A new approach to the ecology of eusocial insects: The Allee Effects in native and invasive ant species.

The Allee effect has been an influential phenomenon for many aspects of basic and applied ecology[1]. Allee effects occur when the per capita population growth rate declines with decreasing population size, due to the loss of mutually beneficial intraspecific interactions. Allee effects are common in social species[2] but it has not been applied to any species of eusocial insects. The present project pursued a pioneering extension of the study of Allee effects to ants, as a first approach to the study of these phenomena in eusocial insects.

During the first year of the project, we carried out preliminary studies with four ant species, and a variety of experimental nests and food resources. We chose two ant species with similar life traits and closely related, one invasive, the Argentine ant *Linepithema humble* and another non-invasive *Tapinoma nigerrimum* that grew well under laboratory conditions and that allowed for manipulation of the number of queens and workers. We collected ants from supercolonies in Córdoba (Spain). For the two species, ants were placed in independent experimental colonies according to a complete two-way factorial design with three categories of queen and worker numbers (8 replicates per treatment). This resulted in a total of 72 nests per species in addition to the trial nests. The experiment lasted from 5 to 10 months depending on colony survival. Several components of fitness where recorded twice a month, including, number of dead queens and workers, brood produced (eggs, larvae, and pupae) produced per nest. We used of cutting-edge and pioneering laboratory methods, including a new set up for keeping ants alive under laboratory conditions for a long period and that allowed the recording of the productivity of nests by a USB Microscope video camera without destroying the nests. During the second year, we continued colony monitoring for surviving colonies and carried out the analysis of video-recordings. This consisted on noting the number of eggs, larvae, and pupae produced and queens and workers alive.

New framework for the study of Allee effects on social species.
We found several drawbacks of the current framework for the study of Allee effects in social species. The impact of Allee effects on population dynamics is confounded by the fact that Allee effects operate within cooperative groups rather than across entire populations. These effects are further complicated by the presence of different castes within these cooperative groups or colonies. These aspects are not unique to ant species and they present important drawbacks for the current framework used in studies of Allee effects. During this project we explored the complexities surrounding Allee effects within social species in general, using ants as an extreme example. For this part, we collaborated with specialists on five taxa of social species, including bats (S.D. Gregory, University of Adelaide, Australia), primates (C.B. Gómes, Agro-Paris Tech, Paris), cooperative breeders (E. Angulo, CSIC, Spain), and wasps and bees (J.W. Wenzel, Carnegie Museum, USA) to provide a more adequate framework for the study of Allee effects that incorporates different aspects of social biology, including cooperative grouping, reproductive specialization, inter-group dynamics, and the density and distribution of group sizes within a population.

[1] Courchamp F et al. J 2008 Allee Effects in Ecology and Conservation. Oxford University Press.
[2] Kramer A M et al. 2009. The evidence for Allee effects. Population Ecology.

Accordingly, we have developed two new concepts: a new type of Allee effect, the Group Allee effect, and the meta-groups dynamics, both of them specific to social species. The importance of understanding Allee effects for conservation is widely recognized, in particular, there are many social species that are already endangered with declining populations for which correct identification and understanding of Allee effects is crucial. Success in this direction will allow us to be more predictive with regard to conservation biology and wildlife management of social species in general, from invertebrates to mammals.

Allee effect in an invasive ant species.
The results obtained from the laboratory data described above provided the first evidence for Allee effects on ants. The species used for this experiments is one of the worst invasive ant species worldwide. Therefore, this results have important implications for the estimation of the likelihood of invasion risk by this species, which is crucial for its management.

Temporal dynamics of Allee effects in ants.
We determined the temporal variations on different mechanisms that lead to Allee effects in ants using laboratory data for five months in two ants, one invasive and the other non-invasive. This allowed for comparison of the types of Allee effects and the mechanisms creating them in the two species, which were different through time. This work revealed the mechanisms underpinning Allee effects in native and invasive ants.

Allee effects and the risk of ant invasions after climate change.
Our study presents the double originality to approach invasiveness of ant species in the context of climate change and experimentally in the field, when almost all climate change studies are conducted either *in sillico* or *in vitro*. We considered the effect of propagule size (i.e., Allee effect) and use three settings: laboratory colonies as control and two field sites representing simultaneously two points in space, separated by climatic conditions (one currently favorable, one currently not) and two points in time, separated by global climate change (one currently unfavorable, but which will become favorable with time). This study first shows that short-term colony survival of the invasive ant incipient colonies is good in Southern Spain but practically null in Northern France, in good accordance with climate models. This result validates the relevance of conducting both experimental approaches to complement theoretical projections, and field experiments to complement laboratory experiments. The approach presented here has yielded results qualitatively different from those obtained in equivalent laboratory experiments, where it is more difficult to account for complex but crucial variables, such as the interspecific competition found in the field.

Potential Allee effects in the stage of colony foundation in parasitic ants.
We investigated colony foundation behavior of three species of the parasitic ants *Lasius* using field observations and laboratory experiments. Laboratory experiments showed that queens from one of the species *L. interjectus* prefer to group and suffer lower mortality when in a group, which was consistent with field observations of queens entering host colonies in large numbers. This shows how the potential importance of Allee effects for this species, which needs a minimum number of queens to successfully found new colonies. This work has been published in *Insectes Sociaux* in collaboration with J. M. Raczkowski from the University of Ohio (OH, USA).