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

Elodie Vercken, Géraldine Groussier, Laurent Lamy, Ludovic Mailleret

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31

32 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:

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

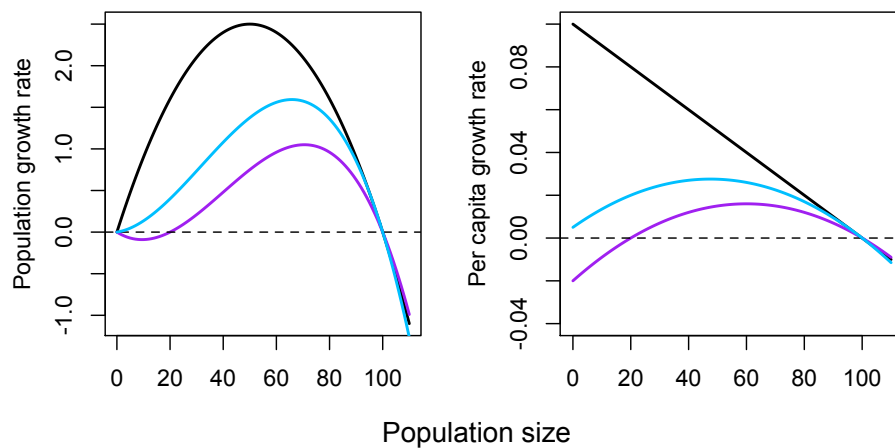
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51 where A quantifies the severity of the Allee effect (weak Allee effect for $A \in (-K, 0]$; strong
52 Allee effect for $A \in (0, K)$), $r > 0$ is the maximum per capita population growth rate in the
53 corresponding logistic model, and K the carrying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

54

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.



71
 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).

75
 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.

85

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.

116

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

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, 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:
$$N_{t+1} \sim s(N_t) + offset(\log(N_t))$$

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 λ_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

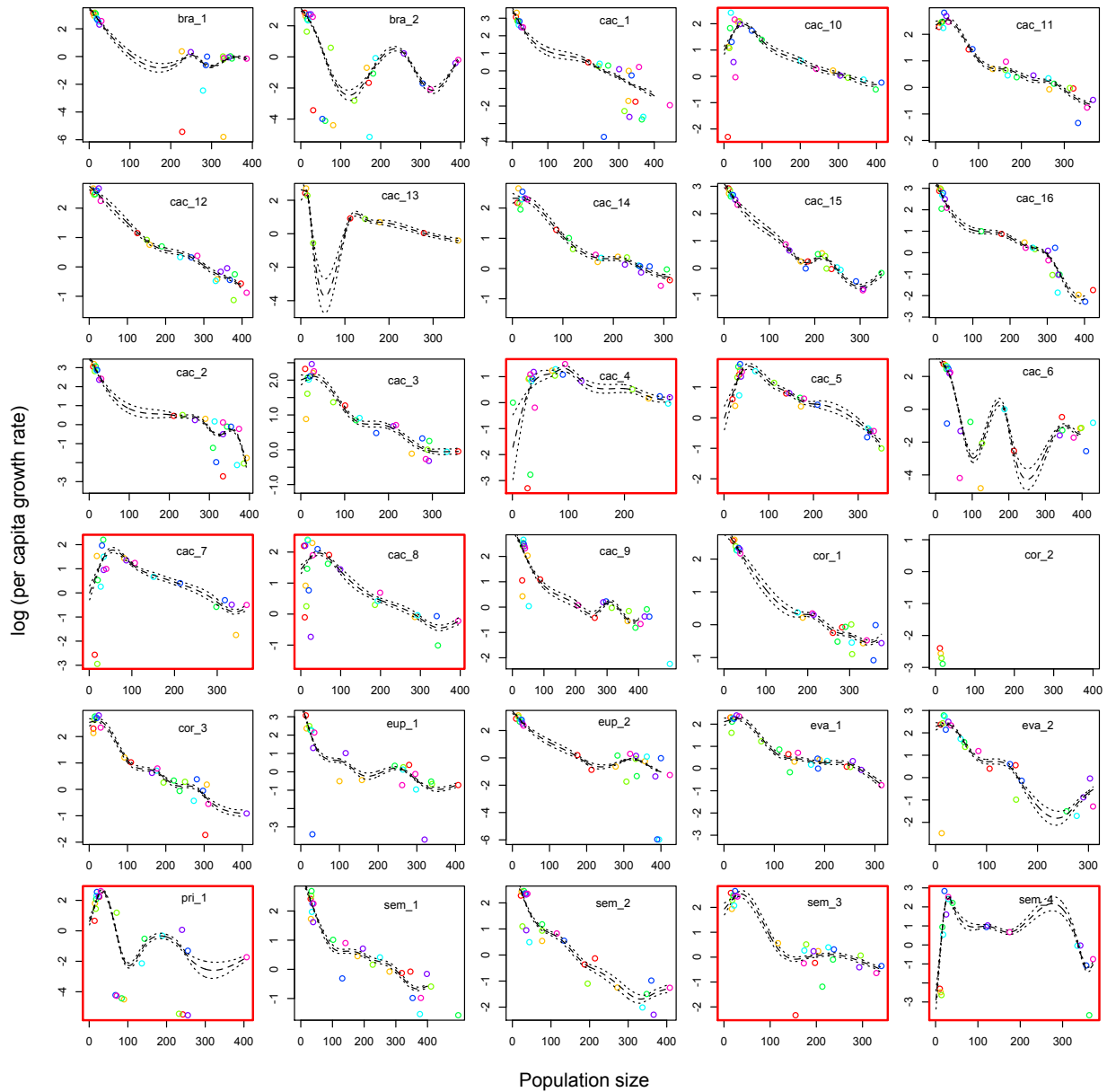
Population dynamics were characterized in each replicate by the maximum per capita growth rate, the maximum and mean population size across all 3 generations for non-extinct populations. These three variables followed Normal distributions and were analyzed using linear mixed models. We also computed 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).

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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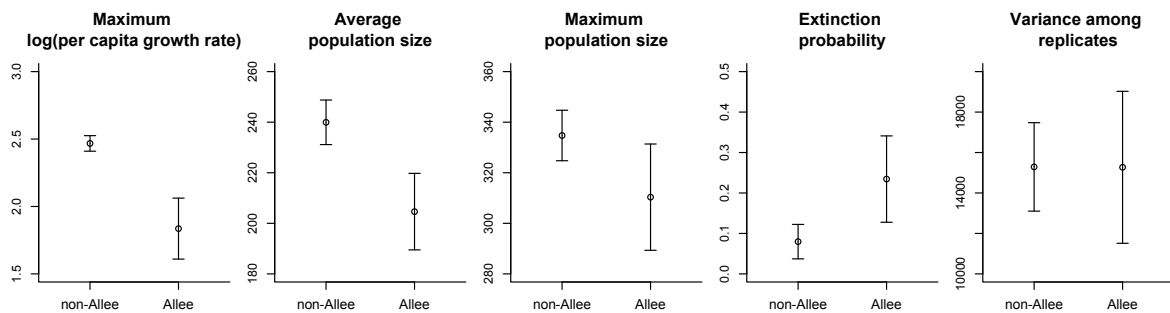
208 Figure 2: Raw data (circle of the same color belong to the same experimental replicate) and
 209 GAM fits (dashed lines: predicted values ; dotted lines: 95% confidence intervals around
 210 prediction) for the relationship between population size and per capita growth rate.

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 ($p=0.98$).



221

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

228

229 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).

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

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.

346

347

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