & Freckleton, 1999). More specifically, Allee effects occur when there are beneficial interactions among individuals that cause the per capita population growth rate to increase with the number of individuals. Conversely, if the number of individuals decreases, they suffer from fewer or less efficient interactions and the per capita population growth rate decreases. The critical population size below which the per capita population growth rate becomes negative is called the Allee threshold. A major consequence of the Allee effect is that populations falling below the Allee threshold become even smaller, thereby entering into a positive feedback loop that can ultimately lead to their extinction (Courchamp, Clutton-Brock, & Grenfell, 1999).

Allee effects are typically categorised into two types: component and demographic (Stephens et al., 1999). A component Allee effect is observed at the level of a single vital rate (i.e. a component of fitness sensu Stephens et al., 1999), the mean (per capita) value of which increases with population size. Typical examples include reproduction rate or offspring survival, which are lower at low population size. A demographic Allee effect is observed at the level of overall population dynamics as described in the first paragraph (a positive relationship between the per capita population growth rate and population size). A demographic Allee effect always implies the presence of at least one component Allee effect, whereas a component Allee effect does not necessarily generate a demographic Allee effect (Stephens et al., 1999). A demographic Allee effect can be weak or strong; it is strong when an

Allee threshold exists (Berec, Angulo, & Courchamp, 2007). Evidence of a demographic Allee effect, however, tells us nothing about its mechanism, knowledge of which is crucial for the design of management and control strategies; to know the mechanism one needs to investigate the underlying component Allee effects (Berec et al., 2007).

1.1 | Mechanisms leading to Allee effects

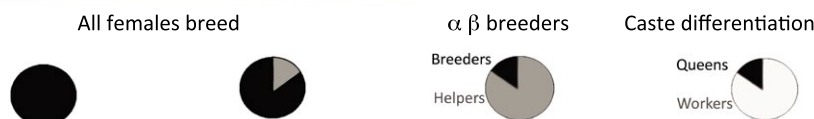
The mechanisms leading to component Allee effects are numerous and range from simple, non-cooperative facilitation to obligate cooperative behaviour (Courchamp et al., 2008; Kramer et al., 2009). As an example of Allee effects linked to facilitation (i.e. passive or mutualistic behaviour), Allee showed that some aquatic species aggregate to improve the chemical quality of their environment with a presumed improvement in survival (Allee, 1938; Allee & Bowen, 1932). Allee effects through chemical or physical facilitation also occur in many plant species (Ghazoul, 2005). This is linked to niche construction theory, in which activities of organisms modify the environmental states that affect their own fitness (Laland et al., 2015). There are also examples of proto-cooperative behaviour (sensu W.C. Allee) that could produce a component Allee effect (i.e. cooperative or altruistic behaviour; West, Griffin, & Gardner, 2007). Broadly speaking, at least two individuals are required to cooperate to reproduce in sexually reproducing species, although in some cases, such as in externally fertilising species, a large number of conspecifics can be critical for successful fertilisation (Gascoigne, Berec, Gregory, & Courchamp, 2009). Similarly, the presence of a large number of conspecifics can ameliorate harsh environmental conditions and thereby improve survival for species that hibernate or thermoregulate in groups (Stephens, Frey-roos, Arnold, & Sutherland, 2002) or that minimise predation risk by aggregating (Gascoigne & Lipcius, 2004; Sorato, Gullett, Griffith, & Russell, 2012).

Figure 1 illustrates examples of Allee effects related to cooperative behaviour. In some social species, individuals actively cooperate

(a) Care



(b) Breeding



(c) Foraging

(d) Defence

FIGURE 1 Examples of cooperative behaviours and their associated social organisation: (a) communal care received from other group members; (b) reproductive skew; (c) cooperation for foraging (it varies from sharing information on food availability as in bats, to having individuals dedicated to group foragers as in ant colonies); and (d) group defence (it may be achieved by passive cooperative behaviour such as predator dilution, to strong cooperative anti-predator behaviour, such as soldiers in ants) [Colour figure can be viewed at wileyonlinelibrary.com]

for defence against predators; in others, cooperative behaviour has become obligate, such as in African wild dogs (*Lycaon pictus*) or meerkats (*Suricata suricatta*), who require a minimum number of helpers for hunting, babysitting, pup defence and feeding, predator surveillance or defence against kleptoparasites (Clutton-Brock et al., 1999; Courchamp & Macdonald, 2001). Highly social species have been hypothesised to be particularly vulnerable to Allee effect-driven extinction at low population sizes (Courchamp et al., 1999, 2008; Stephens & Sutherland, 1999). Yet, there are just a few cases describing a demographic Allee effect in social species (but see Keynan & Ridley, 2016), and empirical confirmation of this hypothesis is still lacking (Angulo, Rasmussen, Macdonald, & Courchamp, 2013; Bateman, Ozgul, Coulson, & Clutton-Brock, 2012; Somers, Graf, Szykman, Slotow, & Gusset, 2008; Woodroffe, 2011).

1.2 | The importance of social structure

Social species are different from asocial species because dynamics of their populations are influenced by another level of organisation: the social group. A typical group is a social unit, such as a pack of African wild dogs or a pride of lions. The way individuals interact within social groups can be different from the way individuals interact between them. For example, most cooperation occurs among individuals of the same group, while mating may occur between individuals from different groups. On the other hand, competitive interactions may be stronger among individuals from different groups than among individuals of the same group.

Making predictions about patterns of population dynamics for social species is challenging without the aid of an appropriate conceptual framework. Because individuals form aggregations to maximise their fitness (Ebensperger, Rivera, & Hayes, 2012; Kingma, Santema, Taborsky, & Komdeur, 2014; Silk, 2007), we might expect Allee effects to occur at the level of social organisation in which the benefit is highest (groups, populations). However, Allee effects occurring at different levels of organisation simultaneously will make any assessment of strong demographic Allee effects rather intricate.

We review available evidence of Allee effects at different levels of social organisation, using examples across various species with contrasting social structure, including carnivores, bats, primates and eusocial insects. We present a unifying conceptual framework that categorises Allee effects in relation to species social structure. We distinguish Allee effects operating at the population level and those operating at the group level. Other authors have defined and used similar terms: *group-level Allee effect* (Bateman, Coulson, & Clutton-Brock, 2011; Bateman et al., 2012; Luque, Giraud, & Courchamp, 2013) and *group Allee effect* (Angulo et al., 2013; Keynan & Ridley, 2016), but clear descriptions of both the processes involved and the resulting implications are needed.

We also integrate demographic factors, namely the number of groups and group size heterogeneity, and behavioural factors represented by intergroup interactions. In particular, we develop a mathematical model to study effects of group size heterogeneity and intergroup interactions on the strength of population-level

demographic Allee effects, given a strong group-level demographic Allee effect. We find that both these factors affect the strength of population-level demographic Allee effects. Specifically, populations with high group size heterogeneity and in which the individual social groups cooperate have been found to buffer most the Allee effects, and may thus provide an explanation for why extinctions due to Allee effects are rare in social species.

2 | COMPONENT ALLEE EFFECTS IN SOCIAL SPECIES

Classically, Allee effects are characterised as a causal relationship in which the predictor is population size and the response variable is either the per capita population growth rate (demographic Allee effects) or any per capita vital rate contributing to it (component Allee effects) (Box 1). In social species, component Allee effects should manifest themselves at different levels of social organisation (hereafter *levels*) depending on the vital rate presenting Allee effects. Accordingly, component Allee effects can occur at the population level when the vital rate corresponds to individuals of the whole population, such as the survival of dispersing individuals, or at the group level when the vital rate corresponds to individuals in any single group, such as per capita productivity in the group. Consequently, the vital rate (response variable) determines the level at which the Allee effect is manifested (as shown in Box 1). Below, we provide examples of component Allee effects at each of these levels in different social species.


2.1 | Group-level component Allee effects


Because benefits of cooperative behaviour occur mainly within groups, many vital rates are positively related to group size and thus imply component Allee effects at the group level. Although the common predictor of such vital rates is group size, it could also be the number of adults or males in the group, or even other variables, as shown in the examples that follow.
























It has been suggested that bats benefit from social foraging. Food resources are often ephemeral and patchily distributed, and can be located more easily if several animals search for them. Velvety free-tailed bats (*Molossus molossus*) from the same colony forage together more frequently than expected by chance (Dechmann, Kranstauber, Gibbs, & Wikelski, 2010). Bats might also transfer information about feeding sites among colony members (Wilkinson, 1992). For example, greater spear-nosed bats (*Phyllostomus hastatus*) emit social calls to recruit and coordinate foraging with unrelated group members (Wilkinson & Wenrick-Boughman, 1998). Benefits of these kinds of social behaviour could manifest themselves in several vital rates of all members of the foraging group and are likely to depend on colony size (Kerth, 2008). Similarly, in gray bats (*Myotis grisescens*), juveniles reared in larger roosts grow faster than those in smaller roosts, which has been attributed to the communal warming effect in larger roosts (Gregory & Jones, 2010; Tuttle, 1976).

Box 1 Types and levels of Allee effect using two examples of highly social species: the wild dog and the Argentine ant

In social species, Allee effects can be detected at three different levels: the population, the group and the subgroup. For each level, we distinguish two types of Allee effects: component and demographic. The Allee effect is a relationship in which the response variable (y-axis) is any per capita vital rate and the predictor (x-axis) is related to numbers of individuals. The vital rate determines the level and type at which the Allee effect appears. In the Table below, we provide examples of vital rates and of predictor variables. In order to understand the examples of variables used, we describe briefly the main characteristics of the two study cases:

 A wild dog population consists of a number of social groups of different sizes called packs. In each pack, only the alpha male and female reproduce. The rest of the adults are helpers; they hunt, fend off kleptoparasites and take care of the pups together. Once a year, the alpha pair produces pups; pups remain in the group until the age of dispersion. Adults of the same sex and cohort disperse together; a new pack is formed when two dispersal groups of different packs and sexes join.

 An Argentine ant population consists of a number of nests, some of them interconnected. In each nest, there are hundreds of workers and many queens (polygyny) that produce eggs. Individuals among interconnected nests recognize each other and cooperate. Once a year, sexual individuals are produced. Some females will mate and remain in the nest, other will disperse accompanied by workers.

Y-axis	Response variables: vital rates		X-axis	Predictor variables
	Component	Demographic		
Population level	 Survival of sexuals	 <i>Per capita</i> population growth rate	Population size	Number of individuals 
	 Survival of dispersers			
	 Colony foundation	 		
	 Pack formation			
Group level	 <i>Per capita</i> productivity	 <i>Per capita</i> colony/pack growth rate	Group size	Colony / pack size
	 Individual survival			
	 Hunting success	 		
	 Pup guarding			
	 Production of sexuals		 Colony survival	
	 Nest defense		 Pack life span	
	 Kleptoparasitism protection		 Pack extinction risk	
Subgroup level	Individual survival of specific sex or age class having specific functional roles within the group (queens / helpers)		Subgroup size	Reproductive number (queens / alpha pair)
	 	Non-reproductive number (workers / helpers)		

In primates, reproductive success may be higher in larger groups, even when most group members breed and care for their own offspring independently. This is the case for the Zanzibar red colobus (*Procolobus kirkii*) living in mangrove forests: larger groups demonstrate higher rates of infant survival than smaller groups (Nowak & Lee, 2011). The benefits of group living in primates are considered to include more effective anti-predator strategies and reduced per capita effects of intergroup competition in larger groups (Snaith &

Chapman, 2008). For example, in ursine colobus monkeys (*Colobus vellerosus*), large groups are more effective at vigilance when resting (Teichroeb & Sicotte, 2012). More subtly, the effectiveness of anti-predator strategies could depend on the number of individuals of a particular sex in a group. In African red colobus monkeys (*Piliocolobus tephrosceles*), the rate of successful defence of a group is correlated positively with both group size and the number of males in the group (Stanford, 2002).

Approximately 15% of all carnivores occur in social groups of varying cohesion. Spotted hyenas (*Crocuta crocuta*) or brown hyenas (*Parahyaena brunnea*) display groups where aggregation is not essential for group persistence; groups are not highly cohesive, adhering to fission–fusion group dynamics (Sanderson, Jobbins, & Alexander, 2014). Social group structures are, however, essential to obligate cooperative breeders, where breeding is generally restricted to only a few of the potentially reproductive individuals of the group (Box 1). In African wild dogs, it has been shown that group vital rates, such as per capita productivity or pup survival, are related to group size (Angulo et al., 2013). Moreover, group reproductive performance is linked more strongly to the number of males than to the number of females in the pack (McNutt & Silk, 2008). In meerkats, lower probability of litter survival and higher juvenile mortality have been observed in small groups, owing to the higher costs of foraging or babysitting when too few adults are present (Clutton-Brock, Hodge, & Flower, 2008; Clutton-Brock et al., 1998; Russell et al., 2002).

Mature colony size of eusocial insects exhibits tremendous variation among species, from fewer than 10 individuals (e.g. colonies of halictid bees) to tens of millions (e.g. army ants, Wilson, 1971). Although there are just a few studies explicitly investigating Allee effects in eusocial insects (Luque et al., 2013; Mikheyev, Tchinguomba, Henderson, & Alonso, 2008), many studies identified a variety of mechanisms through which colonies benefit from increasing the number of individuals. For example, per capita productivity of a colony (i.e. the production of new workers) increases with colony size in many eusocial insect species (Luque et al., 2013). Similarly, the likelihood of reproduction of a colony (i.e. the production of sexuals that disperse to form new colonies) is positively related to colony size (Cole, 2009). In the ant *Pogonomyrmex occidentalis*, the colony needs to attain a given size to produce sexuals (Cole & Wiernasz, 2000). Moreover, in the Argentine ant (*Linepithema humile*), queen productivity is positively correlated with worker abundance and to queen abundance, suggesting a positive feedback between worker and queen abundances that could explain the enormous colony sizes attained by this species (Luque et al., 2013). Larger colonies of the Argentine ant are also more efficient at nest building and maintenance, which should affect survival rates of adults and brood (Halley, Burd, & Wells, 2005).

2.2 | Population-level component Allee effects

In social species, few processes influencing vital rates at the population level occur outside groups. For example, increasing the number of individuals in the population could accrue benefits through non-active mechanisms, such as environmental conditioning or niche construction, conferring higher vital rates in all individuals of the population (Courchamp et al., 1999). This may occur in harvester ants, whose activity causes changes in plant species composition near their nests and may thus provide better soil and food conditions for new ant colonies (MacMahon, Mull, & Crist, 2000).

In addition, mate finding, a common mechanism causing Allee effects (Fauvergue, 2013; Gascoigne et al., 2009; Kramer et al., 2009),

could occur outside groups and thus be relevant at the population level. If this is the case, the success of finding mates might be a function of the number of individuals in the population or the number (or density) of groups in the whole population (hereafter *group number*). For example, in African wild dogs, the probability of finding suitable mates increases with an increase in pack number (Somers et al., 2008) (see Box 1).

Other processes occurring at the population level include dispersal of individuals between groups. Significant risks are associated with dispersal movements (Bonte et al., 2012). When population size or the number of groups is large, finding other dispersers or another group to join occurs in less time than when population size or the number of groups is small. Thus, survival rates of dispersing individuals may be positively related to the number of groups or the number of individuals in the population (Angulo et al., 2013; Keynan & Ridley, 2016). For example, in meerkat populations, successful dispersal of males may depend on the availability of extragroup females (Mares, Bateman, English, Clutton-Brock, & Young, 2014).

3 | DEMOGRAPHIC ALLEE EFFECTS IN SOCIAL SPECIES

In social species, we can distinguish demographic Allee effects at two levels of social organisation. First, we can have a group-level demographic Allee effect that represents group performance and is usually measured as the per capita group growth rate. Second, we can have a population-level demographic Allee effect that represents performance of the whole population and is usually measured as the per capita population growth rate. For a closed population, the per capita population growth rate and mean “Darwinian” fitness are equivalent. At the group level, Darwinian fitness and the per capita group growth rate are not necessarily equivalent, because the group is not normally closed. However, natural populations are normally open (migration rates exist and there is a possibility of losing individuals if only emigration occurs, such as in source–vs. sink populations). In both cases, open or closed group or population, the per capita growth rate is a good parameter to estimate its demographic performance.

3.1 | Group-level demographic Allee effect

Component Allee effects at the group level can have demographic implications through their manifestation as a group-level demographic Allee effect (arrow 1 in Figure 2a,b). In some polygynous ant species (i.e. when several queens live together), the number of queens is related to higher colony survival and growth (Wilson, 1971). An increase in colony size implies a larger worker force that increases colony growth and survival. This occurs through a superior ability to locate and dominate resources (Chapman & Bourke, 2001; Holway & Case, 2001) and to monopolise larger territories (Hora et al., 2005; Walters & Mackay, 2005). For example, in Argentine

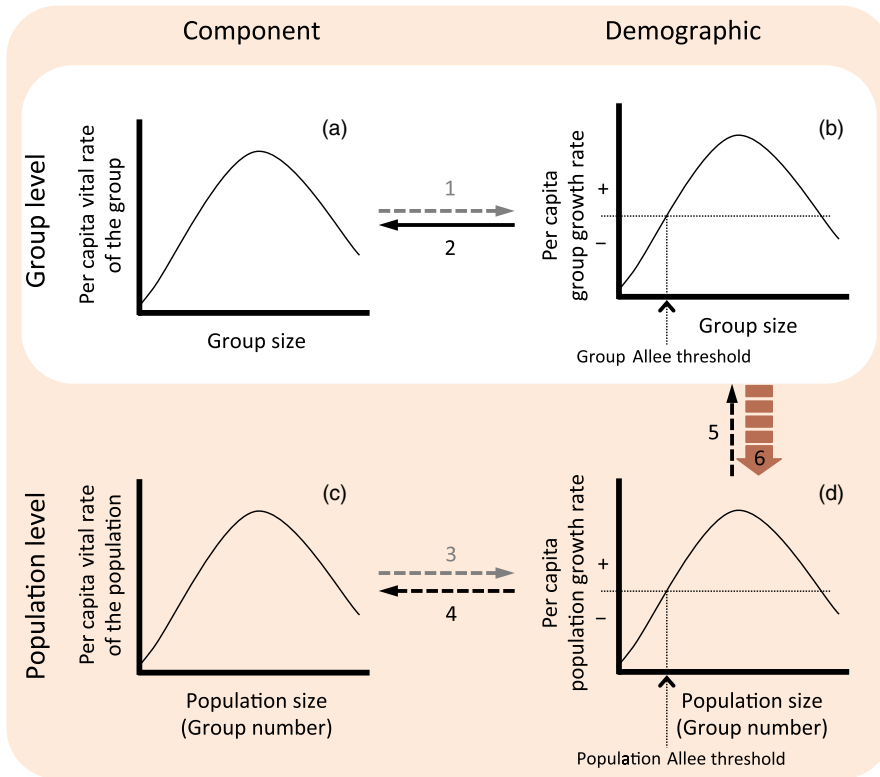


FIGURE 2 Component and demographic Allee effects, at the group level and population level, and their relationships with one another (arrows). At all levels, component Allee effects (a and c) may generate a demographic Allee effect (b and d respectively; arrows 1 and 3). A group-level demographic Allee effect (b) always implies at least one group or subgroup-level component Allee effect (arrow 2). At the population level, a population-level demographic Allee effect (d) implies either or both a population-level component Allee effect (c, arrow 4) or a group-level demographic Allee effect (arrow 5). A group-level demographic Allee effect might generate a population-level demographic Allee effect (arrow 6). Curves represent the positive contribution of individual vital rates with increasing numbers and show a decline representing possible negative density dependence at high numbers [Colour figure can be viewed at wileyonlinelibrary.com]

ants, colony survival increases with worker abundance due to better colony defence and foraging success (Luque et al., 2013).

Many studies on cooperative breeders also reveal demographic implications of component Allee effects at the group level. Theoretical and empirical studies on African wild dogs suggest that several component Allee effects at the group level (e.g. decreased per capita productivity or pup survival in smaller packs) can combine to depress group growth rates and increase group extinction risk, although extinction of small groups could be also due to density-independent stochasticity in mortality rates (Angulo et al., 2013; Buettner, Davies-Mostert, du Toit, & Mills, 2007; Courchamp & Macdonald, 2001; Creel, Mills, & McNutt, 2004; Woodroffe, 2011). On the other hand, Woodroffe (2011) found a group-level component Allee effect in the litter size of African wild dogs that did not give rise to a group demographic Allee effect. In meerkats, a group-level component Allee effect in breeding and survival could induce group extinction when environmental conditions are not favourable (Clutton-Brock et al., 1998, 1999), even though a group-level component Allee effect in meerkat survival alone contributed little to depress group growth rates (Bateman, Ozgul, Nielsen, Coulson, & Clutton-Brock, 2013; Bateman et al., 2012). This supports a general theory that component Allee effects need not result in demographic Allee effects.

3.2 | Influence of the number of groups and group size

The relationship between group number and group size can be represented in three dimensions with two factors (i.e. group number

and group size) influencing a per capita vital rate (Figure 3). When between-group interactions are positive (groups cooperate), a component or demographic Allee effect at the group level may be attenuated as group number increases (i.e. the effect of increasing group size and group number may be additive, decreasing the Allee threshold and the probability of group extinction; Figure 3a). For example, in locations where Argentine ants are introduced as an alien species, increasing group number is beneficial because individuals from different colonies do not fight but rather cooperate and move freely between nests (Giraud, Pedersen, & Keller, 2002). A larger number of colonies may result in a competitive advantage over other ant species in the area and increase colony growth rates (i.e. the group-level demographic Allee effect is attenuated by increasing group number).

In African wild dogs, increasing group number does not appear to have such an effect, as groups favour intergroup avoidance (Rasmussen, Gusset, Courchamp, & Macdonald, 2008). In this case, component or demographic Allee effects at the group level may be similar in populations with different numbers of groups (Figure 3b). The relationship between group size and number may be even more complex. For example, a large group among many other groups may have higher demographic rates than a large group among just a few. In the red imported fire ant (*Solenopsis invicta*), colonies founded by many queens are more successful than colonies founded by fewer queens, but only when there are many colonies present (i.e. the group-level demographic Allee effect occurs only with a large number of groups). This occurs due to the intraspecific raiding behaviour in this species. The probability of a colony winning in these raids increases with queen abundance. Winning colonies acquire brood and workers from losing colonies, thereby gaining mass (the group-level demographic Allee

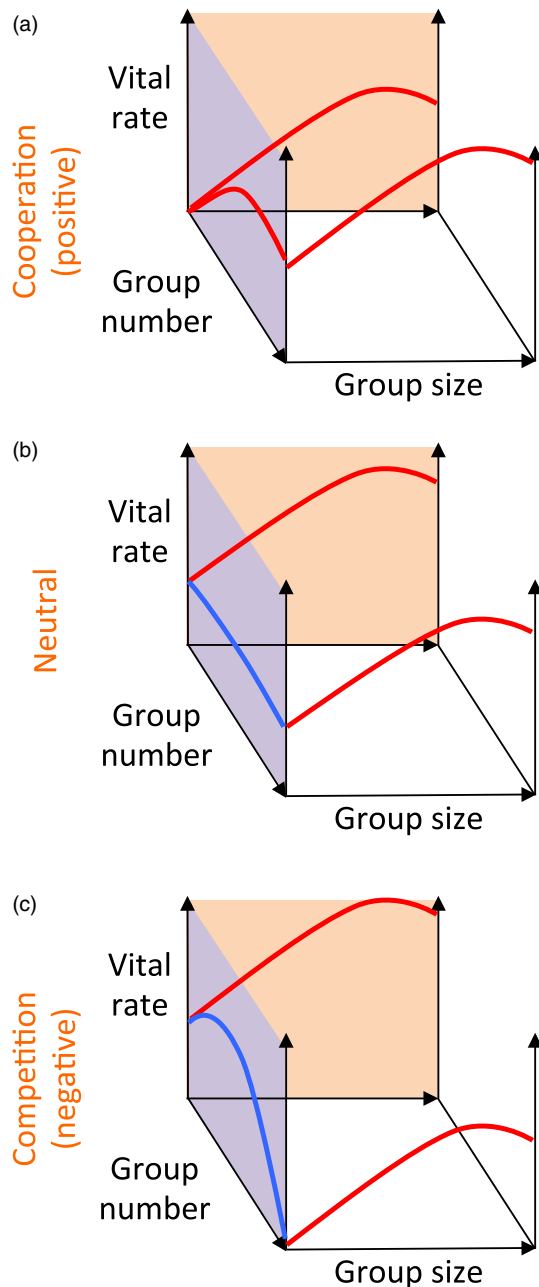


FIGURE 3 Examples of potential interactions between the number of groups in the population (group number) and the group size on vital rates, in relation to the type of interactions among groups: (a) cooperative interaction; (b) neutral interaction and (c) competitive interaction. A component or demographic Allee effect is represented by a red line, while no Allee effect is represented by a blue line [Colour figure can be viewed at wileyonlinelibrary.com]

effect) and increasing their probability of survival and reproduction (the group-level component Allee effect) (Adams & Tschinkel, 1995a, 1995c). This would not occur with low group numbers because the probability of raids decreases.

In some territorial cooperative breeders, such as meerkats, increasing the group number may be detrimental, especially for the smallest groups, which suffer most from intraspecific competition

(Clutton-Brock et al., 1999). This effect will likely be strongest at high population densities because geographic distance has been shown to be a reliable predictor of intergroup encounters (Drewe, Madden, & Pearce, 2009). In this case, with negative interactions among groups (groups compete), a component or demographic Allee effect at the group level may be exacerbated as group number increases (i.e. the effect of increasing group size increases the probability of group extinction; Figure 3c).

3.3 | Influence of group size heterogeneity and intergroup interactions

If all groups in a population were of similar size, then it would be straightforward to predict population extinction due to Allee effects. It has been hypothesised that Allee effects acting at the group level should scale up to the population level (arrow 6 in Figure 2) (Courchamp, Clutton-Brock, & Grenfell, 2000; Stephens et al., 1999). Theoretical studies suggest that if group growth rates are synchronised, then patterns of group growth are likely to resemble patterns of population growth because, in part, the population is made up of homogeneous group sizes (Bateman et al., 2011; Courchamp et al., 2000). Moreover, group size synchrony would pose a risk in addition to that of overall dynamical synchrony (Earn, Rohani, & Grenfell, 1998). Yet, recent empirical studies of cooperative breeders suggest that this process is not universal, and the implications of group-level demographic Allee effect on overall population dynamics remain uncertain (Bateman et al., 2012; Woodroffe, 2011) and might depend on the heterogeneity of group sizes (Angulo et al., 2013). The occurrence of a population-level demographic Allee effect might be also influenced by the type of intergroup interactions. Interestingly, both these factors may be parallel to those driving metapopulation dynamics, namely patch connectivity and patch size heterogeneity (Harrison & Taylor, 1997; Swart & Lawes, 1996).

To study the impacts of these factors, we develop a simple simulation model that considers dynamics of a population distributed in social groups and assumes that there is a strong demographic Allee effect at the group level (see Appendix S1). We explore whether this situation results in a strong demographic Allee effect at the population level, and, if yes, how its strength varies with the level of group size heterogeneity and the type of intergroup interactions. In particular, we model variation in group size heterogeneity in the population and how intergroup interactions affect group growth dynamics, considering nine scenarios: three levels of group size heterogeneity (low, medium, high) and three types of intergroup interactions (competitive, neutral, cooperative). For each scenario, we look for the resulting population-level Allee threshold by varying the initial total population size and assessing the extinction probability of the population (see Appendix S1 for technical details).

A strong population demographic Allee effect emerged from a strong group demographic Allee effect (Figure 4). More importantly, as group size heterogeneity decreased, the Allee threshold became larger and the extinction probability of at least small populations increased. The life cycle of some temperate wasps is seasonally synchronised and there is

no competition among colonies (Michener, 1990; Mitesser, Weissel, & Strohm, 2006). These species thus appear to fall under the low heterogeneity and neutral interactions scenario for which a relatively strong demographic Allee effect is predicted at the population level (Figure 4f).

In African wild dogs, it has been suggested that the presence of group-level demographic Allee effects and the absence of population extinction could be due to mutual intergroup avoidance, with larger packs allowing smaller packs to utilise adjacent territories without harassment (Angulo et al., 2013). This behaviour is consistent with the high heterogeneity and neutral interactions scenario (Figure 4d), suggesting a testable prediction that the strength of a potential population-level demographic Allee effect might be low due to asynchrony in pack dynamics.

Our models also show that the Allee threshold is reduced and the population extinction probability declines as interactions go from competitive through neutral to cooperative (Figure 4 and Appendix S1). In addition, because the effects of group size heterogeneity are larger for competitive interactions than for cooperative ones, the scenario with the lowest population-level demographic Allee threshold is a combination of high group size heterogeneity and cooperative intergroup interactions (Figure 4g). The cooperative scenarios (Figure 4g,h,i) could be exemplified by many invasive ant species in which there is no intraspecific aggression but rather an active cooperation among nests: supercoloniality (Passera, 1994).

Our results may also have important practical implications. Group size heterogeneity may be driven by the variable quality and

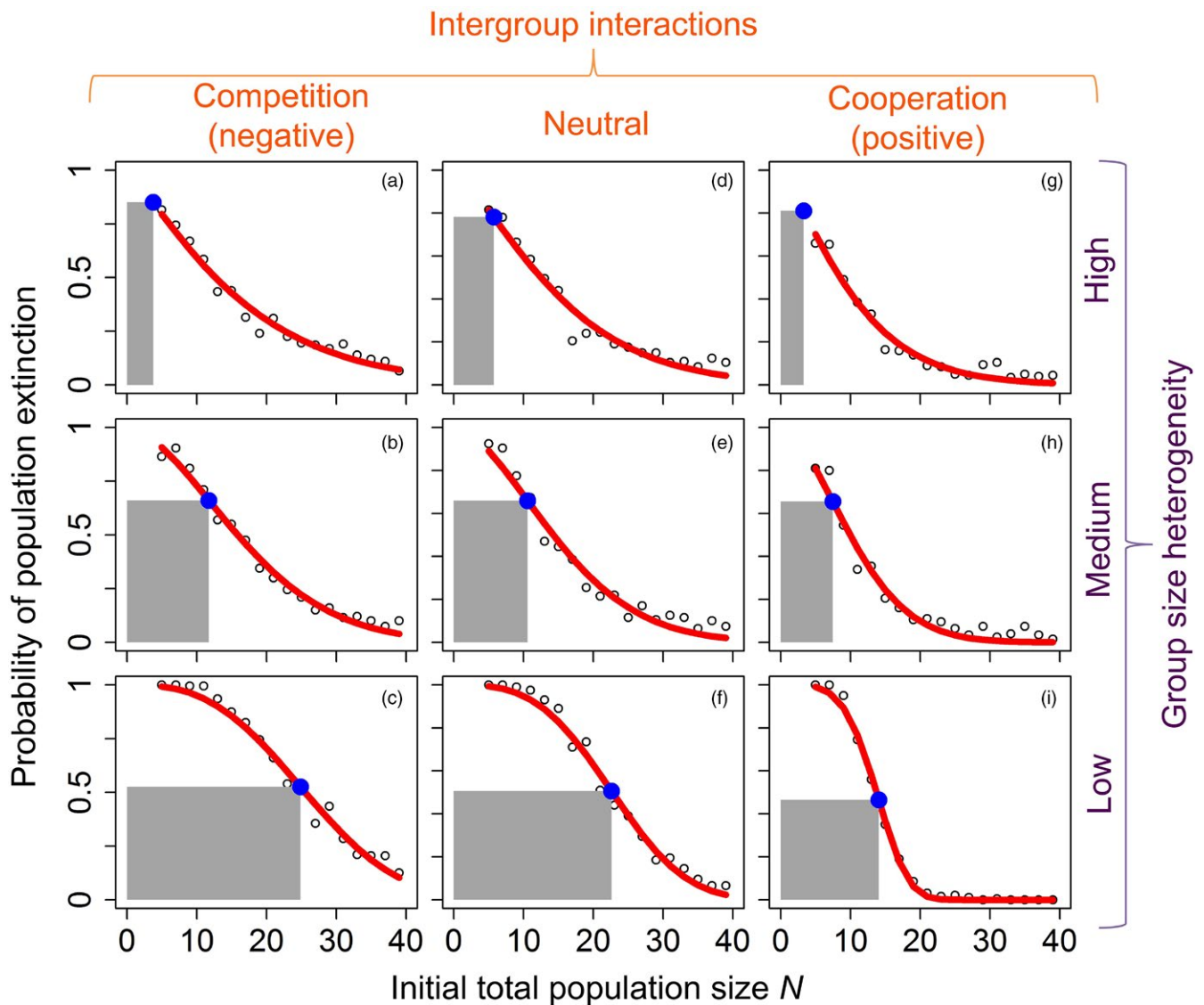


FIGURE 4 Population extinction probability as a function of the initial total population size, for three degrees of group size heterogeneity and three types of intergroup interactions. The open black dots are the simulation results, the red curves are fits of an extinction probability function, and the blue solid dots are inflection points of that function, which correspond to deterministic Allee thresholds. The shaded areas emphasise locations of the Allee thresholds, can be compared across scenarios, and relate to the strength of the population-level demographic Allee effect. This figure shows results for just one of the four model variants and results for all those variants are consistent. For more details see Appendix S1 [Colour figure can be viewed at wileyonlinelibrary.com]

patchy distribution of suitable habitat (Johnson, Kays, Blackwell, & Macdonald, 2002). However, as anthropogenic activities degrade quality and quantity of suitable habitat, group sizes might homogenise which, according to our results, means an increased likelihood of population extinction due to Allee effects. Habitat degradation, such as resource depletion, might increase the group sizes required for group establishment, reducing variability in group sizes. For example, small groups of African wild dogs are compromised energetically and are expected to be significantly more impacted than large groups due to human activity preventing successful hunts (such as hunting or ecotourism) or promoting interspecific competition (including kleptoparasitism) (Rasmussen & Macdonald, 2012; Rasmussen et al., 2008). Other external factors that decrease survival rates (such as diseases, Sanderson et al., 2014) could also create a disease-driven Allee effect (similarly to the predation-driven Allee effect, Angulo, Roemer, Berc, Gascoigne, & Courchamp, 2007) and the loss of individuals should compromise small groups specifically.

4 | THE SUBGROUP-LEVEL ALLEE EFFECT

In species with strong social behaviour, a third level of organisation may be described: the subgroup (see Box 1). Examples of a typical subgroup include a reproductive status in obligate cooperative breeders or a caste in social insects. Most eusocial insects form colonies in which extreme cooperation between individuals leads to task specialisation and reproductively distinct castes of queens, soldiers and sterile workers, which can have different vital rates.

The subgroup-level Allee effect could also be categorised theoretically into component and demographic Allee effects. For a component Allee effect at the subgroup level, the per capita vital rate corresponds to the individuals of a given subgroup, such as queen survival (see Box 1). Subgroup-level component Allee effects may result from interactions within a single subgroup (e.g. queen survival increases with queen abundance; Adams & Tschinkel, 1995b) and also from interactions between different subgroups (e.g. queen survival increases with worker abundance; Luque et al., 2013; Ruel, Cerdá, & Boulay, 2012). Several benefits have been associated with increasing numbers of queens that congregate to initiate new colonies. For example, faster nest construction improves queen survival by lowering the risk of being preyed upon or desiccating above-ground (Rissing & Pollock, 1991; Zanette & Field, 2011).

It may be also possible to distinguish individuals of specific age or sex as pertaining to subgroups, because they could have different vital rates and different functions within the group. For example, helpers or adult males in obligate cooperative breeders, found in bird and mammal species, can also be described as such (Box 1, Clutton-Brock, Russell, & Sharpe, 2003; Clutton-Brock et al., 2001; Courchamp, Rasmussen, & Macdonald, 2003; Keynan & Ridley, 2016; Madden, Drewe, Pearce, & Clutton-Brock, 2011).

The subgroup level is not as clear-cut as the group level, given that most subgroups are sterile or non-reproductive (e.g.

ant soldiers, but see English, Browning, & Raihani, 2015) and hence there is no possibility of a simple component vital rate related to reproduction. More complex processes are possible, such as ant workers producing males or queens (Amor, Ortega, Boulay, & Cerdá, 2017), or extra-alpha pair copulations from helpers (see below, Keynan & Ridley, 2016; Leclaire, Nielsen, Sharp, & Clutton-Brock, 2013; Woodroffe, 2011). Moreover, performance of a subgroup may depend entirely on the other constituents of the group. For this reason, even if we could unambiguously describe a subgroup-level demographic Allee effect, which would represent performance of the subgroup and could be measured as the per capita growth rate of the subgroup, its impacts for population dynamics are less straightforward. More knowledge on the benefits of differentiating Allee effects at the subgroup level is needed.

5 | CONCLUSIONS AND FURTHER RESEARCH

The dynamics of social species must account for their specificities, in particular for Allee effects. Additional research is needed to further unravel the complex mechanisms and relationships that might give rise to Allee effects in social species. Two key components should comprise future research: (1) studying the effect of varying group number on population-level demographic Allee effects, and how this variation interacts with the type of social interactions and the degree of group size heterogeneity; and (2) testing the predictions of our scenarios by investigating with empirical data the conditions under which the type of social interactions combines with the degree of group size heterogeneity to generate (or suppress) demographic Allee effects in a range of social species. In obligate cooperative breeders, it would be beneficial to analyse data combined from different populations.

Many authors point to a disconnection between the apparently abundant component Allee effects at the group level and the scarcity of demographic Allee effects at the population level (Angulo et al., 2013; Somers et al., 2008; Woodroffe, 2011). We propose that even under the presence of strong group demographic Allee effects, cooperative intergroup interactions and high levels of group size heterogeneity may preclude population demographic Allee effects. Validation of this hypothesis will certainly help us better understand the population dynamics of social species, many of which are of primary importance for both fundamental and applied ecology, from the evolution of sociality to the conservation of endangered species.

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AUTHORS' CONTRIBUTIONS

E.A., G.M.L. and F.C. designed research and drafted the manuscript; E.A. and F.C. reviewed Allee effects in cooperative breeders; G.L. reviewed Allee effects in ants. S.D.G. reviewed Allee effects in bats. J.W.W. reviewed Allee effects in eusocial insects. C.B.G. reviewed Allee effects in primates. L.B. developed and simulated the mathematical model. All authors contributed critically to the drafts of the manuscript and read and approved its final version.

DATA ACCESSIBILITY

This article does not contain data.

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Online Supporting Information

Allee effects in social species

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Effects of group size heterogeneity and intergroup interactions on strength of population demographic Allee effect

Here, we develop a simple simulation model that considers the dynamics of a population distributed in social groups. Assuming that each group has a strong demographic Allee effect at the group level, we explore whether it results in a strong demographic Allee effect at the population level. We further explore how the strength of the population demographic Allee effect varies with the level of group size heterogeneity and the type of intergroup interactions.

Group dynamics with a strong demographic Allee effect

We employ a phenomenological model of group dynamics that produces a strong demographic Allee effect. Denoting by $N_i(t)$ the size of group i at time t , the model is as follows:

$$N_i(t + 1) = \lambda N_i(t) \cdot \left(\frac{1}{1 + N_i(t)/\beta} \right) \cdot \left(\frac{N_i(t)}{N_i(t) + L} \right) \quad (\text{eqn 1})$$

In the absence of both fractions we have a geometric growth (a discrete-time equivalent of the classical exponential growth), where λ is the *per capita* growth rate of the group. The fraction

$1/(1 + N_i(t)/\beta)$ then represents a level of within-group competition that limits the maximum group size; the positive parameter β accounts for the strength of this competitive interaction. The geometric growth combined with this competitive term is commonly referred to as a Beverton-Holt formulation of discrete-time dynamics (a discrete-time equivalent of the classical logistic dynamics) (Brännström & Sumpter 2005). The second fraction $N_i(t)/(N_i(t) + L)$ is a generic term often used to trigger a strong demographic Allee effect in population models, here in the group, and thus represents a level of within-group cooperation; the positive parameter L scales the strength of this cooperative interaction (McCarthy 1997; Schreiber 2003). The resulting *per capita* group growth rate as a function of the group size, as implied by (eqn 1), is exemplified in Fig. 1. This function crosses the replacement line $N_i(t + 1) / N_i(t) = 1$ (red line in Fig. 1) at two important points. The lower of these points is the group Allee threshold or the critical group size below which the group growth rate is negative and the group goes extinct (under deterministic dynamics) due to an insufficient number of individuals in the group. The upper of these points is a stable equilibrium attained by the group of an initial size above the Allee threshold (again under deterministic dynamics).

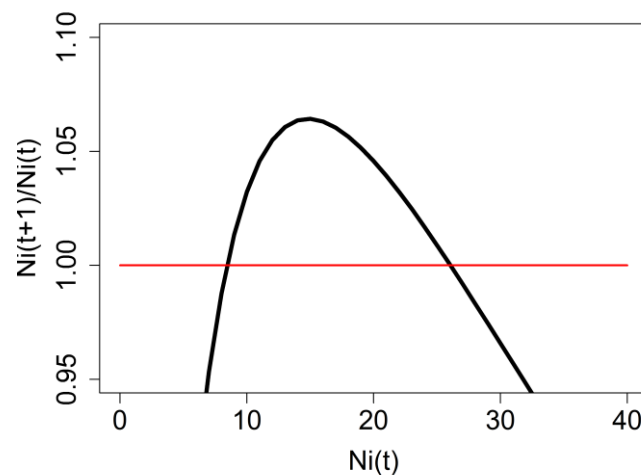


Figure 1: The *per capita* group growth rate as a function of group size, demonstrating a strong group demographic Allee effect. Fixing model parameters to $\lambda = 2$, $\beta = 40$ and $L = 5.5$ gives the group Allee threshold at about 8.5 (group size corresponding to the lower crossing of the red

line and black curve) and the stable equilibrium at about 26 (group size corresponding to the upper crossing of the red line and black curve).

In simulations of group and population dynamics, we use two variants of the model (eqn 1), both accounting for environmental stochasticity. First, we assume that the mean value of the parameter λ is constant and the same for all groups forming the population but its actual value varies among groups and from year to year following a Gamma distribution (Melbourne & Hastings 2008). We refer to this way of modelling stochasticity as *intragroup stochasticity* because it affects just one component of group dynamics. Alternatively, we consider a kind of Moran effect (Royama 1992). Assuming G groups, we implement this effect by adding to the model composed of G equations of type (eqn 1) a multivariate normal random variable with the zero mean and a $G \times G$ variance-covariance matrix Σ that has (for the sake of simplicity) all diagonal elements equal to σ^2 and all non-diagonal elements equal to $\rho\sigma^2$. This simple structure of Σ means that each group is exposed to environmental variance σ^2 and that there is a correlation ρ between dynamics of different groups due to spatially correlated environmental effects. We refer to this way of modelling stochasticity as *intergroup stochasticity* because it affects the overall group growth rate. Both approaches allow us to set different levels of group size heterogeneity by varying variance of the Gamma distribution and the correlation parameter ρ , respectively, which we need for assessing the effect of group size heterogeneity on the occurrence and strength of the population demographic Allee effect.

Simulation framework

Before we specify how we deal with group size heterogeneity and how we introduce intergroup interactions, we present our general simulation framework. Fixing the number of groups to G , then for each adopted level of group size heterogeneity (low, medium, high) and type of intergroup interactions (competitive, neutral, cooperative) we vary the initial total population size N , from G to 40. For each N we run the population model consisting of G equations –

stochastic versions of the model (eqn 1) – for 500 time steps and 200 replicates, storing the proportion of replicates for which the population as a whole went extinct. This proportion provides an estimate of the extinction probability of the population composed of G groups and starting with N individuals.

We then fit a Weibull distribution function (see below) to simulation data to describe the population extinction probability as a function of the initial total population size N , and compare the resulting functions (also referred to as the extinction probability curves) for all nine scenarios we consider. In particular, we seek a strong population demographic Allee effect by looking for an inflection point of the extinction probability curve because this point represents the stochastic analogue of the deterministic Allee threshold (Dennis 1989).

Specifically, we fit the Weibull distribution function

$$P_{ext}(N) = \exp\left(-\left(\frac{N}{\alpha}\right)^w\right) \quad (\text{eqn 2})$$

to simulation data to obtain estimates of the parameters α (scale parameter) and w (shape parameter). Once the estimate of w is greater than 1, we can calculate the inflection point of $P_{ext}(N)$ as (the second derivative of $P_{ext}(N)$ with respect to N has to equal zero at the inflection point)

$$N_{inf} = \alpha \left(\frac{w-1}{w}\right)^{\frac{1}{w}} \quad (\text{eqn 3})$$

Group size heterogeneity

Following the two types of environmental stochasticity we introduced above, we model group size heterogeneity in two ways. Under intragroup stochasticity, we vary variance of the Gamma-distributed maximum *per capita* group growth rate λ (higher variance of λ means higher group

size heterogeneity). Under intergroup stochasticity, we vary the spatial environmental correlation ρ (lower value of ρ means higher group size heterogeneity).

Intergroup interactions

For simplicity and clarity of presentation, we assume that there is no migration (i.e., no exchange of individuals) between groups and no fission-fusion group dynamics (i.e., number of groups does not vary in time), but only assume that groups may interact in a competitive way, not interact at all (neutral interaction), or interact in a cooperative way. A possible competitive interaction occurs when close enough groups compete for food or territory. For example, larger groups of meerkats harass smaller ones (Clutton-Brock *et al.* 1999; Drewe, Madden & Pearce 2009; Bateman *et al.* 2015). An example of neutral interaction is avoidance behaviour that most African wild dog packs display against each other. Packs tolerate proximity of other packs, simply avoiding using the same area (Angulo *et al.* 2013). Finally, a possible cooperative interaction may occur in the Argentine ant invading a new area. Typical of many invasive ant species is cooperation among different nests in a supercolony, which potentiates enhanced foraging, competition over other species, survival, and population expansion (Sagata & Lester 2009). Enhanced mate finding due to encounters of individuals from different groups (the classic Allee effect) also seems to fit under this category.

We adopt two ways of modelling competitive and cooperative interactions. First, we assume that intergroup interactions effectively augment the current group size. In particular, we let the effective group size due to the intergroup interactions equal $N_e(t) = N_i(t) + cN_o(t)$ where $N_o(t)$ is the total number of individuals in the groups other than the focal group at time t and c is a positive constant determining the interaction strength. Furthermore, following the above examples we assume that when competition among groups occurs, the term $1/(1 + N/\beta)$ of the model (eqn 1) is affected by the augmentation and the model (eqn 1) becomes

$$N_i(t + 1) = \lambda N_i(t) \cdot \left(\frac{1}{1 + N_e(t)/\beta} \right) \cdot \left(\frac{N_i(t)}{N_i(t) + L} \right) \quad (\text{eqn 4})$$

Indeed, as $N_o(t) > 0$ and hence $N_e(t) > N_i(t)$ the effect of other groups is to depress the *per capita* group growth rate of any group in a population of any size relative to the baseline model (eqn 1). On the other hand, when cooperation among groups occurs, we assume that the term $N/(N + L)$ of the model (eqn 1) is affected by $N_e(t)$ and the modified model then is

$$N_i(t + 1) = \lambda N_i(t) \cdot \left(\frac{1}{1 + N_i(t)/\beta} \right) \cdot \left(\frac{N_e(t)}{N_e(t) + L} \right) \quad (\text{eqn 5})$$

Here, since $N_o(t) > 0$ implies $N_e(t) > N_i(t)$ the effect of other groups is to enhance the *per capita* group growth rate of any group in a population of any size relative to the baseline model (eqn 1). Finally, for neutral interactions, we use the original model (eqn 1). We refer to this way of modelling intergroup interactions as *group size modification*.

Alternatively, we impose a population-wide suppression (competition), no change (neutral interaction), or population-wide boost (cooperation) to the group growth rate, depending on the population size. In particular, we consider the group growth rate modifying term $cN_o(t)/(1 + N_o(t)) N_i(t)$, where $N_o(t)$ and c have the same meaning as in the previous paragraph. We add this term to the right-hand side of model (eqn 1) in the case of cooperation, but subtract it in the case of competition; no term is added or subtracted in the case of neutral interaction. Since the modelled group size has the potential to become negative if competition occurs and $N_o(t)$ and/or c are large, we assume that once the group size becomes negative the group is considered extinct and its size is set to zero for the remaining simulation time (since we do not assume exchange of individuals among groups). This actually means that the *per capita* group growth rate is reduced or enhanced by $cN_o(t)/(1 + N_o(t))$, a term that grows from 0 to c as $N_o(t)$ increases. Because this way of modelling competitive and cooperative interactions modifies locations of unstable (group Allee threshold) and stable equilibria of the model (eqn 1), it may represent the situation when the presence of other groups modifies efficiency of

performance of the focal group. We refer to this way of modelling intergroup interactions as *group growth modification*. We believe that these two approaches to modelling competitive and cooperative interactions may approximate numerous realistic cases.

Results

A strong population demographic Allee effect emerges from a strong group demographic Allee effect. The consistent trend is a decline of the population Allee threshold and hence a weakening of the population demographic Allee effect when group size heterogeneity increases and/or intergroup interactions go from competitive through neutral to cooperative (Figs 2-5). In addition, for any initial population size, the population extinction probability declines and the effect of group size heterogeneity appears to become weaker as interactions go from competitive through neutral to cooperative (Figs 2-5). All this appears to occur regardless of how we model group size heterogeneity and the effect of intergroup interactions, and hence to be quite robust.

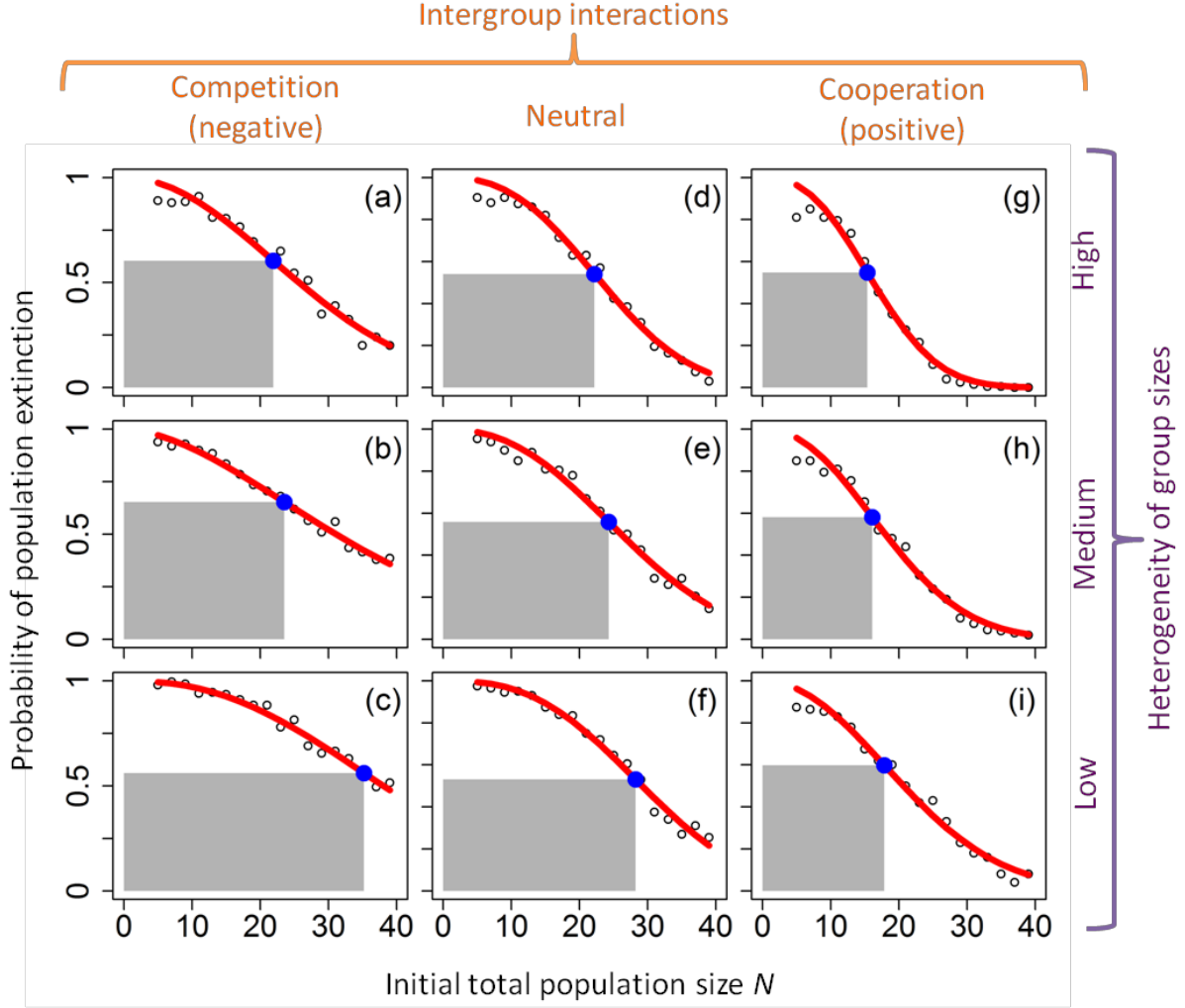


Figure 2: Population extinction probability as a function of the initial total population size N for three levels of group size heterogeneity induced by intergroup stochasticity and three types of intergroup interactions induced by group size modification (panels a, d, g: $\rho = 0.05$ (low group dynamics synchronicity), panels b, e, h: $\rho = 0.5$ (medium group dynamics synchronicity), panels c, f, i: $\rho = 0.95$ (high group dynamics synchronicity)). Parameters: $G = 5$ (i.e., five groups), $c = 0.1$ for cooperative interaction, $c = 0.1$ also for competitive interaction, and $\sigma = 2$. Other parameters are as in Fig. 1. The open black dots are the simulation results, the red curves are fits of the function $P_{ext}(N)$ (eqn 2), and the blue solid dots are their inflection points N_{inf} (eqn 3), which correspond to deterministic Allee thresholds (Dennis 1989). The shaded areas serve to emphasize the size of the population Allee threshold across different scenarios, and therefore the strength of the population demographic Allee effect.

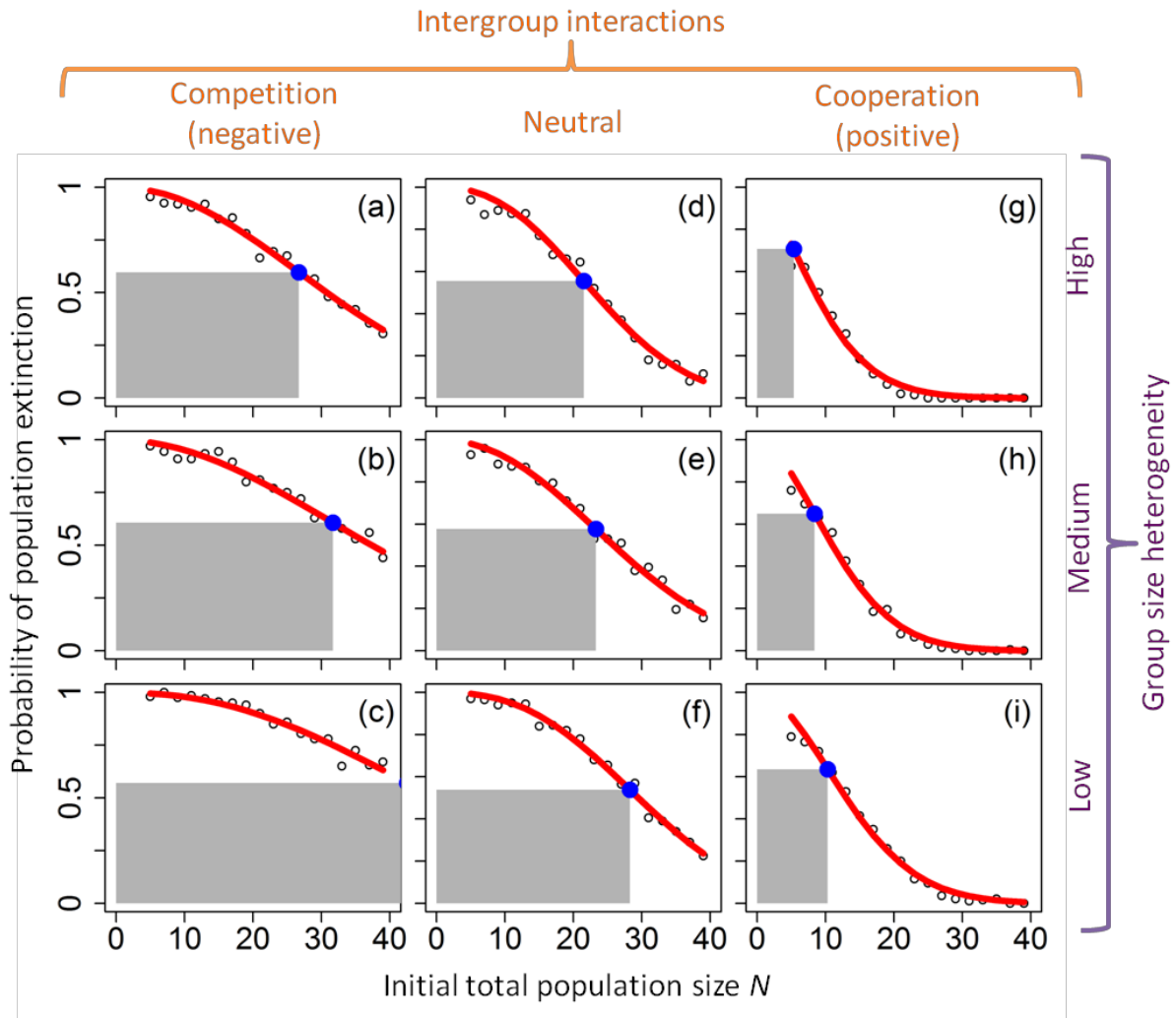


Figure 3: Population extinction probability as a function of the initial total population size N for three levels of group size heterogeneity induced by intergroup stochasticity and three types of intergroup interactions induced by group growth modification (panels a, d, g: $\rho = 0.05$ (low group dynamics synchronicity), panels b, e, h: $\rho = 0.5$ (medium group dynamics synchronicity), panels c, f, i: $\rho = 0.95$ (high group dynamics synchronicity)). Parameters: $G = 5$, $c = 0.25$ for cooperative interaction, $c = 0.05$ for competitive interaction, and $\sigma = 2$. Other parameters and legend are as in Fig. 2.

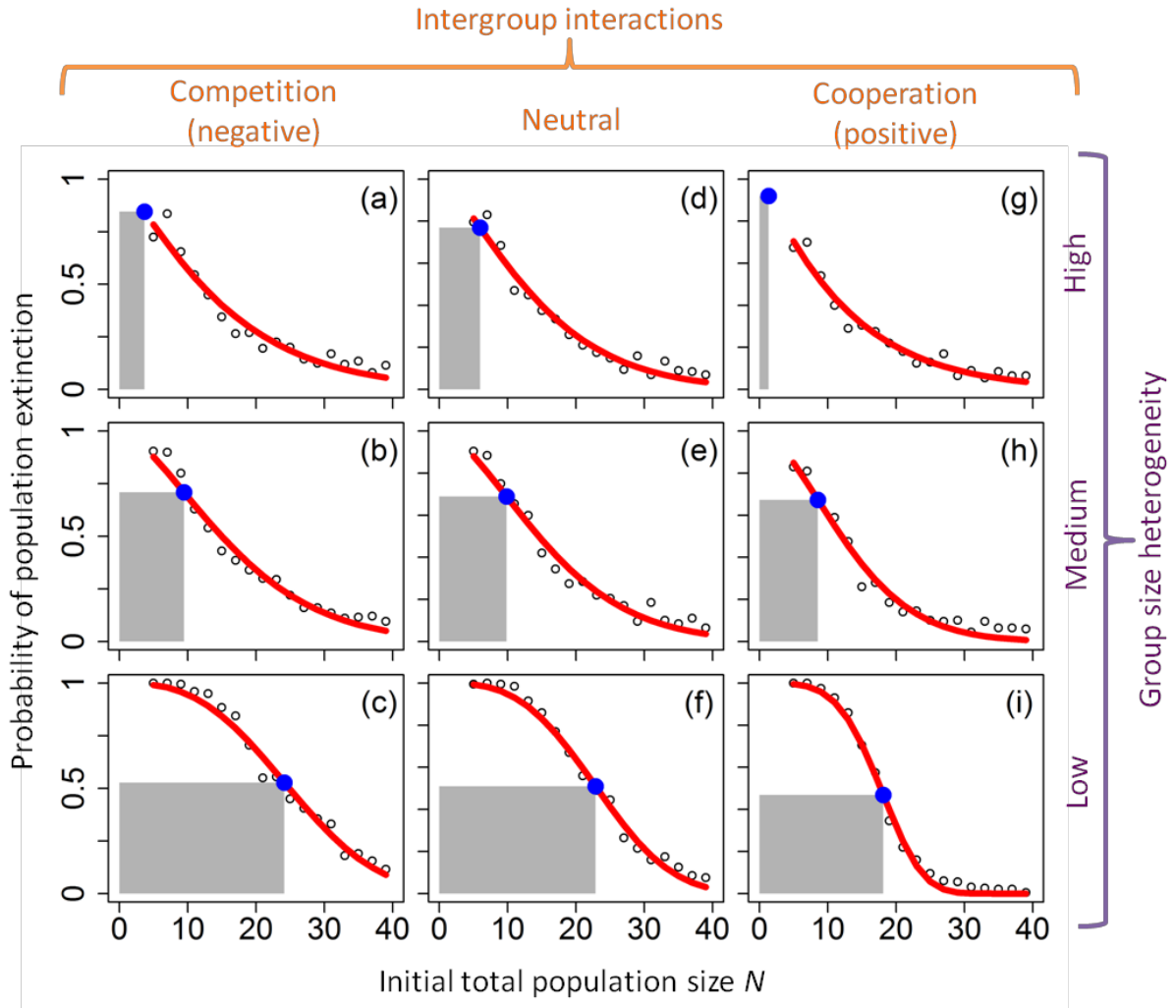


Figure 4: Population extinction probability as a function of the initial total population size N for three levels of group size heterogeneity induced by intragroup stochasticity and three types of intergroup interactions induced by group size modification (panels a, d, g: $\text{var } \lambda = 2$, panels b, e, h: $\text{var } \lambda = 1$, panels c, f, i: $\text{var } \lambda = 0.1$). Parameters: $G = 5$, $c = 0.1$ for cooperative interaction, $c = 0.1$ also for competitive interaction, and $\sigma = 2$. Other parameters and legend are as in Fig. 2.

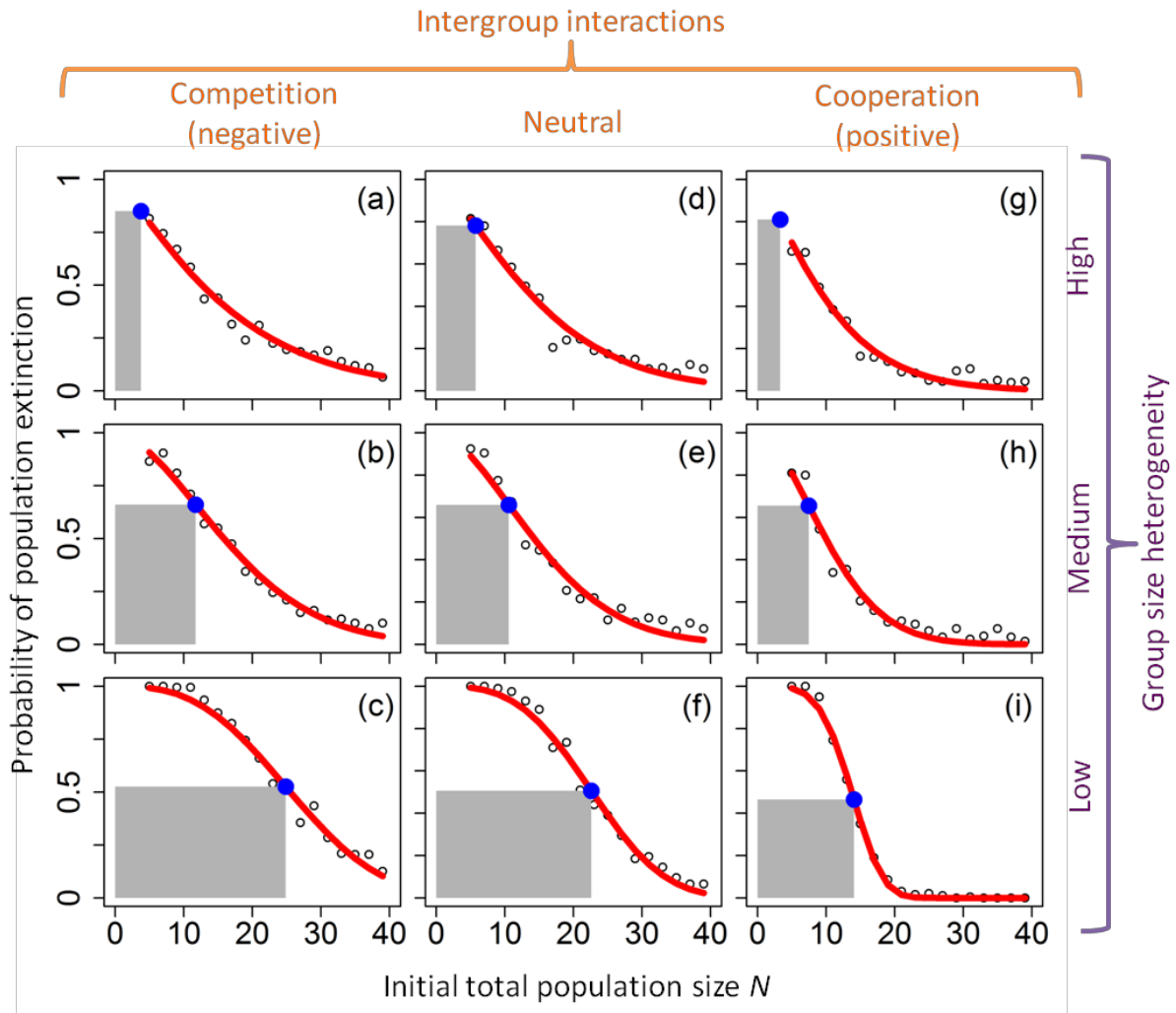


Figure 5: Population extinction probability as a function of the initial total population size N for three levels of group size heterogeneity induced by intragroup stochasticity and three types of intergroup interactions induced by group growth modification (panels a, d, g: $\text{var } \lambda = 2$, panels b, e, h: $\text{var } \lambda = 1$, panels c, f, i: $\text{var } \lambda = 0.1$). Parameters: $G = 5$, $c = 0.25$ for cooperative interaction, $c = 0.05$ for competitive interaction, and $\sigma = 2$. Other parameters and legend are as in Fig. 2.

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