



**HAL**  
open science

# The hidden side of the Allee effect: correlated demographic traits and extinction risk in experimental populations

Elodie Vercken, Géraldine Groussier, Laurent Lamy, Ludovic Mailleret

## ► To cite this version:

Elodie Vercken, Géraldine Groussier, Laurent Lamy, Ludovic Mailleret. The hidden side of the Allee effect: correlated demographic traits and extinction risk in experimental populations. 2020. hal-02570868v2

**HAL Id: hal-02570868**

**<https://hal.science/hal-02570868v2>**

Preprint submitted on 1 Oct 2020 (v2), last revised 20 Apr 2021 (v4)

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# The hidden side of the Allee effect: correlated demographic traits and extinction risk in experimental populations

Elodie Vercken<sup>1</sup>, Géraldine Groussier<sup>1</sup>, Laurent Lamy<sup>1</sup>, Ludovic Mailleret<sup>1,2</sup>

<sup>1</sup>Institut Sophia Agrobiotech - INRAE, Université Côte d'Azur, CNRS, ISA, France

<sup>2</sup>Inria, Biocore, 06902 Sophia Antipolis, France

## ABSTRACT

Because Allee effects have major impacts on the dynamics of small populations, they are routinely included in demographic models for the evaluation of extinction risks. However, the structure of most common models implies that other demographic parameters (like the maximum growth rate) are modified by the inclusion of an Allee effect, which also affects in return the extinction risk of the population. Whether such correlations between demographic traits occur in natural populations or merely reflect a practical constraint related to model formalism is of primary importance to understand better the dynamics of small populations. We investigated this question using 20 populations of *Trichogramma* wasps raised under similar conditions, of which 3 were subject to an Allee effect. We showed that these 3 populations were also characterized by lower maximum growth rate and lower carrying capacity, and that their extinction probability was higher than for non-Allee populations. These results provide the first empirical demonstration of a correlation between the presence of positive density-dependence and impaired demographic performance, which increases the extinction risk of population, especially during the establishment phase.

**Keywords:** experimental population dynamics ; establishment success ; introduced populations ; parasitoids ; microcosms ; demographic stochasticity

## INTRODUCTION

Allee effects characterize small populations in which *per capita* population performance increases with population density, a phenomenon also known as positive density-dependence (Dennis 1989; Courchamp et al. 2008). As the presence of an Allee effect is often considered a major risk factor for population extinction (Lande 1988; Boukal and Berec 2002), Allee effects are commonly included in population dynamics models for the management of small populations, either for conservation or management purposes (Tobin et al. 2011; Molnár et al. 2014; Hutchings 2015; Wittmann et al. 2018; Bajeux et al. 2019). One of the most common heuristic population dynamics model accounting for an Allee effect is a modified version of the logistic model (Lewis and Kareiva 1993; Amarasekare 1998; Boukal and Berec 2002, with analogous models existing in discrete time, Liebhold and Bascompte 2003; Tobin et al. 2007) that reads:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) \left(\frac{x - A}{K}\right)$$

where  $A$  is the Allee parameter (weak Allee effect for  $A \leq 0$ ; strong Allee effect for  $A > 0$ ),  $r > 0$  is the maximum per capita population growth rate in absence of the Allee effect, and  $K$  the carrying capacity.

However, this modified structure impacts several key population parameters, with potential significant consequences beyond the mere presence of positive density-dependence. For instance, when theoretical parameters  $r$  and  $K$  are held constant, the maximum per capita growth rate is lower in populations subject to an Allee effect as described by the model above than in populations affected by negative density-dependence only (Courchamp et al. 2008; Drake and Kramer 2011, Figure 1). A direct consequence of this lower growth rate is that the establishment or growth phase of an initially small population, in which the population is most vulnerable to stochastic influences, lasts longer in presence of an Allee effect (Veit and Lewis 1996; Dennis 2002; Drake 2004; Sinclair and Arnott 2016) and increases with the magnitude of the Allee effect (Bajeux et al. 2019). Both these parameters (maximum per capita growth rate and duration of the establishment phase) have been shown theoretically and empirically to influence extinction risk (Lande 1993; Liebhold and Bascompte 2003; Drake et al. 2011; Cassey et al. 2014). In theoretical analyses of population dynamics, populations with an Allee

effect are thus characterized not only by the presence of positive density-dependence, but also by lower maximum growth rate, both of which increase the extinction risk of populations.

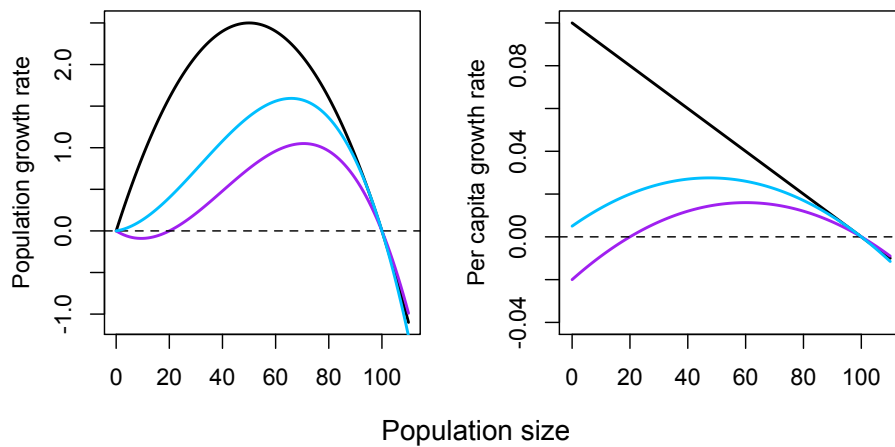


Figure 1: Population growth rate  $\frac{dx}{dt}$  (left) and per capita growth rate  $\frac{1}{x} \frac{dx}{dt}$  (right) for a logistic model (in black), a model with a weak Allee effect ( $A=-5$ , in blue) or a model with a strong Allee effect ( $A=20$ , in purple) when  $r=0.1$  and  $K=100$ . After Drake and Kramer (2011).

Because this non-independence between demographic parameters arises from the structure of population dynamics models, its relevance in natural populations might be questioned. Yet a demographic Allee effect reveals specific processes internal to the population, so it is likely to correlate with other components of population dynamics, like growth rate or carrying capacity. Such characteristics might then add up to increase the probability of population extinction. Alternatively, if the presence of an Allee effect is independent in practice from other demographic parameters, it implies that the extinction risk related to positive density-dependence only might have been overestimated in theoretical studies.

A major difficulty in addressing this issue is to find independent populations subject to an Allee effect or not, whose life histories are close enough to allow quantitative comparisons of demographic parameters. In this study, we analyzed the dynamics of 20 populations of parasitoid wasps of the genus *Trichogramma* raised under similar conditions, and detected the presence of an Allee effect in 3 of these populations. This privileged experimental system allowed us to demonstrate that general components of population dynamics correlate with the presence of an Allee effect, which increases the extinction probability of the populations.

## METHODS

### Biological model

We used parasitoid wasps of the genus *Trichogramma* as biological models. Our study populations were provided by the Biological Resource Center EP-Coll ([doi.org/10.15454/AY4LMT](https://doi.org/10.15454/AY4LMT)), specialized in egg parasitoids. 30 populations were initially chosen from a set of 70 populations collected in the field in 2015 to evaluate the diversity of *Trichogramma* in France (D. Muru, unpublished data). Detailed information on each population is available in Supplementary Material ([doi.org/10.5281/zenodo.3963856](https://doi.org/10.5281/zenodo.3963856), Table S1). A “population” was defined as individuals sampled on the same plant in a given locality, so that several populations could have been collected from the same locality. At the time of the experiment, genetic information about the different populations was not available, so we selected populations to form a representative subset of the geographic diversity from the 2015 field sampling. Seven species were included in the 30 selected populations: *T. brassicae* (2 populations), *T. cacoeciae* (16), *T. cordubensis* (3), *T. euproctidis* (2), *T. evanescens* (2), *T. principium* (1), *T. semblidis* (4). Once genetic information was available, we removed from the analysis the populations whose genetic signature was identical and sampled in the same locality to avoid pseudo-replication. We also removed the data from one *T. cordubensis* population, for which all replicates went extinct at the first generation. The final dataset included 20 populations: *T. brassicae* (1 population), *T. cacoeciae* (10), *T. cordubensis* (2), *T. euproctidis* (1), *T. evanescens* (2), *T. principium* (1), *T. semblidis* (3). *Trichogramma* are haplodiploids, i.e. females are diploid and males are haploid. However, some species are arrhenotokous (sexual reproduction is needed to produce diploid females, and unfertilized eggs develop into males, like *T. brassicae*, *T. euproctidis*, *T. evanescens*, *T. principium*, *T. semblidis*), while others are thelytokous (*T. cacoeciae* and *T. cordubensis*, where females reproduce clonally).

### Monitoring of population dynamics

*Trichogramma* are minute solitary parasitoids of Lepidopteran eggs that can be reared in small volumes. Experimental population units were housed in plastic tubes (diameter 50 mm, length 100 mm). Food for adults was provided ad libitum as drops of honey placed on the tube walls. Hosts for reproduction were provided as 3 mm-diameter patches of *Ephestia kuehniella* eggs

glued on paper strips (10 egg patches at each generation; average number of eggs on a patch and 95% confidence interval: 458 [445–471]). Eggs of *E. kuehniella* were irradiated previously, which prevented host development while allowing parasitoid development. For this experiment, temperature and light conditions were set on a cycle of 16 h daylight (22 °C)/8 h dark (20 °C) with constant 70% humidity. Under these conditions, generation time was 14 days for all populations.

Initial populations were founded by introducing between 10 and 30 parasitized eggs into a tube (for each population, 8 initial density levels with 10-12-14-16-18-20-25-30 parasitized eggs). Because of asynchrony in emergence, the different populations were distributed into 6 experimental blocks, spread over 2 consecutive weeks. At emergence, fresh host eggs were introduced in the tubes and exposed 48h to parasitism, then put aside for parasitoid development until the emergence of the next generation. Population size at the next generation was estimated by counting the total number of parasitized eggs before emergence. Parasitized eggs turn black when the parasitoid reaches the nymphal stage and the number of black eggs directly reflects adult population size at emergence. At the beginning of emergence, fresh host patches were introduced in the tubes and similarly exposed during 48 h to obtain the next parasitoid generation. Parasitoid population dynamics were monitored during three generations after introduction between January and March 2016. Time series of population dynamics are provided as Supplementary Material ([doi.org/10.5281/zenodo.3963856](https://doi.org/10.5281/zenodo.3963856), Figure S1).

### **Detection of Allee effects**

The presence of an Allee effect is indicated by a positive correlation between population size and per capita growth rate. However, this positive correlation is generally present for small population sizes only, and sometimes difficult to evidence due to strong stochastic effects and limited amount of data. We applied two different methods to try and detect this correlation: (i) a correlation test on a subsample of small populations sizes and (ii) non-linear fit over the whole range of population sizes. In both cases, we analyzed the relationship between population size and the "modified per capita growth rate"  $\lambda_{m(i,t)}$  calculated at each generation  $t$  and for each experimental replicate  $i$  as follows:

$$\lambda_{m(i,t)} = \ln\left(\frac{N_{i,t+1}}{N_{i,t}} + 1\right)$$

We chose this metric for the evaluation of growth rate because it is expected to be decreasing linearly when density increases under the hypothesis of simple negative density-dependence. We added 1 to the ratio of densities to be able to include extinction events ( $N_{i,t+1}=0$ ) in the data.

For the regression approach, we selected sub-samples of population sizes  $N_{i,t}$  either inferior to 50 or inferior to 100 individuals, and we fitted a non-parametric Spearman correlation between population size and  $\lambda_{m(i,t)}$ . For the non-linear approach, we fitted a smooth relationship (thin-plate regression spline) between population size and  $\lambda_{m(i,t)}$  using general additive models (package 'mgcv', Wood 2018) in R (R Core Team 2017). We allowed different values (3, 5, 8 or 10) for the dimension parameter  $k$ , which gives the maximum possible degrees of freedom allowed for the smooth term. We acknowledged the presence of an Allee effect for the population if the fitted function was non-monotonic with a maximum  $\lambda_m$  for an intermediate value of population size.

Depending on the method used, different populations were identified as subject to an Allee effect. In what follows, we focused on the non-linear fit with parameter  $k=8$ , which managed to intersect all of the populations identified with the other methods and thus seemed the most conservative approach for the identification of Allee effects (see Table S1, [doi.org/10.5281/zenodo.3963856](https://doi.org/10.5281/zenodo.3963856)).

### **Estimation of demographic parameters and statistical analyses**

Population dynamics were characterized in each replicate by the maximum modified per capita growth rate ( $\lambda_{max}$ ), the maximum population size ( $N_{max}$ ) and the mean population size across all 3 generations for non-extinct populations ( $N_{mean}$ ). These three variables followed Normal distributions and were analyzed using linear mixed models with the presence of an Allee effect as a fixed factor, and population as a random effect. We also analyzed the probability of extinction of a replicate, which followed a binomial distribution, using generalized linear mixed models with the presence of an Allee effect as a fixed factor, and population as a random effect. Both linear mixed models and generalized linear mixed models were fitted using the R package 'glmmADMB' (Skaug et al. 2018). Models including the

presence of an Allee effect were compared with null models including only the random population effect using AIC ( $\Delta AIC = AIC_{\text{null model}} - AIC_{\text{Allee model}}$ ), and if relevant (i.e.  $\Delta AIC > 2$ ), the impact of an Allee effect was interpreted using the p-value of the fixed factor.

We quantified the replicability of population dynamics using a repeatability index RI. The RI was calculated for each population as the mean of the sum of squares between the time series of each pair of replicates (excluding the founding generation where population size was assigned to each replicate).

$$RI = \frac{1}{C_8^2} \sum_{i,j} \sum_{t=1}^3 (N_{i,t} - N_{j,t})^2$$

The RI did not follow any classical distribution, and it was compared among Allee and non-Allee populations using a Kruskal-Wallis test.

All data and scripts for analyses are available with supplementary materials on Zenodo ([doi.org/10.5281/zenodo.3963856](https://doi.org/10.5281/zenodo.3963856)).



## RESULTS

Out of the 20 populations analyzed, 3 displayed an Allee effect (1 population from *T. cacoeciae*, 1 population from *T. principium*, 1 population from *T. semblidis*, Figure 2).

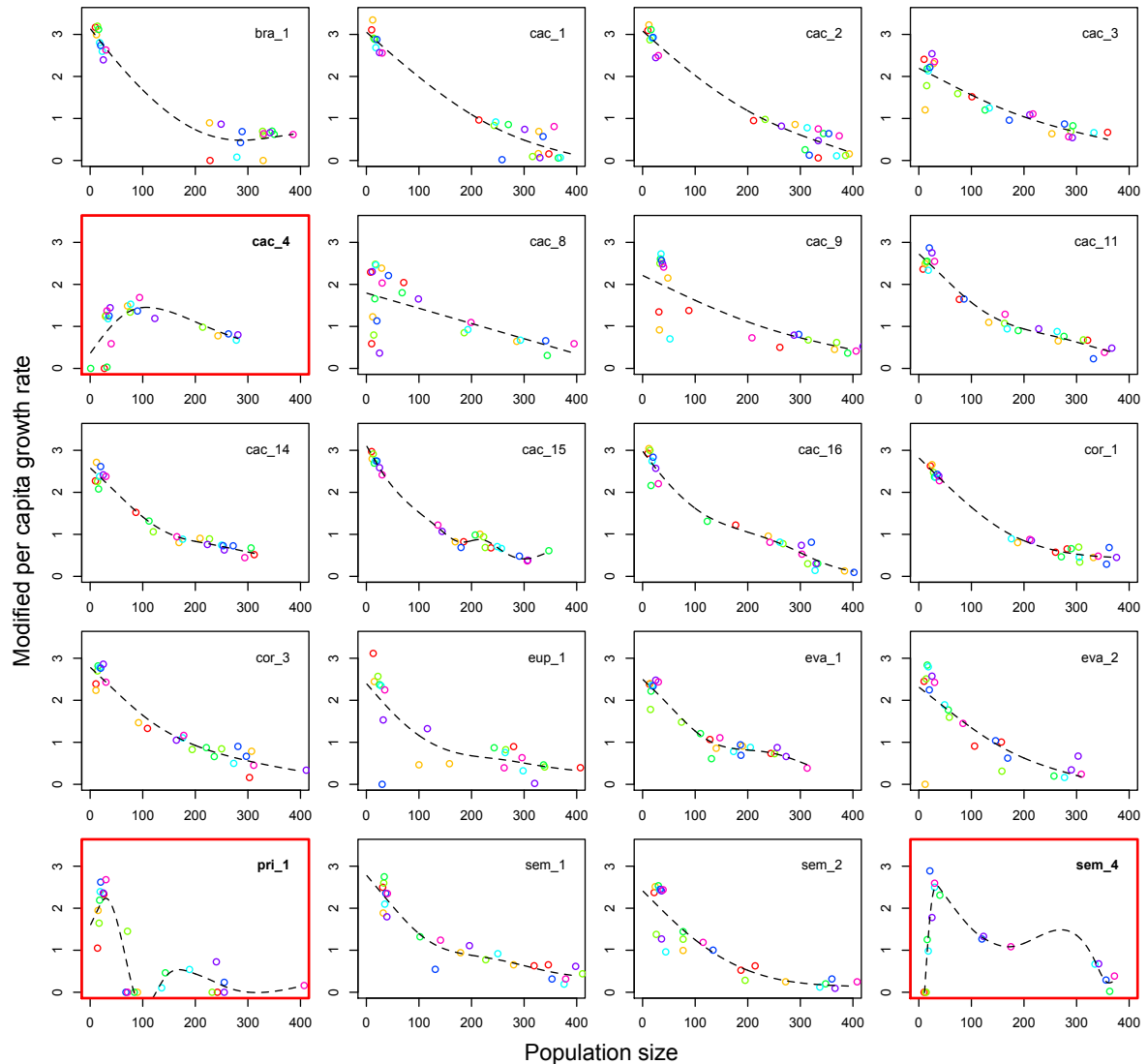


Figure 2: Raw data and GAM fits ( $k=8$ ) for the relationship between population size and modified per capita growth rate  $\lambda_m$ . Red boxes: populations characterized by an Allee effect.

Population dynamics were found to be markedly different between Allee and non-Allee populations (Figure 3). Allee populations were characterized by lower maximum modified per capita growth rate ( $\Delta AIC=5.7$ ,  $p=1.9 \times 10^{-3}$ ), lower maximum population size ( $\Delta AIC=2.0$ ,  $p=0.017$ ), lower average population size ( $\Delta AIC=2.7$ ,  $p=0.021$ ), and higher extinction rate

( $\Delta AIC=6.1$ ,  $p=0.016$ ). Their trajectories also tended to be less repeatable ( $p=0.087$ ) than for non-Allee populations.

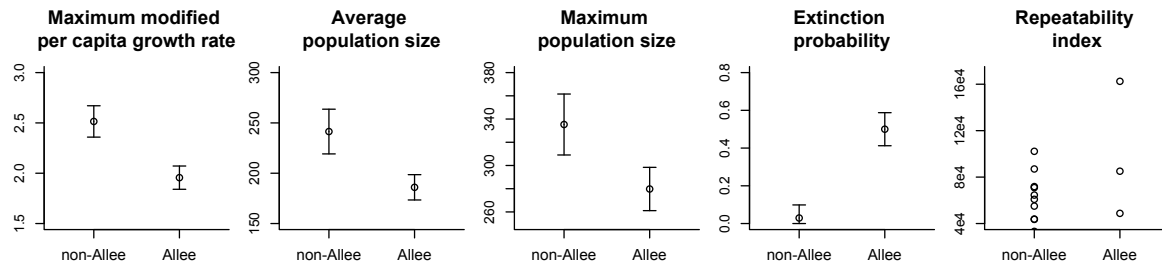


Figure 3: Comparison of demographic parameters between populations with or without an Allee effect. All graphs represent mean  $\pm$  2 SE, except the repeatability index for which raw data are plotted because of the low number of replicates.

## DISCUSSION

Our analysis demonstrated the presence of an Allee effect in some, but not all, *Trichogramma* populations raised in laboratory conditions. This finding further confirms that Allee effects can operate in small volumes and affect population persistence even in favourable, controlled conditions (Gertzen et al. 2011; Kaul et al. 2016). Unlike most classical experimental microcosm systems (e.g., *Tribolium*, *Daphnia*, *Tetrahymena*), our collection of *Trichogramma* populations allows us to compare populations with similar life-histories and raised under the same conditions, in order to single out the impact of the presence or absence of an Allee effect. In this study, we found that *Trichogramma* populations for which an Allee effect was detected were characterized by qualitatively different dynamics from populations with no Allee effect.

The demographic parameters correlated with the presence of an Allee effect have direct consequences on short-term extinction risk. Indeed, low per capita growth rates and low population sizes interact to maintain the population in a unfavorable demographic zone, where it is most vulnerable to extinction through the influence of demographic stochasticity (Dennis et al. 2015). This increased stochastic regime is noticeable in our data, as populations subject to an Allee effect show greater variability among replicates, and a higher extinction

rate. In addition, this prolonged demographic bottleneck in presence of an Allee effect might increase genetic drift and inbreeding, so that even populations that manage to grow enough to reach carrying capacity will suffer from higher long-term extinction risk (Fauvergue et al. 2012). This special case of genetic extinction debt was previously reported in laboratory populations of a different species of *Trichogramma* (Vercken et al. 2013). Interestingly, even parameters related to equilibrium dynamics (like maximum population size) differed between Allee and non-Allee populations. This suggests that the influence of the Allee effect on population dynamics persists beyond the early establishment phase and can affect the demographic trajectory over wide ranges of densities.

In our case, the mechanism responsible for the presence of positive density-dependence in some populations only has not been identified. Out of the 3 populations subject to an Allee effect, the population of *T. cacoeciae* is strictly parthenogenous, so mate limitation is unlikely to be the major factor impairing population performance at small density, although it can still play a role in the two other populations. Alternatively, strong demographic stochasticity could act as a generic mechanism inducing positive density-dependence, even in parthenogenous populations. Classical ecology theory predicts that, if individual variance in reproductive success is high (e.g., because of random differences in fecundity and survival), the realized per capita growth rate will be reduced (May 1973; Melbourne 2012), especially at low density (Lande 1993), which can generate an Allee-like effect (Lande 1998). However, such a purely stochastic process has been argued to be qualitatively different from a deterministic Allee effect, the latter being characterized by an inflection point in the relationship between initial population size and extinction probability (Dennis 2002). Yet, the presence of such an inflection point is a characteristic of strong Allee effects only, while the detection of positive density-dependence in the per capita growth rate can be considered as a generic evidence for the presence of an Allee effect (Johnson et al. 2006; Kramer et al. 2009; Gregory et al. 2010), including stochastic Allee-like effects that are more similar to weak Allee effects.

Although the weak or strong nature of an Allee effect induces major qualitative differences in dynamics in theoretical models related to the existence of an unstable equilibrium in the case of a strong Allee effect (Dennis 1989; Lewis and Kareiva 1993; Wang and Kot 2001), the same ecological mechanisms are expected to be involved in both cases (e.g., mate limitation,

cooperation, predation, (Courchamp et al. 2008). In practice, the distinction between weak and strong Allee effect in empirical data thus relies only on the quantitative estimation of the per capita growth rate at small density, where stochastic variance is the highest and therefore the estimation is least precise (Kramer et al. 2009). In our three Allee populations, two have an estimated negative growth rate at low density, all three confidence intervals being large enough to include both positive (i.e., weak Allee effect) and negative (i.e., strong Allee effect) values. Furthermore, estimations of Allee effects in nature have demonstrated that the intensity of the Allee effect can vary geographically (Tobin et al. 2007), and results from stochastic models have demonstrated that weak Allee effects can be amplified by stochasticity (demographic or environmental) so as to induce a lower unstable equilibrium, similar to an Allee threshold (Roth and Schreiber 2014; Dennis et al. 2015). This converging evidence suggests that the dichotomous distinction of weak and strong Allee effect, though essential in deterministic theoretical approaches, might be less relevant in stochastic modelling or in nature where the “strength” or “intensity” of an Allee effect could be quantified continuously.

These results provide the first empirical demonstration of a correlation between the presence of positive density-dependence and impaired demographic performance during establishment phase. If the presence of an Allee effect is correlated with other demographic parameters, in particular the maximum per capita growth rate, then it remains a major risk factor for population extinction, even in the case of a weak Allee effect, or if the population introduced is superior to the theoretical Allee threshold for a strong Allee effect. The non-independence between these demographic parameters is thus likely to be of critical importance for the prediction of the establishment success of introduced species.

#### ACKNOWLEDGEMENTS

We are especially grateful to Sylvie Warot, for the most helpful molecular determination of *Trichogramma* species, and to Nicolas Ris for making the Biological Resource Center possible so that all of us (and many others) can enjoy working on *Trichogramma*. This work was funded by the Agence Nationale de la Recherche as part of the TriPTIC project (ANR-14-CE18-0002).

## References

- Amarasekare P. 1998. Allee effects in metapopulation dynamics. *Am Nat.* 152(2):298–302. doi:10.1086/286169.
- Bajeux N, Grogard F, Mailleret L. 2019. Influence of the components of propagule pressure, Allee effects, and stochasticity on the time to establish introduced populations. *J Theor Biol.* 471:91–107. doi:10.1016/j.jtbi.2019.03.012.
- Boukal DS, Berec L. 2002. Single-species Models of the Allee Effect: Extinction Boundaries, Sex Ratios and Mate Encounters. *J Theor Biol.* 218(3):375–394. doi:10.1006/jtbi.2002.3084.
- Cassey P, Prowse TAA, Blackburn TM. 2014. A population model for predicting the successful establishment of introduced bird species. *Oecologia.* 175(1):417–428. doi:10.1007/s00442-014-2902-1.
- Courchamp F, Berec L, Gascoigne J. 2008. Allee effects in ecology and conservation. Oxford, England: Oxford University Press.
- Dennis B. 1989. Allee effects: population growth, critical density, and the chance of extinction. *Nat Resour Model.* 3:481–538.
- Dennis B. 2002. Allee Effects in Stochastic Populations. *Oikos.* 96(3):389–401.
- Dennis B, Assas L, Elaydi S, Kwessi E, Livadiotis G. 2015. Allee Effects and Resilience in Stochastic Populations. *Theor Ecol.* 9. doi:10.1007/s12080-015-0288-2.
- Drake JM. 2004. Allee effects and the risk of biological invasion. *Risk Anal Off Publ Soc Risk Anal.* 24(4):795–802. doi:10.1111/j.0272-4332.2004.00479.x.
- Drake JM, Kramer AM. 2011. Allee Effects. *Nat Educ Knowl.* 3(10):2.
- Drake JM, Shapiro J, Griffen BD. 2011. Experimental demonstration of a two-phase population extinction hazard. *J R Soc Interface R Soc.* 8(63):1472–1479. doi:10.1098/rsif.2011.0024.
- Fauvergue X, Vercken E, Malausa T, Hufbauer RA. 2012. The biology of small, introduced populations, with special reference to biological control. *Evol Appl.* 5(5):424–443. doi:10.1111/j.1752-4571.2012.00272.x.
- Gertzen EL, Leung B, Yan ND. 2011. Propagule pressure, Allee effects and the probability of establishment of an invasive species (*Bythotrephes longimanus*). *Ecosphere.* 2(3):UNSP 30. doi:10.1890/ES10-00170.1.
- Gregory SD, Bradshaw CJA, Brook BW, Courchamp F. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology.* 91(7):2151–2161.

Hutchings JA. 2015. Thresholds for impaired species recovery. *Proc R Soc B*. 282(1809):20150654. doi:10.1098/rspb.2015.0654.

Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON. 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature*. 444(7117):361–363. doi:10.1038/nature05242.

Kaul RB, Kramer AM, Dobbs FC, Drake JM. 2016. Experimental demonstration of an Allee effect in microbial populations. *Biol Lett*. 12(4):20160070. doi:10.1098/rsbl.2016.0070.

Kramer AM, Dennis B, Liebhold AM, Drake JM. 2009. The evidence for Allee effects. *Popul Ecol*. 51(3):341–354. doi:10.1007/s10144-009-0152-6.

Lande R. 1988. Genetics and demography in biological conservation. *Science*. 241(4872):1455–1460. doi:10.1126/science.3420403.

Lande R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. *Am Nat*. 142(6):911–927.

Lande R. 1998. Demographic Stochasticity and Allee Effect on a Scale with Isotropic Noise. *Oikos*. 83(2):353–358. doi:10.2307/3546849.

Lewis MA, Kareiva P. 1993. Allee dynamics and the spread of invading organisms. *Theor Popul Biol*. 43(2):141–158.

Liebhold AM, Bascompte J. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecol Lett*. 6(2):133–140.

May RM. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, New Jersey: Princeton University Press.

Melbourne BA. 2012. Demographic stochasticity. In: Hastings A, Gross L, editors. *Encyclopedia of Theoretical Ecology*. p. 706–712.

Molnár PK, Lewis MA, Derocher AE. 2014. Estimating Allee Dynamics before They Can Be Observed: Polar Bears as a Case Study. *PLoS ONE*. 9(1). doi:10.1371/journal.pone.0085410. [accessed 2018 Jun 4]. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3888426/>.

R Core Team. 2017. R: a language and environment for statistical computing. <https://www.R-project.org/>.

Roth G, Schreiber SJ. 2014. Pushed beyond the brink: Allee effects, environmental stochasticity, and extinction. *J Biol Dyn*. 8(1):187–205. doi:10.1080/17513758.2014.962631.

Sinclair JS, Arnott SE. 2016. Strength in size not numbers: propagule size more important than number in sexually reproducing populations. *Biol Invasions*. 18(2):497–505. doi:10.1007/s10530-015-1022-0.

Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B. 2018. Package 'glmmADMB'. Generalized Linear Mixed Models using 'AD Model Builder'. Version 0.8.3.4. <http://glmmadmb.r-forge.r-project.org>, <http://admb-project.org>.

Tobin PC, Berec L, Liebhold AM. 2011. Exploiting Allee effects for managing biological invasions. *Ecol Lett.* 14(6):615–624. doi:10.1111/j.1461-0248.2011.01614.x.

Tobin PC, Whitmire SL, Johnson DM, Bjornstad ON, Liebhold AM. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecol Lett.* 10(1):36–43. doi:10.1111/j.1461-0248.2006.00991.x.

Veit RR, Lewis MA. 1996. Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *Am Nat.* 148(2):255–274.

Vercken E, Vincent F, Mailleret L, Ris N, Tabone E, Fauvergue X. 2013. Time-lag in extinction dynamics in experimental populations: evidence for a genetic Allee effect? *J Anim Ecol.* 82(3):621–631. doi:10.1111/1365-2656.12051.

Wang MH, Kot M. 2001. Speeds of invasion in a model with strong or weak Allee effects. *Math Biosci.* 171(1):83–97.

Wittmann MJ, Stuis H, Metzler D. 2018. Genetic Allee effects and their interaction with ecological Allee effects. *J Anim Ecol.* 87(1):11–23. doi:10.1111/1365-2656.12598.

Wood S. 2018. Package 'mgcv'. Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. Version 1.8-24.