

IN FOCUS

Numbers count: caste-specific component Allee effects and their interactions



A queen and worker of the Argentine ant *Linepithema humile*. The numbers of queens and of workers in a colony each have positive relationships with components of fitness. Photo and copyright: Alexander Wild.

In Focus: Luque, G., Giraud, T. & Courchamp, F. (2013) Allee effects in ants. *Journal of Animal Ecology*, **82**, 956–965.

Allee effects, positive relationships between fitness and the number or density of conspecifics, are surprisingly widespread and are of profound importance for understanding ecological dynamics. Lucque *et al.* (2013) provide the first explicit demonstration of Allee effects in a social insect. Using laboratory colonies of the Argentine ant, they show that there are component Allee effects of both workers and queens which interact with negative frequency-dependent effects. Such Allee effects are central to the ecology and evolution of social insects, the societies of which provide a rich, experimentally tractable resource for understanding the mechanisms and impact of Allee effects.

It is a general rule in ecology that a greater density of conspecifics means more competition for resources such as food, mates and nest sites, and such intraspecific competition is accordingly a major regulating factor in population dynamics. A surprising diversity of organisms, however, show instead a positive relationship between individual fitness or population growth, and the number or density of conspecifics (Stephens, Sutherland & Freckleton 1999). These ‘Allee effects’ can be either on the total fitness of the organism (a demographic Allee effect) or on a component of fitness such as growth (a component Allee effect). Allee effects are of great importance in ecology, affecting parasite epidemiology, extinction, invasions, mating success and population dynamics (Courchamp, Clutton-Brock & Grenfell 1999;

Stephens & Sutherland 1999; Kokko & Rankin 2006). Most studies have investigated component Allee effects, and evidence for demographic Allee effects is in general more limited (Gregory *et al.* 2010), but the existence and importance of demographic Allee effects are very obvious in social species. Group-living organisms from social microbes like the amoeba *Dictyostelium discoideum*, to social vertebrates like African wild dogs *Lycaon pictus*, need a minimum number of individuals in their group for part or all of their life cycle in order to achieve positive inclusive fitness (Strassmann, Zhu & Queller 2000; Courchamp & Macdonald 2001). Social species therefore intrinsically have group-level, demographic Allee effects (i.e. total individual inclusive fitness positively related to the number of individuals in a group). Whether they might also have population-level Allee effects (i.e. individual fitness depending also on the number of groups in a population) is less clear, and it could even be the case

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that sociality is associated with a buffering of population-level Allee effects (Angulo *et al.* 2013).

Although eusocial insects are one of the pinnacles of sociality and represent a major transition in evolution, only one study has explicitly considered their Allee effects previously (Mikheyev *et al.* 2008). In this issue, Luque, Giraud & Courchamp (2013) investigate Allee effects using laboratory colonies of the Argentine ant, *Linepithema humile*. Colonies of this species can be highly polygynous, with many queens in a colony, and can function with a wide range in numbers of queens or workers. Luque and colleagues exploited this fact to set up 72 colonies with 1, 3 or 6 queens and 10, 30 or 300 workers, in a full factorial design, and maintained the colonies under controlled conditions with *ad libitum* food. Worker mortality and brood production after 25 days were recorded, revealing that the numbers of both queens and workers are associated with component Allee effects on several variables that determine colony growth (Fig. 1). The study extends previous studies reporting positive relationships between the number of workers in Argentine ant colonies and their brood production or competitive success (Hee *et al.* 2000; Holway & Case 2001; Walters & Mackay 2005). The fact that effects were detected here in spite of the colonies being kept under relatively benign conditions suggests that these effects are independent of the various environmental factors that are often involved in Allee effects and that the effects could be greater still under natural conditions. The Argentine ant studied here is a remarkable insect. It is a highly successful invasive species that forms unicolonial populations in its introduced range, with the main supercolony in southern Europe stretching over 6000 km (Giraud, Pedersen & Keller 2002). The presence of component Allee effects suggests that Argentine ant colonies likely require a colony with a sufficient number of workers for an invasion to be successful (Hee *et al.* 2000; Holway & Case 2001; Walters & Mackay 2005), unlike some invasive ant species that can become established from just a single queen (Mikheyev, Bresson & Conant 2009).

The study provides the first explicit demonstration of Allee effects in a social insect, but the general pattern of a positive relationship between the number of workers in a social insect colony and the growth, survival or fitness of the colony, is well known (Schmid-Hempel, Winston & Ydenberg 1993; Bourke & Franks 1995; Field *et al.* 2000; Strohm & Bordon-Hauser 2003; Table S1). In those species that have polygynous colonies, the number of queens too has been found in some, but not all, cases to show a positive relationship with colony growth, survival or fitness (Schmid-Hempel, Winston & Ydenberg 1993; Bourke & Franks 1995). However, the precise relationships are often complex. The relationships with number of workers are often nonlinear or disproportionate, with larger colonies generally having lower per capita brood production and growth, something that has been termed 'Michener's paradox' (Michener 1964; Naug & Wenzel



Fig. 1. Allee effects in Argentine ants. The effects of the number of workers and number of queens in a colony on (a) relative worker survival as a proportion of the best surviving category, (b) per capita queen productivity (brood/queen) and (c) per capita worker productivity (brood/worker). Colonies were kept under controlled conditions with *ad libitum* food. There are positive relationships between the number of queens and worker survival, the number of workers and queen productivity, and the number of queens and worker productivity. In both the latter cases, the strength of the Allee effects is affected significantly by the numbers of the other caste. Redrawn from Luque, Giraud & Courchamp (2013).

2006; Cao & Dornhaus 2013). The relationship with queen number can sometimes be strongly convex (Bartz & Holldobler 1982; Tschinkel & Howard 1983), and per capita egg production per queen is also often negatively related to the number of queens in the colony (Michener 1964; Bourke & Franks 1995). In addition, the number of workers or queens in a colony can alter the sex ratio of reproductives (males and new queens) produced (Keller *et al.* 1996; Bono & Herbers 2003), which will then impact the ultimate fitness of individuals in the colony depending on the relative fitness of males compared to new queens and their respective relatedness to focal individuals.

Importantly, Luque, Giraud & Courchamp (2013) show how component Allee effects can interact with other frequency-dependent effects. While the effects on worker mortality were straightforward, those on queen productivity and worker productivity were more complex (Fig. 1). There was a positive effect of the number of workers on queen productivity and specifically of an increase from 30 to 300 workers. However, the strength of this effect was negatively related to the number of queens, with the number of queens being negatively correlated with queen productivity for colonies with 300 workers. Similarly, there was a positive effect of the number of queens on worker productivity, but the strength of this effect was negatively related to the number of workers in the colony, with the number of workers being negatively correlated with worker productivity for colonies with 3 or 6 queens. In addition to having component Allee effects, both worker and queen numbers therefore had negative effects on per capita productivity that moderated the Allee effect of the other caste.

The study by Luque, Giraud & Courchamp (2013) illustrates two essential aspects for understanding Allee effects. First, not every individual in a group or population is the same. Many studies of Allee effects simply consider the total number or density of individuals, but the impact of each individual on the group or population will vary. This is well illustrated by the distinct queen and worker Allee effects shown by Luque, Giraud & Courchamp (2013) in Argentine ant colonies. It is likely that there will be similar influences of the caste, age, experience, health, sex, etc. of individuals on Allee effects in other social animals, and indeed in solitary animals as well. Secondly, component Allee effects will often interact with each other and with negative frequency-dependent effects, and understanding these interactions will be critical to understand the ultimate impact on population growth or individual fitness, and whether a demographic Allee effect is the result. Compared to many other highly social animals, social insects are in many ways easier to work with, as is illustrated by the ability of Luque, Giraud & Courchamp (2013) to compare mortality and brood production for 72 manipulated colonies under controlled conditions. Social insects provide some of the richest examples of Allee effects, and their experimentally

tractability makes them valuable models for understanding the ecology and evolution of such effects.

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Supporting Information

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

Table S1. A selection of the social insect species for which positive relationships have been shown between the number of workers or queens in a group and some component of fitness (i.e. a component Allee effect; orange rows), or negative relationships with per capita productivity (blue rows) have been reported. Note that this is not an exhaustive list and there are undoubtedly many more examples in the literature.