Allee effects in ants

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Summary

1. Allee effects occur when the aggregation of individuals result in mutually beneficial intra-specific interactions whereby individual fitness, or per capita growth rate, increases with the number of individuals. Allee effects are common in social species due to their cooperative behaviours, such as breeding, feeding or defence. Allee effects have important implications for many aspects of basic and applied ecology. Over the past decades, the study of Allee effects has influenced population dynamics, community ecology, endangered species management and invasion biology.

2. Despite the fact that cooperation is the basis of their social structure, Allee effects have received little attention among eusocial insects. Extreme cooperation is common, and reproductive specialization of individuals occurs due to division of labour. These life-history traits suggest that the potential contribution of each caste to reproduction and survival may be differential and nonadditive.

3. We studied Allee effects in the invasive Argentine ant (*Linepithema humile*). In this species, many queens and workers are present in colonies, which allowed us to explore the differential effects of castes on the presence of Allee effects. In the laboratory, we measured brood production and individual survival in experimental colonies that differed in the initial numbers of queens and workers.

4. Our results highlight the differential effect of queens and workers on survival and productivity. We found three positive density-dependent relationships indicative of component Allee effects at the colony level: both workers and queens had a positive effect on the productivity of the other caste, and queens had a positive effect on worker survivorship.

5. Our experimental results suggest a potential positive feedback between worker and queen abundance, which may have contributed to the evolution of large colony sizes. Our study provides the first evidence of Allee effects in eusocial insects and highlights the need to consider castes separately in population dynamics. Division of labour and differential reproductive rates are factors that should be integrated into the study of Allee effects.

Key-words: colony dynamics, inverse density dependence, population dynamics, social groups, inverse density dependence

Introduction

Many species show a positive relationship between their population size and growth rate (Courchamp, Clutton-Brock & Grenfell 1999). This relationship, coined the Allee effect after the ecologist W.C. Allee, relates to the aggregation of individuals or some form of cooperation (Allee 1931). The mechanisms leading to Allee effects are numerous, including mate limitation, chemical or physical facilitation and social interactions that lead to forms of cooperation (Courchamp, Berec & Gascoigne 2008; Gascoigne *et al.* 2009; Kramer *et al.* 2009). The Allee

effect has played a prominent role in many biological disciplines, including population and community ecology (Courchamp, Clutton-Brock & Grenfell 1999). It can cause population decline in species with low densities and therefore has important implications for conservation biology (Stephens & Sutherland 1999). Allee effects also influence the dynamics and risk of non-native species invasions, as founding populations are often small (Taylor & Hastings 2005; Tobin, Berec & Liebhold 2011).

When Allee effects are observed at the level of a single fitness component, such as the probability of survival or successfully raising offspring, they are commonly referred to as 'component Allee effects' (Stephens, Sutherland & Freckleton 1999). A 'demographic Allee effect' results when the cumulative effects of all component Allee effects

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and all negative density-dependent effects produce an overall increase in population growth rate with increasing abundance. Whether component Allee effects result in a demographic Allee effect depends on the strength of negative density dependence. (Stephens, Sutherland & Freckleton 1999; Courchamp, Berec & Gascoigne 2008).

Allee effects have been documented across a wide range of species. Examples include lower reproductive output of flowering plants as population size decreases, reduced reproductive success in small colonies of seabirds and mate-finding failure among gypsy moths at low densities (Courchamp, Berec & Gascoigne 2008; Schippers *et al.* 2011; Tobin, Onufrieva & Thorpe 2013). Social interactions that lead to cooperation can relate to Allee effects through cooperative breeding, feeding and defence in a wide variety of social animals (Kramer *et al.* 2009). Noteworthy, however, is the absence of Allee effect studies in eusocial insects, despite the fact that cooperation is the basis of their social structure (but see Mikheyev *et al.* 2008).

Unique life-history traits may influence how component Allee effects could impact social species. First, as cooperation occurs within relatively small groups of individuals, Allee effects can also operate at the group level (i.e. group-level Allee effects; Bateman *et al.* 2012; Bateman, Coulson & Clutton-Brock 2011). Decreasing group size may negatively affect the probability of survival or reproduction. For example, pup survival decreases with pack size in wild dogs (Clutton-Brock *et al.* 1998; Courchamp & Macdonald 2001). Some studies have shown the benefit of increasing the number of individuals in colonies of eusocial insects through a variety of mechanisms (Wenzel & Pickering 1991; Johnson 2004; Bouwma, Nordheim & Jeanne 2006). Second, division of labour often implies that individuals have differential impacts on reproduction and survival (Courchamp & Macdonald 2001; Creel & Creel 2002). Some eusocial insect species present an extreme case of division of labour through reproductively distinct castes (i.e. queens and workers) that contribute differentially to reproduction and survival and therefore to the overall colony growth rate. For example, many ant species reproduce by fragmentation from the maternal nests with queens accompanied by workers (Holway, Suárez & Case 1998; Hee *et al.* 2000; Suárez, Holway & Case 2001). In the Argentine ant (*Linepithema humile*), queens cannot survive without workers: a single queen must be supported by a group of workers (Hee *et al.* 2000). For many social insects, colony demography may not be a simple additive function of the effects of different castes, but rather a result of the interaction between them. Allee effects may result from interactions within a single caste (e.g. per capita queen fitness increases with queen abundance) and from interactions between castes (e.g. per capita queen fitness increases with worker abundance). Whether these component Allee effects generate a demographic Allee effect at the colony level will depend on their cumulative impact across all castes.

In this study, we investigated whether component Allee effects are present in the Argentine ant. Native to South America, the Argentine ant is a cosmopolitan invasive species that is responsible for a suite of ecological impacts, particularly in Mediterranean and island ecosystems (Krushelnycky, Holway & LeBrun 2010; Vogel *et al.* 2010). It is a highly polygynous species that forms supercolonies with hundreds of queens and workers. In the laboratory, we experimentally manipulated colony size and caste proportions (i.e. number of queens and workers) to explore the potential differential contributions of castes to colony growth. We measured two key traits related to colony growth: productivity and survival. Further, we decomposed these two traits by caste. More specifically, we tested whether we could detect, in each of the worker and queen castes: (i) positive density dependence between per capita productivity and/or survival in a given caste and colony size as a whole; and (ii) positive density dependence between per capita productivity and/or survival in a given caste and caste abundance. The results demonstrate the importance of partitioning colony size into caste abundance to identify and understand component Allee effects in social species with reproductively distinct castes.

Materials and methods

Ants were collected in February 2010 live from nature in Cordoba, Spain, which is part of the primary European supercolony (*sensu* Giraud, Pedersen & Keller 2002) and transferred to the laboratory (Orsay, France). In the laboratory, we created independent experimental colonies that differed in their numbers of queens and workers. These initial colonies did not contain brood. We used a complete two-way factorial design with three categories of initial queen numbers (1, 3 and 6) and three categories of initial workers (10, 30, and 300). Each treatment contained 8 replicates ($n = 72$ nests, with a total of 240 queens and 8160 workers). We considered existing data and observations for the Argentine ant to select the appropriate numbers of queens and workers to experimentally test for Allee effects (i.e. 1 queen and 10 workers is the minimum number of queens and workers necessary to produce workers; Hee *et al.* 2000). We did not consider queen age, since fecundity is independent of age for the Argentine ant (Keller & Passera 1990).

Our laboratory colonies were housed in plastic, foraging boxes ($18 \times 12 \times 7$ cm), with metal mesh tops for aeration and plaster bottoms. The boxes were connected to three nest tubes (1 cm in diameter and 10 cm long) connected to a water source through cotton. Brood and most workers were always inside the tubes. Ants were fed *ad libitum* with sugar water (8%) and a protein-based solution (Dussutour & Simpson 2008). Laboratory temperature was maintained at 25 ± 2 °C. Boxes were maintained and cleaned on a weekly basis. We cleaned the foraging boxes by removing mounds of dead individuals created by the workers, and any loose food. Cleaning did not disturb the ants; most workers and all queens and brood remained inside the tubes connected to the foraging boxes.

After 25 days, we estimated brood produced by observations made with video recordings, using a digital USB Microscope Video Camera (DigiMicro 2.0, New York, USA). Metal mesh

Table 1. Results of model fitting for caste mortality and productivity, with maximum parsimony models shown in bold ranked by model AICc (QAICc is given for Worker mortality). For each model, inclusion of a variable is represented by a '+', and the degrees of freedom (d.f.), log likelihood (logLik), ΔAICc and Akaike weight (ω) are shown. Also shown for each parameter is its importance weight. Variables in the models were queen and worker abundance (Q and W, respectively) and their interaction ($Q : W$) and colony size (Colony) as the sum of queens and workers

Response variable	Explanatory variables					d.f.	logLik	ΔAICc	ω
	Intercept	Q	W	$Q : W$	Colony				
Queen mortality	**−0·97**				**−0·47**	**2**	**−37·2**	**0**	**0·535**
	−2·71					**1**	**−39·1**	**1·8**	**0·213**
	−2·20		**+**			**3**	**−37·1**	**2·0**	**0·193**
	−2·40	+				3	−39·0	5·8	0·030
	−1·88	+	+			5	−36·9	6·2	0·024
	−1·95	+	+	+		9	−33·4	9·2	0·005
Importance weight	**1**	0·06	0·22	0·01	0·53				
Worker mortality	**−1·44**	**+**				**3**	**−342·1**	**0**	**0·880**
	−1·82	**+**	**+**			**5**	**−339·7**	**4·0**	**0·118**
	−1·47	+	+	+		9	−333·3	12·6	0·002
	−1·82					1	−536·9	49·0	<0·001
	−2·21				0·07	2	−535·5	50·8	<0·001
	−2·20		+			3	−534·6	52·8	<0·001
Importance weight	**1**	1	0·12	<0·01	<0·01				
Queen productivity	**0·91**	**+**	**+**	**+**		**10**	**−79·7**	**0**	**0·989**
	−0·81				0·78	3	−93·5	10·5	0·005
	1·62	+	+			6	−90·4	11·2	0·004
	1·28		+			4	−93·2	12·0	0·002
	2·26					2	−124·2	69·7	<0·001
	2·59	+				4	−123·1	71·8	<0·001
Importance weight	**1**	0·99	0·99	0·99	0·01				
Worker Productivity	**1·35**	**+**	**+**	**+**		**10**	**−79·4**	**0**	**0·925**
	1·94	**+**	**+**			**6**	**−87·1**	**5·2**	**0·070**
	2·36		+			4	−92·5	11·2	0·003
	2·84				−0·26	3	−94·7	13·3	0·001
	1·40	+				4	−95·2	16·7	<0·001
	1·82					2	−99·6	21·0	<0·001
Importance weight	**1**	**0·99**	**0·99**	**0·92**	<0·01				

was used with cotton, so that ants could not embed brood inside the cotton. Video recordings, thus, allowed us to reliably record brood production (i.e. eggs, larvae and pupae) inside the nest tubes. At the time of the recordings none of the nests had any pupae, so brood consisted of eggs and different larval stages. In addition, we recorded the number of dead queens and workers by physically removing them from the containers upon the completion of the experiment. The duration of our experiment is based on previous studies that used similar timing (e.g. Tschinkel 1993; Bouwma, Nordheim & Jeanne 2006).

We calculated mortality and productivity at the level of the caste (i.e. per queen and per worker). Brood produced (hereafter referred to as productivity) is commonly used as a proxy for fitness in eusocial insects, including for workers (Michener 1964; Jeanne & Nordheim 1996; Karsay & Wenzel 1998; Bouwma, Nordheim & Jeanne 2006; Cole 2009). Indeed, as a worker is sterile, its inclusive fitness is a function of its relatives' brood (Queller & Strassmann 1998; Bargum & Sundström 2007), which should also depend on worker survival, as they take care of the brood.

Mortality was modelled by using a binomial distribution (logistic regression analysis). The response variable was a matrix with the number of individuals dead and alive. The global models' goodness-of-fit was assessed using likelihood ratio G^2 test. Productivity was calculated for queens and workers by dividing the brood produced by the number of either workers or queens. Thus, pro-

ductivity was a continuous variable bounded by zero and was modelled by fitting a log-normal distribution. The model for queen productivity followed a normal distribution and had homogeneous variances. We transformed worker productivity by Box–Cox transformation to fit the normal distribution and homogeneity of variance. Significant results did not vary from model selection using Box–Cox-transformed or log-transformed data (Table S1 and S2, Supporting information). Therefore, we present the estimates of log-transformed data that are easier to interpret.

We modelled caste-level mortality and productivity against two default models of colony size: (i) colony size as a single factor (determined by simply summing queens and workers); and (ii) colony size split into two factors, queen and worker abundance. We used the information-theoretical-based approach of AIC multi-model inference to compare models (Burnham & Anderson 2002). The competing hypotheses were determined by the potential explanatory variables: colony size, workers, queens and their interaction. Models were ranked according to their AICc (a corrected measure of AIC for small samples), and ΔAICc was computed for each model (AICc of the model minus the AICc of the 'best model'). From the ΔAICc, we computed the Akaike weights (ω) of the models. The Akaike weight of a model can be interpreted as the estimated probability that each model in the set is the 'best model' (Burnham, Anderson & Huyvaert 2011). For models showing over-dispersion, Quasi AICc (QAICc) was used (Grueber *et al.* 2011).

Table 2. Explanatory variable estimates for caste mortality and productivity, along with their interactions. Below are parameter model estimates and 95% confidence intervals for each response variable from model averaging from the top models (ΔAICc ≤ 7), with the exception of queen productivity for which the 'best model' was used (ΔAICc ≤ 7, see Table 1). Parameter estimates have a significant effect when the 95% CIs do not include zero. Queens had three levels, with one-queen nests as the reference category (Q3 = 3 queens, Q6 = 6 queens). Workers had three levels, with 10-worker nests as the reference category (W30 = 30 workers, Q300 = 300 workers)

Response variable	Explanatory variable	Estimate	95% CI inf	95% CI sup
Queen mortality	Intercept	−1·64	−3·7302	0·4433
	Colony	−0·47	−1·0017	0·0524
	Q3	−0·20	−1·9470	1·5488
	Q6	−0·02	−2·0889	1·2114
	W30	−0·44	−1·6951	0·6732
	W300	−1·46	−3·0772	0·1441
Worker mortality	Intercept	**−1·48**	**−1·7834**	**−1·1787**
	Q3	−0·05	−0·1939	0·0831
	Q6	**−1·71**	**−1·9283**	**−1·4970**
	W30	0·27	−0·2190	0·7646
	W300	0·40	−0·0313	0·8510
Queen productivity	Intercept	**0·91**	**0·3617**	**1·4666**
	Q3	0·73	−0·0477	1·5150
	Q6	0·36	−0·4143	1·1484
	W30	**1·35**	**0·5743**	**2·1370**
	W300	**3·67**	**2·8971**	**4·460**
	Q3 : W30	**−1·76**	**−2·8726**	**−0·6626**
	Q6 : W30	−0·73	−1·8409	0·3691
	Q3 : W300	**−1·83**	**−2·9376**	**−0·7277**
	Q6 : W300	**−1·99**	**−3·0972**	**−0·8872**
Worker productivity	Intercept	**1·39**	**0·7727**	**2·0106**
	Q3	**1·46**	**0·5284**	**2·3395**
	Q6	**1·43**	**0·6011**	**2·2759**
	W30	0·07	−0·7809	0·9297
	W300	−0·06	−0·9718	0·8483
	Q3 : W30	**−1·68**	**−2·7845**	**−0·5822**
	Q6 : W30	−0·64	−1·7428	0·4595
	Q3 : W300	**−1·54**	**−2·6387**	**−0·4363**
	Q6 : W300	**−1·44**	**−2·5391**	**−0·3367**

Significant effects are in bold. 95% CI inf and sup, 95% Confidence Interval inferior and superior, respectively

We calculated the importance weight of each explanatory variable by calculating the sum of the Akaike weights of the models that contained a particular variable. The explanatory variables are reported with their relative importance weights, parameter estimates and 95% confidence intervals (CI). Parameter estimates have a significant effect when the 95% CIs do not include zero. We used model averaging when there was more than one model with ΔAICc < 7 (Burnham, Anderson & Huyvaert 2011).

Values are presented as mean ± SE. Statistical analyses were conducted using R (Development-Core Team 2011) with an α-level of 0·05. Model-selection approach was performed using the MuMIn package (Bartón 2012). Data deposited in the Dryad repository: http://dx.doi.org/10.5061/dryad.1qf3s.

Results

Overall, both worker and queen survivorship were high throughout the 25-day experiment. Out of the 72 nests, 17 (24%) had 100% worker survivorship and 46 (64%) had >85% worker survivorship. Sixty nests (83%) had 100% queen survivorship. Eggs were present in all colonies after day three of the experiment. Only two colonies did not contain eggs by the end of the experiment; both of them had single queens that had died.

For queen mortality, the two global binomial models fitted the data well (likelihood ratio goodness-of-fit: worker and queen abundance separate: $G^2 = 48·52$, d.f. = 63, $P = 0·9104$; colony size: $G^2 = 56·08$, d.f. = 70, $P = 0·8863$). Our model analysis yielded three top models with ΔAICc < 7 (Table 1). The estimate parameter for colony size was negative and had the highest importance weight; however, it did not show significant support (Tables 1 and 2). All confidence intervals for the parameter estimates included zero, so there is little evidence that any of the explanatory variables affected queen mortality. This indicates that queen mortality was not significantly impacted by colony size or by the separate queen or worker abundance.

For worker mortality, the two global binomial models did not fit the data (likelihood ratio goodness-of-fit: worker and queen abundance separate: $G^2 = 459·52$, d.f. = 63, $P < 0·001$; colony size: $G^2 = 863·75$, d.f. = 70, $P < 0·001$) because of overdispersion. This overdispersion was corrected in model selection using QAICc (Burnham & Anderson 2002). The two models with ΔAICc < 7 contained queen and worker abundance (Table 1). With an importance weight of 1, the support was strong for the importance of queen abundance relative to the other factors. Moreover, the queen abundance estimate was significant for nests with six queens but not significant for worker abundance (Table 2). This indicates that worker mortality decreased significantly with the initial number of queens, while it was not affected by the number of workers (Fig. 1b). The model with only colony size had a much lower AIC and no support (Table 1). As worker mortality is affected only by queen abundance, the large numbers of workers relative to queens masked any effect when colony size was the explanatory factor in our model (Fig. 1a).

For queen productivity analysed with queen and worker abundance as separate variables, the global log-normal model fitted the data well ($R^2 = 0·71$, $F_{8,63} = 19·27$, $P < 0·001$). When using colony size as the only predictor, the model was still significant but with a lower R^2 ($R^2 = 0·57$; $F_{1,70} = 94·05$, $P < 0·001$). The single 'best model' included queen and worker abundance and their interaction, with all three having high importance weights (Table 1). The support for the importance of colony size was very low (Table 1, Fig. 2a). The parameter estimate for worker abundance was positive and had significant support (Table 2), indicating that queen productivity increased with worker abundance (Fig. 2b). While its parameter estimate was also positive, there was no significant support for a queen abundance effect (Table 2). Nevertheless, the interaction between worker and queen
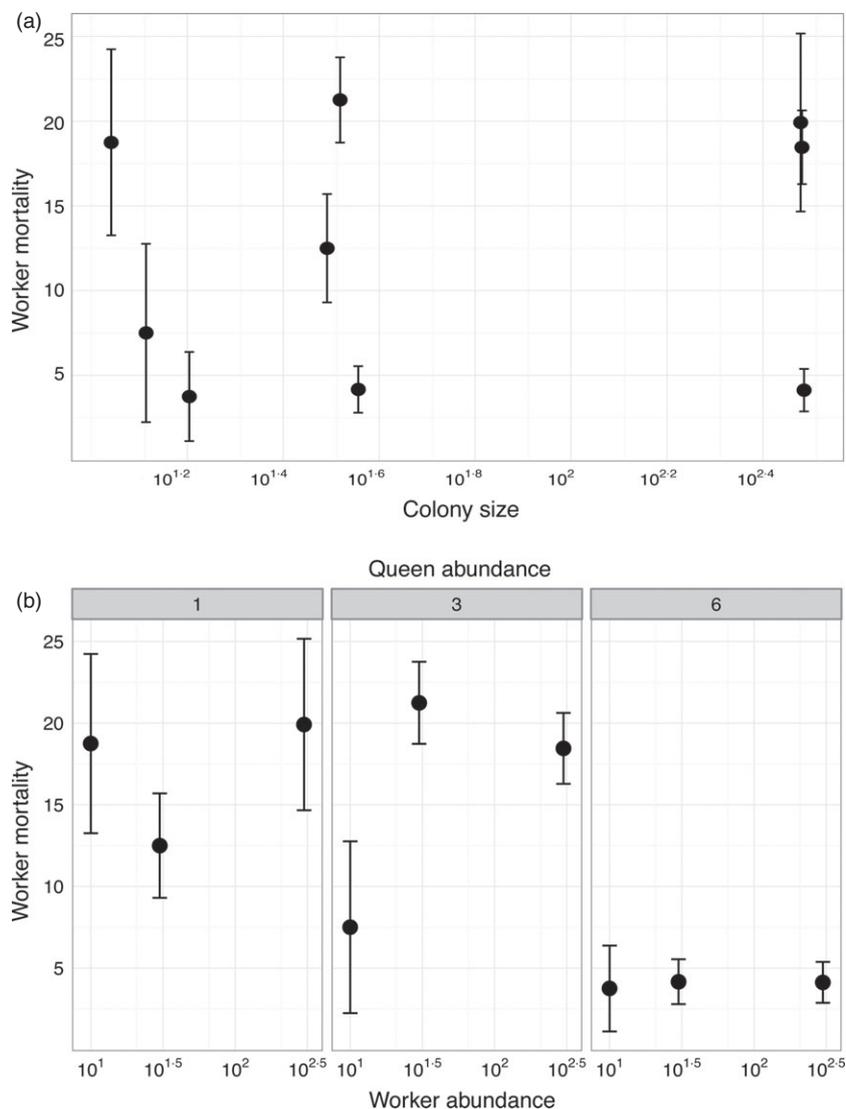
Fig. 1. (a) Worker mortality rate and initial total colony size (i.e. queen plus worker abundance). (b) Worker mortality (percentage of workers that died) for colonies with different initial worker and queen abundance. *X*-axes are log10 transformed. Error bars are ±SE.

abundance was significant: the positive effect on queen productivity by worker abundance decreased as queen abundance increased.

For worker productivity, both global models were significant (queen and worker abundance as separate variables: $R^2 = 0.43$; $F_{8,63} = 5.93$, $P < 0.001$; colony size as the single variable: $R^2 = 0.13$; $F_{1,70} = 10.24$, $P < 0.001$). The model with only colony size had very low support (Table 1, Fig. 3a). The two top models included queen and worker abundance and their interaction, with all three having high importance weights (Table 1). Queen abundance was positive and had significant support (Table 2), indicating that worker productivity increased with queen abundance (Fig. 3b). While its parameter estimate was also positive, there was no significant support for a worker abundance effect (Table 2). This was clearly represented by the case of one queen, where increasing worker abundance did not impact worker productivity (Fig. 3b, first panel with one queen). The interaction between queen and worker abundance was significant:

increasing queen abundance had a positive effect on worker productivity, but only with low worker abundance (Fig. 3b).

Discussion

The results of our experiments document the presence of component Allee effects in the Argentine ant. We found three positive density-dependent relationships indicative of component Allee effects at the colony level, namely (i) between the number of workers in a colony and queen productivity (Fig. 2b); (ii) between the number of queens in a colony and worker productivity (Fig. 3b); and (iii) between the number of queens in a colony and worker survival (Fig. 1a). Our results thus highlight the different effects of queens and workers on survival and productivity of the two castes. None of our models with colony size as a single factor significantly explained mortality or productivity, even in models using queens and worker as separate factors. This suggests that colony size as a whole,
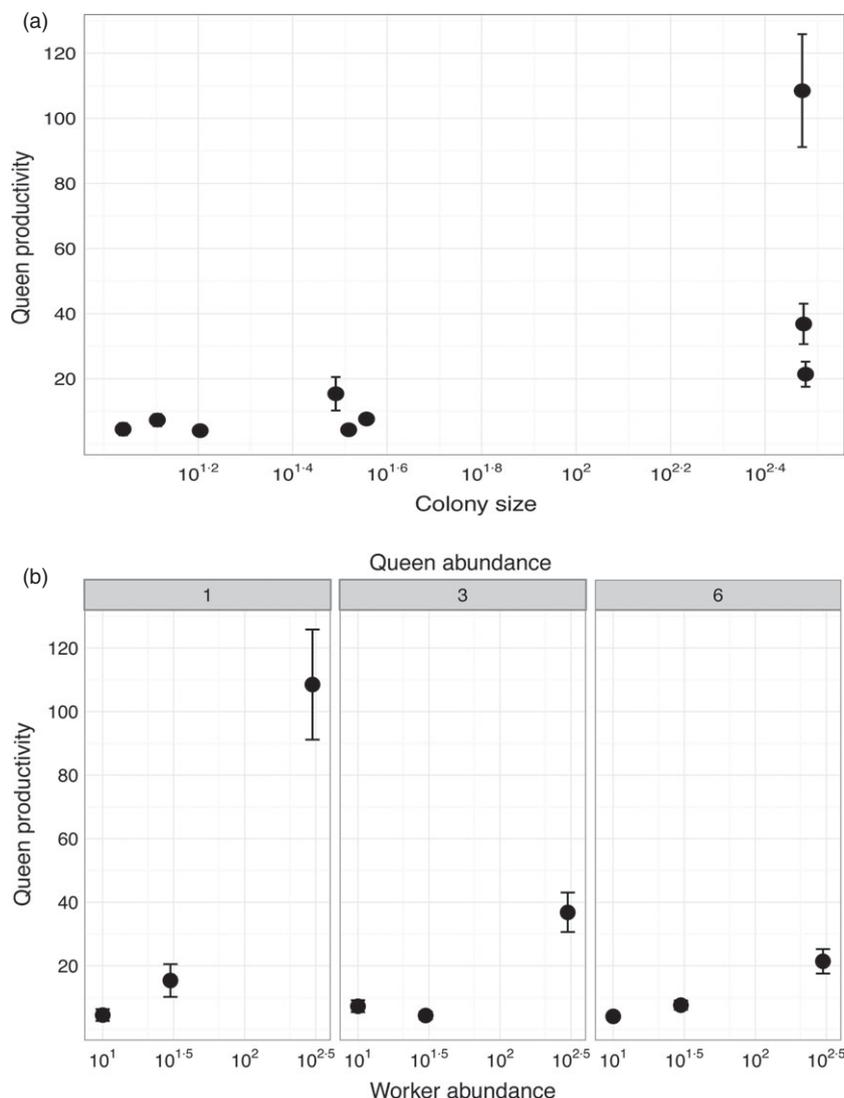
Fig. 2. (a) Queen productivity (brood produced divided by the number of queens) and initial total colony size (i.e. queen plus worker abundance). (b) Queen productivity with different initial worker and queen abundance. (b) Worker productivity (brood produced divided by the number of workers) with different initial worker and queen abundance. *X*-axes are log10 transformed. Error bars are ±SE.

without separating queen and worker castes, is inadequate to fully understand colony dynamics.

The first component Allee effect that we observed was an increase in queen productivity with worker abundance. This is not surprising since the Argentine ant queens need workers to rear brood (Hee *et al.* 2000). However, the benefit of adding workers decreased with increasing queen abundance. This was because at high worker abundance, queen productivity decreased when adding more queens. The decrease in queen productivity with an increase in queen abundance generally observed in ants was detected here only for high worker abundance (Keller & Vargo 1993; Keller 1995). Actually, this effect has been reported in species in which groups of queens gather to found new colonies, while in the Argentine ant, workers and queens are always present together to found colonies. Our results suggest that the relationship between queen productivity and queen abundance can be modified by the number of workers, probably increasing the benefit of queens gathering together.

The second component Allee effect observed was an increase in worker productivity with increasing queen abundance. However, the benefit of increasing queens seemed to disappear at high worker abundance, suggesting that the number of workers was then too low compared to queen abundance for all workers to be efficient in rearing brood. An alternative explanation could be that space became limiting, and 300 workers were taking care of the maximum number of brood that could fit inside the nest tubes. This seems unlikely, however, because there were always empty nest tubes available that were not occupied.

The third component Allee effect, a positive effect of queens on worker survival, appears less intuitive; it could be a result of workers feeding on queens' eggs. Egg cannibalism is common in ants, at least at the early stages of colony foundation, when both queens and workers are in low abundance (Tschinkel 1993; Ito 2005). In contrast, we did not observe a relationship in the reciprocal interaction: worker abundance and queen survival. Likewise, worker
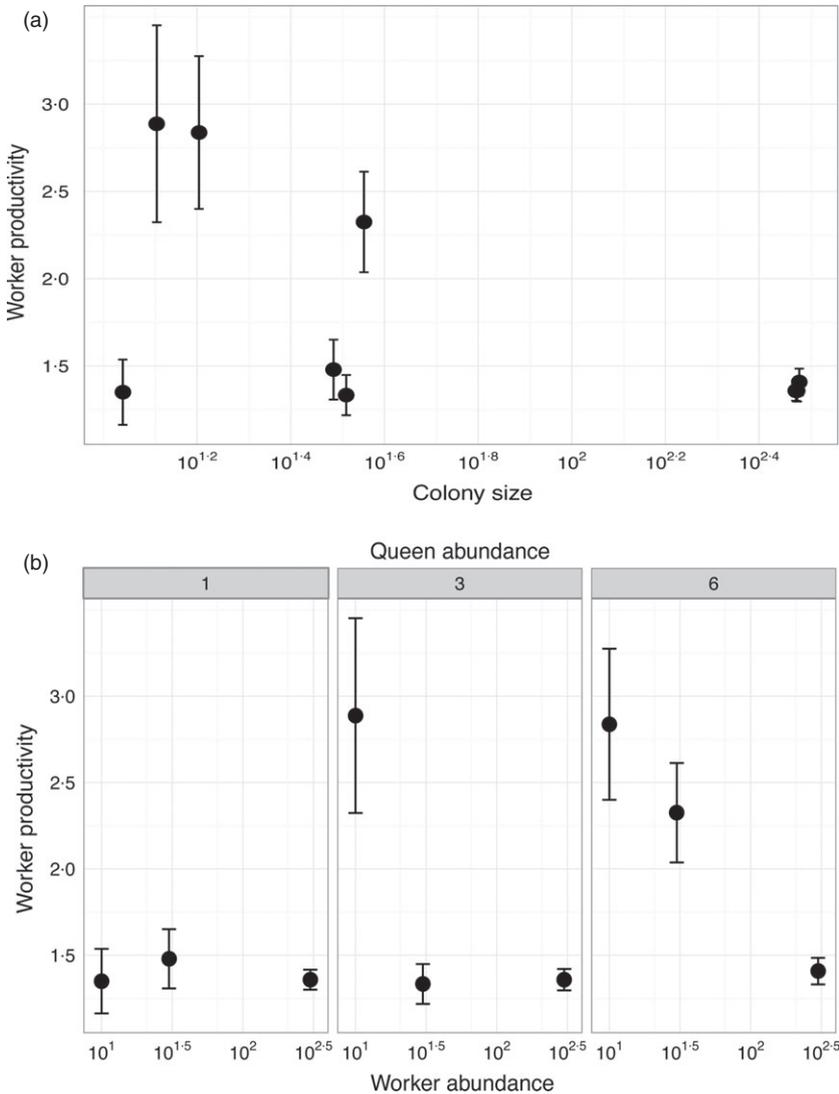
Fig. 3. (a) Worker productivity (brood produced divided by the number of workers) and initial total colony size (i.e. queen plus worker abundance). (b) Worker productivity with different initial worker and queen abundance. *X*-axes are log10 transformed. Error bars are ±SE.

and queen abundance did not show any density dependence effect on the survival of their own castes. In temporary polygynous species, increasing queen abundance often decreases queen survival, through either queen or worker aggression (Tschinkel & Howard 1983). However, density dependence is not necessarily expected in the Argentine ant, a permanently polygynous species, where coexistence occurs between large numbers of queens and workers in mature colonies (Markin 1970). The opposite pattern, positive density dependence between queen abundance and survival, has been documented in species where only queens form new colonies and provide resources to each other to raise the initial workers (Johnson 2004). The Argentine ant, in contrast, reproduces by fragmentation from maternal nests with queens accompanied by workers (Holway, Suárez & Case 1998; Hee *et al*. 2000; Suárez, Holway & Case 2001). With respect to worker abundance, an effect may be revealed in the presence of interspecific competition. For example, worker abundance can determine the outcome of competitive encounters in ant species (Holway & Case 2001; Palmer 2004).

Demographic Allee effects are generated – or not – by the cumulative effects of different components related to growth rate. This applies to our results in the cases where there may be density-dependent effects that counter component Allee effects. For example, in colonies with high number of workers, increasing the number of queens improved worker survival, but decreased queen productivity. A component Allee effect related to a specific caste abundance may interact with the effect of the other caste abundance. In our results, component Allee effects related to productivity were modified by the abundance of the alternative caste but not cancelled out. Indeed, the benefit of queens on worker productivity decreased with queen abundance but was present in all cases. Furthermore, there may be additional direct or indirect benefits under natural conditions that could be gained with large colony sizes. For example, cooperative groups may be more advantageous in challenging habitats (Duffy & Macdonald 2010), and large ant colony sizes may enhance the ability to persist against adverse environmental conditions (Kaspari & Vargo

1995). The advantage of increasing the number of workers or queens may be accentuated under harsh environmental conditions, high predator pressure or intense competition in favourable environments (e.g. Pedersen & Boomsma 1999; Herbers & Johnson 2007). In addition, colony size may affect behaviour towards other species. The Argentine ant may behave more aggressively only when their numbers are high, allowing it to out-compete other species (Sagata & Lester 2009). Therefore, challenging habitats may produce additional component Allee effects that could not be observed in the laboratory conditions.

The three positive density dependence patterns observed here show that workers and queens castes each have a positive effect on the productivity of the other caste and that queens have a positive effect on worker survivorship. The fact that both queens and workers benefited from an increase in the number of individuals from the other caste may lead to a positive feedback loop (Fig. 4). Such feedbacks could contribute to the large colony sizes observed in the field. In the Argentine ant and other ant species, queen abundance has been shown to vary according to ecological constraints (e.g. resources, competition and predation; Pedersen & Boomsma 1999; Ingram 2002). Further, Argentine ant queens and workers are able to discriminate and kill sexual larvae and thereby potentially control colony caste ratios (Markin 1970; Vargo & Passera 1991). Thus, Argentine ants may be able to influence queen/worker caste ratios to maximize productivity, as has already been shown in the pharaoh ant, *Monomorium pharaonis* (Schmidt *et al.* 2011). This mechanism could allow the Argentine ants to achieve a potentially unlimited colony size (Suárez, Holway & Tsutsui 2008; Helantera *et al.* 2009; Moffett 2012).

While we observed Allee effects at the colony level in Argentine ants, the population-level implications are less certain (i.e. multiple colonies). Sociality has been suggested to promote strong Allee effects and consequently to increase the susceptibility to population extinction (Stephens & Sutherland 1999; Courchamp, Clutton-Brock & Grenfell 2000). However, as cooperation due to sociality usually occurs only among individuals within colonies, cooperative mechanisms do not necessarily lead to Allee effects at the population level (i.e. multiple colonies). Thus, an increase in the number of colonies does not necessarily relate to an increase in population growth. Nevertheless, Allee effects at the level of the colonies could lead to population-level Allee effects provided colony growth rates are synchronized, and populations are composed of colonies of the similar sizes (Stephens, Sutherland & Freckleton 1999; Bateman, Coulson & Clutton-Brock 2011). For example, Mikheyev *et al.* (2008) suggested that the invasive, little fire ant *Wasmania auropunctata* was not substantially affected by Allee effects, which they measured as the probability of establishment related to the potential number of introductions due to human disturbance. However, initial colony size in each potential introduction was not considered. Introduction events could have contained large colonies with high probability of establishment and small colonies with a lower probability of establishment, caused by the presence of Allee effects. The impacts of Allee effects in ants would benefit from considering colony size dynamics and its interaction with population-level dynamics.

Our study demonstrates the importance of measuring the dynamics of different fitness components in eusocial species, since castes may influence fitness components in different ways. Studying the caste-specific components of fitness and their interactions will likely prove useful in understanding the benefits of increasing colony size in ants, and more generally the population dynamics of eusocial insects. In the case of invasive species, a high number of ant species are causing economic and ecological impacts, and control or eradication programs are being developed (Hoffmann, Abbot & Davis 2010). Detecting Allee effects in these invasive ant species can be important in the development of control strategies (Rabitsch 2011; Tobin, Berec & Liebhold 2011). For instance, in species for which only the number of queens drives Allee effects, eliminating queens may be the priority, while little effort would be directed towards workers. Detecting Allee effects and the components driving them may prove also useful for the management of social insects whose populations are drastically declining (e.g. honey bees). Disentangling the driving forces that trigger Allee effects, including caste abundance, their ratios and population-level effects, will contribute valuable information in the understanding of the basic and applied ecology of eusocial species.
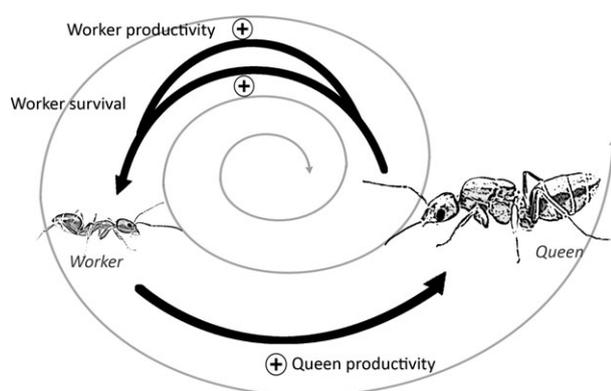

Fig. 4. Diagram showing three component Allee effects (black arrows): increasing the number of queens led to an increase in worker productivity and to an increase in worker survival, while increasing the number of workers increased queen productivity. The fact that both queens and workers benefited from an increase in the alternative caste may lead to a positive feedback loop (outwards grey arrow) that could help explain large colony sizes (e.g. supercolonies) in the Argentine ant. Alternatively, the same relationship could drive the colony into a vortex of extinction if the number of individual in one caste is insufficient (inwards grey arrow).

Acknowledgements

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Supporting Information

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

Table S1. Results of model fitting for worker productivity after Box Cox transformation (variable with exponent -1).

Table S2. Explanatory variable estimates along with their interactions for worker productivity after Box Cox transformation.