

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

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## ABSTRACT

Because Allee effects (i.e., the presence of positive density-dependence at low population size or density) 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 30 populations of *Trichogramma* wasps raised under similar conditions, of which 8 were subject to an Allee effect. We showed that these 8 populations were also characterized by lower maximum growth rate and lower population size, 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

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## INTRODUCTION

33 Allee effects (or “demographic” Allee effects, Stephens et al. 1999) characterize small  
34 populations in which *per capita* performance increases with population density, a  
35 phenomenon also known as positive density-dependence (Odum and Allee 1954, Dennis  
36 1989; Courchamp et al. 2008). Consequently, populations subject to Allee effects have lower  
37 per capita growth rates when population density decreases. In some cases, referred to as a  
38 “strong” Allee effects, there is a critical density threshold below which the population declines  
39 and ultimately goes extinct. In contrast, in presence of “weak” Allee effects, population  
40 growth is reduced at low density but always remains positive (Courchamp et al. 2008). As the  
41 presence of an Allee effect is often considered a major risk factor for population extinction  
42 (Lande 1988; Boukal and Berec 2002), Allee effects are commonly included in population  
43 dynamics models for the management of small populations, either for conservation or  
44 management purposes (Tobin et al. 2011; Molnár et al. 2014; Hutchings 2015; Wittmann et  
45 al. 2018; Bajeux et al. 2019). One of the most common heuristic population dynamics model  
46 accounting for an Allee effect is a modified version of the logistic model (Lewis and Kareiva  
47 1993; Amarasekare 1998; Boukal and Berec 2002, with analogous models existing in discrete  
48 time, Liebhold and Bascompte 2003; Tobin et al. 2007) that reads:

$$49 \quad \frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) \left(\frac{x-A}{K}\right) \quad (1)$$

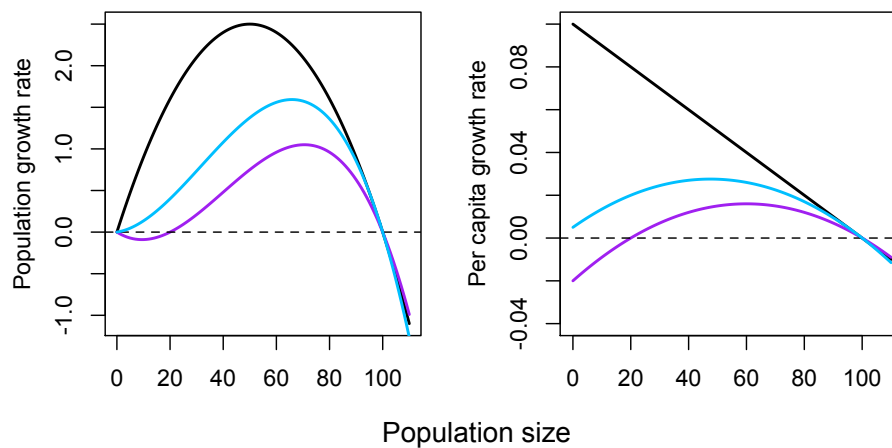
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51 where  $A$  quantifies the severity of the Allee effect (weak Allee effect for  $A \in (-K, 0]$ ; strong  
52 Allee effect for  $A \in (0, K)$ ),  $r > 0$  is the maximum per capita population growth rate in the  
53 corresponding logistic model, and  $K$  the carrying capacity.

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55 However, this modified structure impacts in return several key population properties, with  
56 potential significant consequences beyond the mere presence of positive density-  
57 dependence. For instance, when theoretical parameters  $r$  and  $K$  are held constant, the  
58 maximum value reached by the per capita growth rate  $\frac{1}{x} \frac{dx}{dt}$  over  $x$  is always lower in  
59 populations subject to an Allee effect as described by the model above than in populations  
60 following a logistic model (Courchamp et al. 2008; Drake and Kramer 2011). A direct  
61 consequence of this lower growth rate is that the establishment or growth phase of an initially

62 small population, in which the population is most vulnerable to stochastic influences, lasts  
 63 longer in presence of an Allee effect (Veit and Lewis 1996; Dennis 2002; Drake 2004; Sinclair  
 64 and Arnott 2016) and increases with the magnitude of the Allee effect (Bajeux et al. 2019).  
 65 Both these parameters (maximum per capita growth rate and duration of the establishment  
 66 phase) have been shown theoretically and empirically to influence extinction risk (Lande 1993;  
 67 Liebhold and Bascompte 2003; Drake et al. 2011; Cassey et al. 2014). In theoretical analyses  
 68 of population dynamics, populations with an Allee effect are thus characterized not only by  
 69 the presence of positive density-dependence, but also by lower maximum growth rate, both  
 70 of which increase the extinction risk of populations.



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

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 76 Because this non-independence between demographic properties arises from the structure  
 77 of population dynamics models like model (1), its relevance in natural populations might be  
 78 questioned. Yet a demographic Allee effect reveals specific processes internal to the  
 79 population, so it is likely to correlate with other components of population dynamics, like  
 80 growth rate or carrying capacity. Such characteristics might then add up or even interact to  
 81 increase the probability of population extinction. Alternatively, if the presence of an Allee  
 82 effect is independent in practice from other demographic properties, it implies that the  
 83 extinction risk related to positive density-dependence only might have been overestimated in  
 84 theoretical studies.

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86 A major difficulty in addressing this issue is to find independent populations whose life  
87 histories are close enough to allow quantitative comparisons of demographic properties, but  
88 that still present variation regarding the Allee effect. Previous studies that aimed at estimating  
89 the frequency of Allee effects by analyzing population time series from several species found  
90 very little evidence of Allee effects (Myers et al. 1995; Saether et al. 1996; Gregory et al. 2010).  
91 However, as these approaches were based on model-fitting, they were constrained by the  
92 structure of the models they used. In these studies, either several alternative models were  
93 compared (some including negative density-dependence only, others including also positive  
94 density-dependence, see for instance Gregory et al. 2010), or a generic model allowing for  
95 some degree of positive density-dependence was fitted and the presence of an Allee effect  
96 was derived from the estimates of model parameters (Myers et al. 1995; Perälä and Kuparinen  
97 2017). Yet, while such theoretical models are extremely useful to examine the theoretical  
98 consequences of Allee effects on population eco-evolutionary dynamics, there is no reason  
99 why real populations should comply with their underlying hypotheses (e.g., continuous  
100 density-dependent response, negative quadratic relationship). This is especially true for  
101 models that don't aim at fitting closely to the ecology of a given population (for which enough  
102 prior knowledge might exist to allow for an informed decision about modelling), but at  
103 comparing general patterns across populations or species.

104 An alternative method to detect Allee effects from population time series might be to test for  
105 the presence of positive density-dependence in the per capita growth rate at low density,  
106 without any a priori on the shape of the general density-dependence function (see for instance  
107 Stenglein and Deelen 2016). For this purpose, we analyzed the relationship between per capita  
108 growth rate and population size in 30 populations of parasitoid wasps of the genus  
109 *Trichogramma* using generalized additive models that allow the fitting of smooth relationships  
110 using spline functions. We detected positive density-dependence at low population size, i.e.  
111 the presence of an Allee effect, in 8 of these populations. Then we compared the demographic  
112 performance – maximum growth rate, population size, and extinction probability - of these  
113 populations to those without an Allee effect. This privileged experimental system allowed us  
114 to demonstrate that general components of population dynamics correlate with the presence  
115 of an Allee effect, which increases the extinction probability of the populations.

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## 117 METHODS

### 118 **Biological model**

119 We used parasitoid wasps of the genus *Trichogramma* as biological models. Our study  
120 populations were provided by the Biological Resource Center EP-Coll  
121 ([doi.org/10.15454/AY4LMT](https://doi.org/10.15454/AY4LMT)), specialized in egg parasitoids. 30 populations were chosen from  
122 a set of 70 populations collected in the field in 2015 to evaluate the diversity of *Trichogramma*  
123 in France (D. Muru, unpublished data). Detailed information on each population is available in  
124 Supplementary Material ([doi.org/10.5281/zenodo.4650051](https://doi.org/10.5281/zenodo.4650051), Table S1). A “population” was  
125 defined as individuals sampled on the same plant in a given locality, so that several  
126 populations could have been collected from the same locality. Seven species were included in  
127 the 30 selected populations: *T. brassicae* (2 populations), *T. cacoeciae* (16), *T. cordubensis* (3),  
128 *T. euproctidis* (2), *T. evanescens* (2), *T. principium* (1), *T. semblidis* (4). *Trichogramma* are  
129 haplodiploids, i.e. females are diploid and males are haploid. However, some species are  
130 arrhenotokous (sexual reproduction is needed to produce diploid females, and unfertilized  
131 eggs develop into males, like *T. brassicae*, *T. euproctidis*, *T. evanescens*, *T. principium*, *T.*  
132 *semblidis*), while others are thelytokous (*T. cacoeciae* and *T. cordubensis*, where females  
133 reproduce clonally).

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### 135 **Monitoring of population dynamics**

136 *Trichogramma* are minute solitary parasitoids of Lepidopteran eggs that can be reared in small  
137 volumes. Experimental population units were housed in plastic tubes (diameter 50 mm, length  
138 100 mm). Food for adults was provided ad libitum as drops of honey placed on the tube walls.  
139 Hosts for reproduction were provided as 3 mm-diameter patches of *Ephestia kuehniella* eggs  
140 glued on paper strips (10 egg patches at each generation; average number of eggs on a patch  
141 and 95% confidence interval: 458 [445–471]). Eggs of *E. kuehniella* were irradiated previously,  
142 which prevented host development while allowing parasitoid development. For this  
143 experiment, temperature and light conditions were set on a cycle of 16 h daylight (22 °C)/8 h  
144 dark (20 °C) with constant 70% humidity. Under these conditions, generation time was 14 days  
145 for all populations.

146 Each population was replicated 8 times, each replicated corresponding to increasing levels of  
147 initial density (each replicate being founded with 10-12-14-16-18-20-25 or 30 parasitized

148 eggs). Because of asynchrony in emergence, the different populations were distributed into 6  
149 experimental blocks, spread over 2 consecutive weeks. At emergence, fresh host eggs were  
150 introduced in the tubes and exposed 48h to parasitism, then put aside for parasitoid  
151 development until the emergence of the next generation. Population size at the next  
152 generation was estimated by counting the total number of parasitized eggs before emergence.  
153 Parasitized eggs turn black when the parasitoid reaches the nymphal stage and the number of  
154 black eggs directly reflects adult population size at emergence. At the beginning of emergence,  
155 fresh host patches were introduced in the tubes and similarly exposed during 48 h to obtain  
156 the next parasitoid generation. Parasitoid population dynamics were monitored during three  
157 generations after introduction between January and March 2016. Time series of population  
158 dynamics are provided as Supplementary Material ([doi.org/10.5281/zenodo.3963856](https://doi.org/10.5281/zenodo.3963856), Figure  
159 S1). All replicates from one *T. cordubensis* population went extinct at the first generation (see  
160 Figure S1), and it was removed from further analyses. The final dataset thus included 29  
161 populations only.

## 162 **Detection of Allee effects**

163 The presence of an Allee effect is indicated by a positive correlation between population size  
164 and per capita growth rate, but usually present for small population sizes only. To account for  
165 the potential non-linearity in density-dependence of the per capita growth rate, we fitted a  
166 thin-plate regression spline on the relationship between  $N_{t+1}$  (population size at generation  
167  $t+1$ ) and  $N_t$  (population size at generation  $t$ ) using general additive models (package ‘mgcv’,  
168 Wood 2018) in R (R Core Team 2017). The function ‘gam’ fits penalized regression splines, and  
169 the optimal degree of smoothness is determined using generalized cross-validation (Wood  
170 2006). To avoid overfitting, we set an upper limit for the smooth term at 7 degrees of freedom  
171 (dimension parameter  $k=8$ ).

172 The definition of the per capita growth rate  $\lambda(N_t) = \frac{N_{t+1}}{N_t}$  transcribed into the following  
173 model:  $N_{t+1} \sim s(N_t) + \text{offset}(\log(N_t))$   
174  $N_{t+1}$  followed a Poisson distribution with a log link to the linear predictors, so that the smooth  
175 function  $s(N_t)$  was directly equal to the log of per capita growth rate  $\lambda_t$ . We acknowledged the  
176 presence of an Allee effect for the population if the fitted function was strictly non-monotonic  
177 within the 95% confidence bands, with a maximum  $s(N_t)$  for an intermediate value of  
178 population size.

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

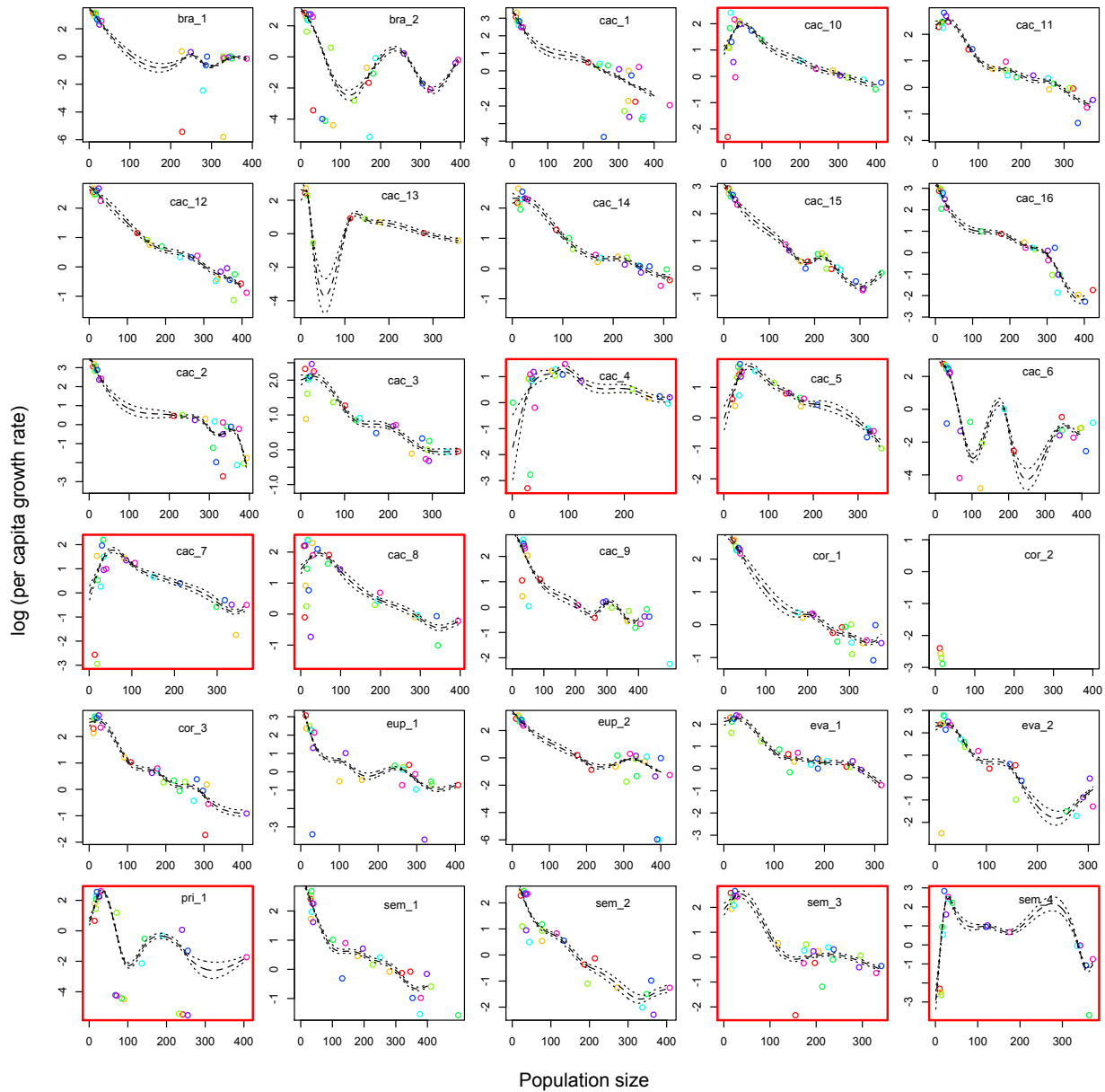
Population dynamics were characterized in each replicate by the maximum per capita growth rate, the maximum and mean population size across all 3 generations for non-extinct populations. These three variables followed Normal distributions and were analyzed using linear mixed models. We also computed the probability of extinction of a replicate, which followed a binomial distribution and was analyzed with a generalized linear mixed models. In order to evaluate potential differences in the amount of demographic stochasticity between the different populations, we estimated the variance between replicates by computing the sum of squares between non-extinct replicates of the same population at the first generation. This variable followed a negative binomial distribution and was analyzed with a generalized linear mixed models. Both linear mixed models and generalized linear mixed models were fitted using the R package 'lme4' (Bates et al. 2015) using Maximum Likelihood estimation following (Zuur et al. 2009). For all variables, a full model, including the presence of an Allee effect as a fixed factor and population nested within species as a random effect, was compared with a null model including the random effect only using a likelihood ratio 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)).

202 RESULTS

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204 Out of the 30 populations analyzed, 8 displayed an Allee effect (5 populations from *T.*  
 205 *cacoeciae*, 1 population from *T. principium*, 2 population from *T. semblidis*, Figure 2).

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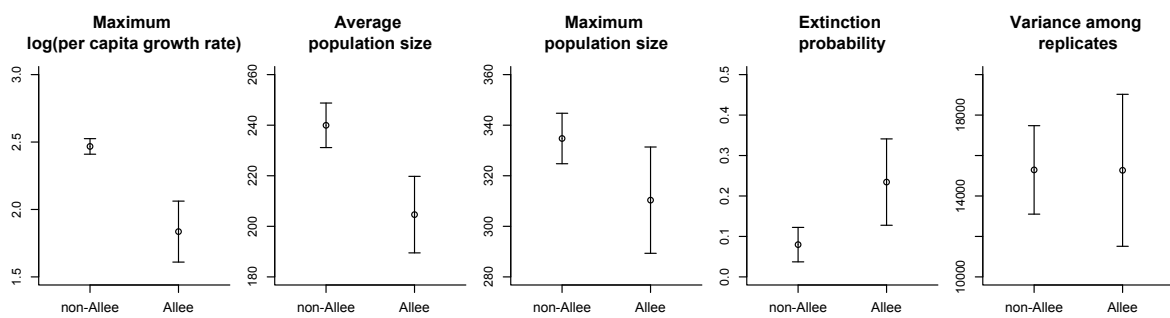
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208 Figure 2: Raw data (circle of the same color belong to the same experimental replicate) and  
 209 GAM fits (dashed lines: predicted values ; dotted lines: 95% confidence intervals around  
 210 prediction) for the relationship between population size and per capita growth rate.  
 211 Experimental data were modified as  $\log\left(\frac{N_{t+1}+1}{N_t}\right)$  so that extinction events could be  
 212 represented. Red boxes: populations characterized by an Allee effect.



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Population dynamics were found to be markedly different between Allee and non-Allee populations (Figure 3). Allee populations were characterized by lower maximum per capita growth rate ( $p=1.4 \times 10^{-4}$ ), lower mean population size ( $p=0.013$ ), and higher extinction probability ( $p=7.6 \times 10^{-3}$ ). Maximum population size was also marginally smaller ( $p=0.06$ ). There was no difference in the variability among replicates between Allee and non-Allee populations ( $p=0.98$ ).



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222 Figure 3: Comparison of demographic parameters between populations with or without an  
223 Allee effect. All graphs represent mean +/- 2 SE.

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## 227 DISCUSSION

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Our analysis demonstrated the presence of an Allee effect in some, but not all, *Trichogramma*  
230 populations raised in laboratory conditions. This finding further confirms that Allee effects can  
231 operate in small volumes and affect population persistence even in favourable, controlled  
232 conditions (Gertzen et al. 2011; Kaul et al. 2016). Unlike most classical experimental  
233 microcosm systems (e.g., *Tribolium*, *Daphnia*, *Tetrahymena*), our collection of *Trichogramma*  
234 populations allows us to compare a diversity of populations with similar life-histories and  
235 raised under the same conditions, in order to single out the impact of the presence or absence  
236 of an Allee effect. In this study, we found that *Trichogramma* populations for which an Allee  
237 effect was detected were characterized by qualitatively different dynamics from populations  
238 with no Allee effect, with lower per capita growth rate, lower population size and increased  
239 extinction probability. The demographic parameters correlated with the presence of an Allee  
240 effect have direct consequences on short-term extinction risk. Indeed, low per capita growth

241 rates and low population sizes interact to maintain the population in a unfavorable  
242 demographic zone, where it is most vulnerable to extinction through the influence of genetic,  
243 demographic, and environmental stochasticity (Dennis et al. 2015).

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245 This high-risk, low-density phase, might be transitory when a newly founded population  
246 struggles to establish, but it might also be encountered more regularly, for instance during  
247 recovery phases after a perturbation. Modelling results and empirical data from fish stock  
248 populations show that the presence of an Allee effect delays population recovery after a major  
249 decline, such that a population could stay at a low level for a long time where its vulnerability  
250 to external stressors and therefore its extinction risk were substantially increased (Kuparinen  
251 et al. 2014).

252 Expanding populations are also exposed to repeated low-density phases at every new  
253 colonization beyond the occupied area. It is already widely acknowledged that populations  
254 subject to an Allee effect experiment colonization failures when the number of migrants for a  
255 new colonization event falls below the critical threshold population persistence, which  
256 reduces their spread rate (Lewis and Kareiva 1993; Kot et al. 1996; Wang and Kot 2001).  
257 However, if population growth is also reduced even at intermediate densities, it will take  
258 longer for a newly colonized population to reach a large enough size so it can send enough  
259 migrants to overcome the colonization threshold and proceed with the expansion. Indeed, in  
260 a simulation study, Walter et al. (2017) showed that expanding populations with lower Allee  
261 thresholds were characterized by shorter colonization times and higher population densities.

262 In addition to these direct effects of low population size and reduced population growth, this  
263 prolonged demographic bottleneck in presence of an Allee effect might increase genetic drift  
264 and inbreeding, so that even populations that manage to reach carrying capacity will suffer  
265 from higher long-term extinction risk (Fauvergue et al. 2012). This special case of genetic  
266 extinction debt was previously reported in laboratory populations of a different species of  
267 *Trichogramma* (Vercken et al. 2013). Furthermore, even parameters related to equilibrium  
268 dynamics (like maximum population size) differed between Allee and non-Allee populations.  
269 This suggests that the influence of the Allee effect on population dynamics may persist beyond  
270 the early establishment phase and affect the demographic trajectory over wide ranges of  
271 densities.

273 In our case, the mechanism responsible for the presence of positive density-dependence in  
274 some populations has not been identified. Out of the eight populations subject to an Allee  
275 effect, five belong to the species *T. cacoeciae* that is strictly parthenogenous. Mate limitation  
276 is thus unlikely to be the main factor impairing population performance at small density in our  
277 system, although it could still play a role in the other three populations. In sexual populations  
278 of *Trichogramma*, sex-ratio is usually female-biased (between 60-80% of individuals being  
279 females, Martel 2003). This means that, in small populations, the number of males may be too  
280 low to mate all females, especially when mating is allowed for a limited time as was the case  
281 in our experimental system. Such populations are arrhenotokous, i.e. unmated females may  
282 still produce male offspring, so that mate limitation should not theoretically affect the  
283 population growth rate and the number of eggs produced at the next generation. However,  
284 several studies on arrhenotokous parasitoids have shown that unmated females lay fewer  
285 eggs, especially in the beginning of their adult life (Fauvergue et al. 2008; Abe et al. 2010),  
286 which may have played a role in the emergence of positive density-dependence in our  
287 populations of *T. principium* and *T. semblidis*. In addition to this first mechanism, patch  
288 exploitation strategy and parasitism pattern in both sexual and asexual populations of  
289 *Trichogramma* might have responded to conspecific density. Direct observations of  
290 oviposition behavior suggest that females may adjust their oviposition rate to the competition  
291 level they experience: females reared in isolation will wait longer before they start laying eggs  
292 and examine host eggs suitability more thoroughly than females reared in group (G. Groussier,  
293 pers. obs). Furthermore, previous results on *T. minutum* showed that female search rate and  
294 residence time on a patch are increased in presence of conspecifics (Mills and Lacan 2004;  
295 Robert et al. 2016), which should increase parasitism rate in a single-patch context. In  
296 contrast, Robert et al. (2016) found no response of *T. petoi* to intraspecific competition, which  
297 confirms that major differences in patterns of density-dependence may emerge between  
298 *Trichogramma* species.

299  
300 Apparent positive density-dependence may also emerge in some cases even in the absence  
301 of specific ecological mechanisms. Demographic stochasticity in particular may introduce an  
302 unstable equilibrium at low population size below which most population trajectories tend to  
303 decline towards extinction (Lande 1998; Saether and Engen 2004). However, such a  
304 phenomenological Allee-like effect does not seem to be the most likely explanation to our

305 results. First, positive density-dependence was detected on population growth rate and not  
306 on extinction probability, which does fit the original definition by Odum and Allee (1954) and  
307 is considered as a generic evidence for the presence of an Allee effect (Johnson et al. 2006;  
308 Kramer et al. 2009; Gregory et al. 2010). Second, the dispersion of data at low density does  
309 not support the hypothesis of an extreme variability driving artefactually the signal of positive  
310 density-dependence (Figure 2). While it remains undeniable that population dynamics at low  
311 density are subject to complex interactions between the Allee effect and stochastic forces, we  
312 are confident that our findings reflect true variation in density-dependence among  
313 *Trichogramma* populations.

314  
315 Independently of the mechanisms responsible for the emergence of an Allee effect, its weak  
316 or strong nature is expected to induce major qualitative differences in dynamics in theoretical  
317 models related to the existence of an unstable equilibrium in the case of a strong Allee effect  
318 (Dennis 1989; Lewis and Kareiva 1993; Wang and Kot 2001). In practice however, the  
319 distinction between weak and strong Allee effect in empirical data relies on the quantitative  
320 estimation of the per capita growth rate at small density, where stochastic variance is the  
321 highest and therefore the estimation is least precise (Kramer et al. 2009). Among our eight  
322 Allee populations, two have an estimated growth rate inferior to 1 at low density (i.e., negative  
323 values for the log of the per capita growth rate, see Fig. 2), four have a growth rate strictly  
324 superior to 1 at low density, while the remaining two have confidence intervals large enough  
325 to include 1, i.e. compatible with both weak and strong Allee effect. Furthermore, estimations  
326 of Allee effects in nature have demonstrated that the intensity of the Allee effect is context-  
327 dependent and can vary geographically (Tobin et al. 2007), while results from stochastic  
328 models have demonstrated that weak Allee effects can be amplified by stochasticity  
329 (demographic or environmental) so as to induce a lower unstable equilibrium, similar to an  
330 Allee threshold (Roth and Schreiber 2014; Dennis et al. 2015). This converging evidence  
331 suggests that the dichotomous distinction of weak and strong Allee effect, though essential in  
332 deterministic theoretical approaches, might be less relevant in stochastic modelling or in  
333 nature where the “strength” or “intensity” of an Allee effect could be quantified continuously.

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336 These results provide the first empirical demonstration of a correlation between the presence  
337 of positive density-dependence and impaired demographic performance during  
338 establishment phase. If the presence of an Allee effect is correlated with other demographic  
339 parameters, in particular the maximum per capita growth rate, then it remains a major risk  
340 factor for population extinction, even in the case of a weak Allee effect, or if the population  
341 introduced is superior to the theoretical Allee threshold for a strong Allee effect. The non-  
342 independence between these demographic parameters is thus likely to be of critical  
343 importance for [predictions of dynamics and extinction risk of any population subject to low-](#)  
344 [density stages, like expanding populations, periodic systems, and populations subject to](#)  
345 [environmental perturbations or extinction-colonization events.](#)

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#### 359 **References**

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- 361 Abe J, Innocent TM, Reece SE, West SA. 2010. Virginity and the clutch size behavior of a  
362 parasitoid wasp where mothers mate their sons. *Behav Ecol Off J Int Soc Behav Ecol.*  
363 21(4):730–738. doi:10.1093/beheco/arq046.
- 364 Amarasekare P. 1998. Allee effects in metapopulation dynamics. *Am Nat.* 152(2):298–302.  
365 doi:10.1086/286169.
- 366 Bajeux N, Grogard F, Mailleret L. 2019. Influence of the components of propagule pressure,  
367 Allee effects, and stochasticity on the time to establish introduced populations. *J Theor Biol.*  
368 471:91–107. doi:10.1016/j.jtbi.2019.03.012.
- 369 Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using  
370 lme4. *J Stat Softw.* 67(1):1–48. doi:10.18637/jss.v067.i01.
- 371 Boukal DS, Berec L. 2002. Single-species Models of the Allee Effect: Extinction Boundaries,  
372 Sex Ratios and Mate Encounters. *J Theor Biol.* 218(3):375–394. doi:10.1006/jtbi.2002.3084.
- 373 Cassey P, Prowse TAA, Blackburn TM. 2014. A population model for predicting the

374 successful establishment of introduced bird species. *Oecologia*. 175(1):417–428.  
375 doi:10.1007/s00442-014-2902-1.

376 Courchamp F, Berec L, Gascoigne J. 2008. Allee effects in ecology and conservation. Oxford,  
377 England: Oxford University Press.

378 Dennis B. 1989. Allee effects: population growth, critical density, and the chance of  
379 extinction. *Nat Resour Model*. 3:481–538.

380 Dennis B. 2002. Allee Effects in Stochastic Populations. *Oikos*. 96(3):389–401.

381 Dennis B, Assas L, Elaydi S, Kwessi E, Livadiotis G. 2015. Allee Effects and Resilience in  
382 Stochastic Populations. *Theor Ecol*. 9. doi:10.1007/s12080-015-0288-2.

383 Drake JM. 2004. Allee effects and the risk of biological invasion. *Risk Anal Off Publ Soc*  
384 *Risk Anal*. 24(4):795–802. doi:10.1111/j.0272-4332.2004.00479.x.

385 Drake JM, Kramer AM. 2011. Allee Effects. *Nat Educ Knowl*. 3(10):2.

386 Drake JM, Shapiro J, Griffen BD. 2011. Experimental demonstration of a two-phase  
387 population extinction hazard. *J R Soc Interface R Soc*. 8(63):1472–1479.  
388 doi:10.1098/rsif.2011.0024.

389 Fauvergue X, Lo Genco A, Lo Pinto M. 2008. Virgins in the Wild: Mating Status Affects the  
390 Behavior of a Parasitoid Foraging in the Field. *Oecologia*. 156(4):913–920.

391 Fauvergue X, Vercken E, Malausa T, Hufbauer RA. 2012. The biology of small, introduced  
392 populations, with special reference to biological control. *Evol Appl*. 5(5):424–443.  
393 doi:10.1111/j.1752-4571.2012.00272.x.

394 Gertzen EL, Leung B, Yan ND. 2011. Propagule pressure, Allee effects and the probability of  
395 establishment of an invasive species (*Bythotrephes longimanus*). *Ecosphere*. 2(3):UNSP 30.  
396 doi:10.1890/ES10-00170.1.

397 Gregory SD, Bradshaw CJA, Brook BW, Courchamp F. 2010. Limited evidence for the  
398 demographic Allee effect from numerous species across taxa. *Ecology*. 91(7):2151–2161.

399 Hutchings JA. 2015. Thresholds for impaired species recovery. *Proc R Soc B*.  
400 282(1809):20150654. doi:10.1098/rspb.2015.0654.

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

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

405 Kot M, Lewis MA, Van Den Driessche P. 1996. Dispersal data and the spread of invading  
406 organisms. *Ecology*. 77(7):2027–2042.

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

409 Kuparinen A, Keith DM, Hutchings JA. 2014. Allee Effect and the Uncertainty of Population  
410 Recovery. *Conserv Biol*. 28(3):790–798. doi:10.1111/cobi.12216.

411 Lande R. 1988. Genetics and demography in biological conservation. *Science*.  
412 241(4872):1455–1460. doi:10.1126/science.3420403.

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

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

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

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

421 Martel V. 2003. Sex allocation and mating structure in the egg parasitoids of the genus  
422 *Trichogramma* (Hymenoptera: Trichogrammatidae). Montréal: Mc Gill University (PhD  
423 Thesis).

424 Mills NJ, Lacañ I. 2004. Ratio dependence in the functional response of insect parasitoids:  
425 evidence from *Trichogramma minutum* foraging for eggs in small host patches. *Ecol*  
426 *Entomol.* 29(2):208–216. doi:10.1111/j.0307-6946.2004.00584.x.

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

430 Myers RA, Barrowman NJ, Hutchings JA, Rosenberg AA. 1995. Population Dynamics of  
431 Exploited Fish Stocks at Low Population Levels. *Science.* 269(5227):1106–1108.  
432 doi:10.1126/science.269.5227.1106.

433 Odum HT, Allee WC. 1954. A Note on the Stable Point of Populations Showing Both  
434 Intraspecific Cooperation and Disoperation. *Ecology.* 35(1):95–97.  
435 doi:<https://doi.org/10.2307/1931412>.

436 Perälä T, Kuparinen A. 2017. Detection of Allee effects in marine fishes: analytical biases  
437 generated by data availability and model selection. *Proc R Soc B Biol Sci.*  
438 284(1861):20171284. doi:10.1098/rspb.2017.1284.

439 R Core Team. 2017. R: a language and environment for statistical computing. [https://www.R-](https://www.R-project.org/)  
440 [project.org/](https://www.R-project.org/).

441 Robert F-A, Brodeur J, Boivin G. 2016. Patch exploitation by non-aggressive parasitoids  
442 under intra- and interspecific competition. *Entomol Exp Appl.* 159:n/a-n/a.  
443 doi:10.1111/eea.12429.

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

446 Saether B-E, Engen S. 2004. Stochastic population theory faces reality in the laboratory.  
447 *Trends Ecol Evol.* 19:351–3. doi:10.1016/j.tree.2004.05.003.

448 Saether B-E, Ringsby T, Røskaft E. 1996. Life History Variation, Population Processes and  
449 Priorities in Species Conservation: Towards a Reunion of Research Paradigms. *Oikos.*  
450 77:217–226. doi:10.2307/3546060.

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

454 Stenglein JL, Deelen TRV. 2016. Demographic and Component Allee Effects in Southern  
455 Lake Superior Gray Wolves. *PLOS ONE.* 11(3):e0150535.  
456 doi:10.1371/journal.pone.0150535.

457 Stephens PA, Sutherland WJ, Freckleton RP. 1999. What Is the Allee Effect? *Oikos.*  
458 87(1):185–190.

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

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

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

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

469 Walter JA, Johnson DM, Haynes KJ. 2017. Spatial variation in Allee effects influences  
470 patterns of range expansion. *Ecography.* 40(1):179–188.  
471 doi:<https://doi.org/10.1111/ecog.01951>.

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

474 Wittmann MJ, Stuis H, Metzler D. 2018. Genetic Allee effects and their interaction with  
475 ecological Allee effects. *J Anim Ecol.* 87(1):11–23. doi:10.1111/1365-2656.12598.  
476 Wood S. 2018. Package ‘mgcv’. Mixed GAM Computation Vehicle with Automatic  
477 Smoothness Estimation. Version 1.8-24.  
478 Wood SN. 2006. Generalized additive models. Boca Raton, FL.: CRC Press.  
479 Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed Effects Models and  
480 Extensions in Ecology with R. 2009 edition. New York, NY: Springer.  
481