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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

INTRODUCTION

Allee effects (or "demographic" Allee effects, Stephens et al. 1999) characterize small populations in which *per capita* performance increases with population density, a phenomenon also known as positive density-dependence (Odum and Allee 1954, Dennis 1989; Courchamp et al. 2008). Consequently, populations subject to Allee effects have lower per capita growth rates when population density decreases. In some cases, referred to as a "strong" Allee effects, there is a critical density threshold below which the population declines and ultimately goes extinct. In contrast, in presence of "weak" Allee effects, population growth is reduced at low density but always remains positive (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:

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

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

However, this modified structure impacts in return several key population properties, 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 value reached by the per capita growth rate $\frac{1}{x}\frac{dx}{dt}$ over x is always lower in populations subject to an Allee effect as described by the model above than in populations following a logistic model (Courchamp et al. 2008; Drake and Kramer 2011). 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.

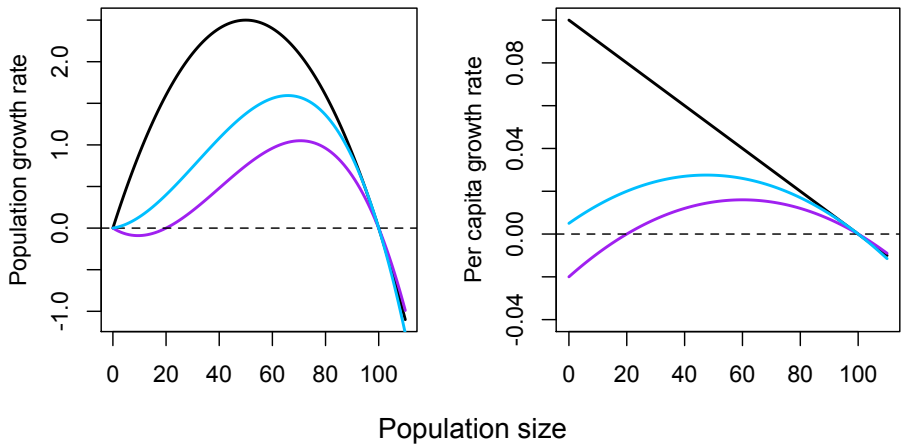

Figure 1: Population growth rate $\frac{dx}{dt}$ (left) and per capita growth rate $\frac{1}{x}\frac{dx}{dt}$ (right) for a logistic model (in black), a model with a weak Allee effect (A=-5, in blue) or a model with a strong Allee effect (A=20, in purple) when r=0.1 and K=100. After Drake and Kramer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

Because this non-independence between demographic properties arises from the structure of population dynamics models like model (1), 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 or even interact to increase the probability of population extinction. Alternatively, if the presence of an Allee effect is independent in practice from other demographic properties, 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 whose life histories are close enough to allow quantitative comparisons of demographic properties, but that still present variation regarding the Allee effect. Previous studies that aimed at estimating the frequency of Allee effects by analyzing population time series from several species found very little evidence of Allee effects (Myers et al. 1995; Saether et al. 1996; Gregory et al. 2010). However, as these approaches were based on model-fitting, they were constrained by the structure of the models they used. In these studies, either several alternative models were compared (some including negative density-dependence only, others including also positive density-dependence, see for instance Gregory et al. 2010), or a generic model allowing for some degree of positive density-dependence was fitted and the presence of an Allee effect was derived from the estimates of model parameters (Myers et al. 1995; Perälä and Kuparinen 2017). Yet, while such theoretical models are extremely useful to examine the theoretical consequences of Allee effects on population eco-evolutionary dynamics, there is no reason why real populations should comply with their underlying hypotheses (e.g., continuous density-dependent response, negative quadratic relationship). This is especially true for models that don't aim at fitting closely to the ecology of a given population (for which enough prior knowledge might exist to allow for an informed decision about modelling), but at comparing general patterns across populations or species.

An alternative method to detect Allee effects from population time series might be to test for the presence of positive density-dependence in the per capita growth rate at low density, without any a priori on the shape of the general density-dependence function (see for instance Stenglein and Deelen 2016). For this purpose, we analyzed the relationship between per capita growth rate and population size in 30 populations of parasitoid wasps of the genus *Trichogramma* using generalized additive models that allow the fitting of smooth relationships using spline functions. We detected positive density-dependence at low population size, i.e. the presence of an Allee effect, in 8 of these populations. Then we compared the demographic performance – maximum growth rate, population size, and extinction probability - of these populations to those without an Allee effect. 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.

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), 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, 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).

134

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

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, Figure S1). All replicates from one *T. cordubensis* population went extinct at the first generation (see Figure S1), and it was removed from further analyses. The final dataset thus included 29 populations only.

Detection of Allee effects

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

The definition of the per capita growth rate $\lambda(N_t) = \frac{N_{t+1}}{N_t}$ transcribed into the following model: $N_{t+1} \sim s(N_t) + offset(\log(N_t))$

N_{t+1} followed a Poisson distribution with a log link to the linear predictors, so that the smooth function $s(N_t)$ was directly equal to the log of per capita growth rate λ_t. We acknowledged the presence of an Allee effect for the population if the fitted function was strictly non-monotonic within the 95% confidence bands, with a maximum $s(N_t)$ for an intermediate value of population size.

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).

RESULTS

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

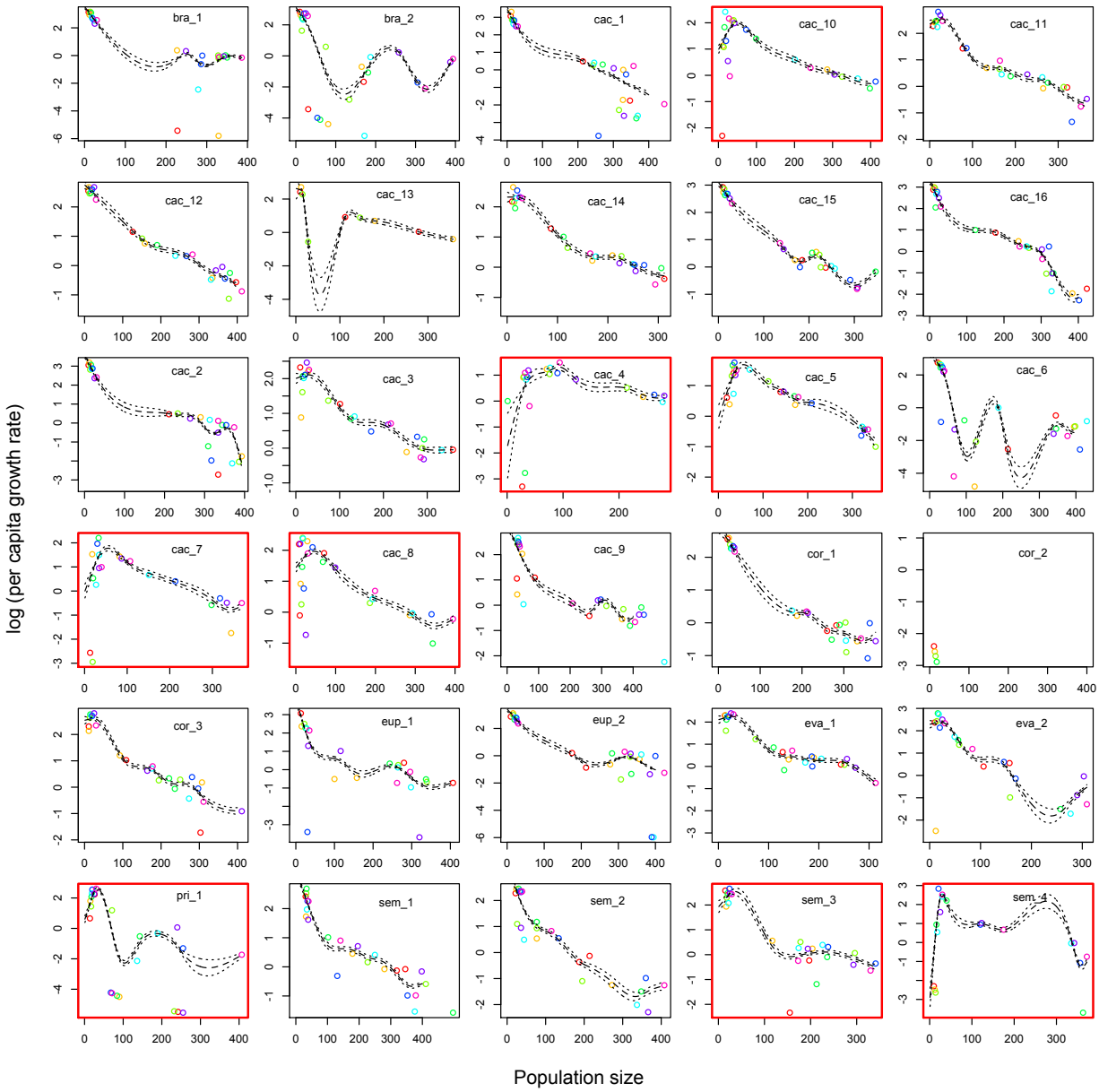

Figure 2: Raw data (circle of the same color belong to the same experimental replicate) and GAM fits (dashed lines: predicted values ; dotted lines: 95% confidence intervals around prediction) for the relationship between population size and per capita growth rate. Experimental data were modified as $log\left(\frac{N_{t+1}+1}{N_t}\right)$ so that extinction events could be represented. 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 per capita growth rate ($p=1.4x10^{-4}$), lower mean population size (p=0.013), and higher extinction probability ($p=7.6x10^{-3}$). 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).

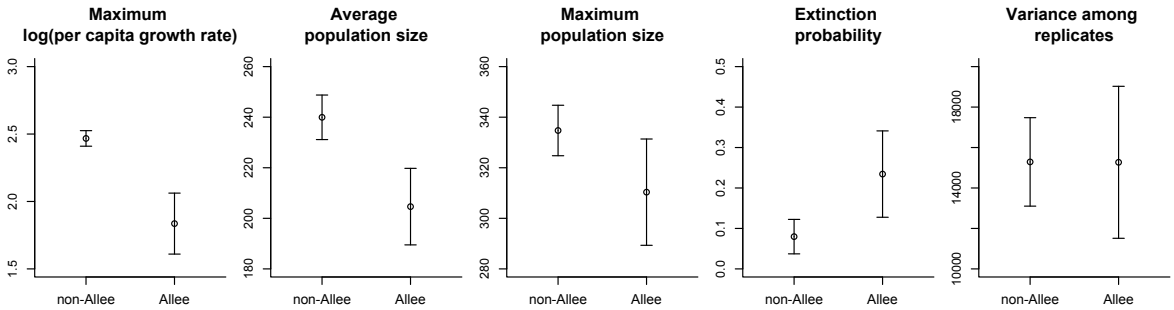

Figure 3: Comparison of demographic parameters between populations with or without an Allee effect. All graphs represent mean +/- 2 SE.

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 a diversity of 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, with lower per capita growth rate, lower population size and increased extinction probability. The demographic parameters correlated with the presence of an Allee 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).
244
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.
272

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.
334
335

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 predictions of dynamics and extinction risk of any population subject to low-density stages, like expanding populations, periodic systems, and populations subject to environmental perturbations or extinction-colonization events.

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