

Experimental demonstration of population extinction due to a predator-driven Allee effect

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Summary

1. Allee effects may result in negative growth rates at low population density, with important implications for conservation and management of exploited populations. Theory predicts prey populations will exhibit Allee effects when their predator exhibits a Type II functional response, but empirical evidence linking this positively density-dependent variation in predator-induced individual mortality to population growth rate and probability of extinction is lacking.

2. Here, we report a demonstration of extinction due to predator-driven Allee effects in an experimental *Daphnia-Chaoborus* system. A component Allee effect caused by higher predation rates at low *Daphnia* density led to positive density dependence in per capita growth rate and accelerated extinction rate at low density.

3. A stochastic model of the process revealed how the critical density below which population growth is negative depends on the mechanistic details of the predator–prey interaction.

4. The ubiquity of predator–prey interactions and saturating functional responses suggests predator-driven Allee effects are potentially important in determining extinction risk of a large number of species.

Key-words: Allee effect, critical density, extinction, functional response, predator satiation

Introduction

Allee effects are a density-dependent phenomenon which can cause the per capita rate of population growth to decline with decreasing population size (Allee 1931; Stephens, Sutherland & Freckleton 1999; Courchamp, Berec & Gascoigne 2008); under conditions of severe density dependence, Allee effects result in negative population growth rates at low density (Wang & Kot 2001; Courchamp *et al.* 2008). Accordingly, understanding Allee effects is important for conserving endangered species, managing exploited populations, and explicating the speciation-extinction process that has given rise to extant biodiversity (Courchamp *et al.* 2008).

Common mechanisms known to cause Allee effects include difficulty in finding mates, cooperative breeding, and cooperative defense (reviewed in Courchamp *et al.* 2008; Kramer *et al.* 2009). More recently, there has been increased interest in the potential for predator–prey interactions to cause an Allee effect in the prey population if predation saturates in the form of a Type II functional response (Dennis 1989, Gascoigne & Lipcius 2004). This positive relationship between survival and density is an example of a component Allee effect. When uncompensated by corresponding changes in reproduction, the excess mortality from the component Allee effect decreases growth rate causing a demographic Allee

effect (Stephens *et al.* 1999; Courchamp *et al.* 2008). When strong, Allee effects induce a critical density below which per capita growth rate is negative and extinction becomes increasingly likely, while weak Allee effects result in reduced, but still positive, growth rate as population size diminishes (Wang & Kot 2001). Because predator–prey interactions and Type II functional responses are ubiquitous (Begon, Harper & Townsend 1996; Sinclair *et al.* 1998; Seitz *et al.* 2001), predator-driven Allee effects are therefore expected to accelerate extinction risk in a large number of species.

As empirical evidence for Allee effects has accumulated, the predator-driven component Allee effect has been increasingly identified as important to the dynamics of natural animal populations (e.g. Sinclair *et al.* 1998; Wittmer, Sinclair & McLellan 2005; Ward, Nislow & Folt 2008). However, only Angulo *et al.* (2007) have identified a component Allee effect in adult survival due to predation that was severe enough to cause a demographic Allee effect and this probable consequence was confounded by concurrent Allee effects in other components of fitness. Thus, to date no existing studies have clearly linked a demographic Allee effect in a population to a component Allee effect caused by predator-induced changes in individual survival.

We have experimentally demonstrated that a predator-driven component Allee effect can cause a demographic Allee effect that is detectable in both population growth and extinction rates. Because extinction rate at low density is

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simultaneously elevated by other factors like demographic stochasticity (Lande, Engen & Sæther 2003), we first used a nonlinear birth-death process to identify a diagnostic pattern in the extinction time distribution that signifies the influence of Type II predation and distinguishes these effects from the effects of demographic stochasticity. We then performed a microcosm experiment in which a predator-driven Allee effect was caused by an experimentally controlled predator-prey (*Chaoborus-Daphnia*) interaction. To our knowledge, this confirmation of a predator-driven Allee effect is the first in which the individual-level effects of saturating predation are scaled up to population-level extinction.

Materials and methods

CONCEPTUAL MODEL

To illustrate how a predator-driven Allee effect and demographic stochasticity jointly determine the extinction time distribution, we consider a model for the dynamics of an idealized prey population under predation by a generalist predator, subject to the assumptions that: (i) population size is restricted to the non-negative integers ($N \in [0, 1, 2, \dots]$); and (ii) changes in population size are due to a combination of reproduction [occurring at rate $b(N)$], non-predation mortality [occurring at rate $m(N)$], and predation [occurring at rate $g(N)$]. For simplicity, we assume reproduction and non-predation mortality are density-independent, $b(N) = \beta N$ ($\beta > 0$) and $m(N) = \mu N$ ($\mu > 0$), justified for small population sizes vulnerable to extinction which do not exhibit a predator-independent Allee effect; in the literature in predator-prey dynamics the term $g(N)$ is commonly called the *functional response* (Holling 1959).

These assumptions are satisfied by a continuous-time birth-death process with rates $N \xrightarrow{\beta N} N + 1$ and $N \xrightarrow{\mu N + g(N)} N - 1$. For concreteness, we adopted a Type II functional response $g(N) = P\alpha N / (1 + \alpha T_h N)$, where $\alpha > 0$ is known as the attack rate, $T_h > 0$ is the handling time (Holling 1959) and predator number P , is constant (set to one for simplicity). On average, the growth of the prey population (N) is approximately,

$$\frac{dN}{dt} = \beta N - \mu N - g(N). \quad \text{eqn 1}$$

When $\beta - \mu \geq \alpha$ this equation has an unstable equilibrium at $N^* = 0$ and grows without bounds. When $\beta - \mu < \alpha$, this equation has a stable equilibrium at $N^* = 0$ and an unstable equilibrium at

$$N^* = \frac{1}{T_h} \left(\frac{1}{\beta - \mu} - \frac{1}{\alpha} \right). \quad \text{eqn 2}$$

This unstable equilibrium is the critical density below which a population subject to deterministic dynamics would inevitably decline to extinction and is the hallmark of a strong Allee effect.

Solutions to the stochastic model were obtained by simulation using Gillespie's direct method (Gillespie 1977), giving exact stochastic integrals, which are needed to precisely estimate extinction time of populations commonly at low densities where demographic stochasticity is important. For parameterizations we studied, extinction by $t = 40$ is practically indistinguishable from the ultimate extinction probability $\Pr(N_\infty = 0)$. Therefore, we plotted the probability of extinction at time 40 against initial population size. A sigmoid relationship in the plot of extinction probability is diagnostic of Allee effects (Dennis

2002), to be compared with $d^2\Pr(N_\infty = 0)/dt$ everywhere positive (J-shaped) characteristic of other kinds of population growth.

This conceptual model was constructed to illustrate the idea we mean to demonstrate – predator-driven Allee effects. However, because there is a size refuge (Pastorok 1981; Spitze 1985) in our experimental system (see below), we also studied an extended model given by

$$\frac{dJ}{dt} = \beta A - \mu J - g(J + A) - \delta J, \quad \text{eqn 3}$$

$$\frac{dA}{dt} = \delta J - \mu A - g(J + A). \quad \text{eqn 4}$$

In this extension, juveniles (J) became adults at a rate $\delta(J)$, adults (A) produced juvenile offspring at rate $\beta(A)$, and both suffered from intrinsic mortality, $\mu(J)$ and $\mu(A)$. The rate of predation $g(J + A)$ depended on total population size, with mortality of each stage dependent on relative susceptibility to predation. This formulation is relevant to a non-visual ambush predator, such as in the experiment below. Results were roughly equivalent when predator functional response varied independently with J and A , as might be expected for other types of predators (Appendix S1, Supporting information). The initial population was assumed to consist of all juveniles.

LABORATORY EXPERIMENT

We started 56 *Daphnia magna* populations at sizes of 1, 2, 4, 8, 16, 32, and 64 (8 replicates/treatment) 1–3 day old individuals. The *D. magna* was from a single clone in laboratory culture, and experimental organisms were obtained from females isolated for two generations (Griffen & Drake 2008). Four hours later, half of the replicates received a single *Chaoborus trivittatus* larva. Larvae used were the largest available (8–11 mm long) and had been starved for 24 h. *Chaoborus* is an important zooplankton predator in natural systems (Wissel & Benndorf 1998) and has several experimentally useful characteristics: (i) as reproduction occurs in the non-aquatic adult stage, the predator population density cannot respond to prey density, i.e. *Chaoborus* density is an exogenous variable just like a generalist predator; (ii) larvae survive without food for extended periods if prey concentrations are low (Wissel & Benndorf 1998); and (iii) as ambush predators (Pastorok 1981), *Chaoborus* larvae do not actively search the chamber, which would rapidly extirpate the prey obscuring the pattern we sought to detect. While some *Daphnia* species respond morphologically to *Chaoborus* presence, *D. magna* do not (Walls, Caswell & Ketola 1991).

Populations were reared in 1.4 L microcosms (31.5 × 21.7 × 2 cm) of clear Plexiglas filled with synthetic freshwater medium (Griffen & Drake 2008) and fed daily with 800 μL of a solution prepared by mixing 0.30 g of powdered *Spirulina* (a blue-green alga, 10.16% N and 44.96% C, JEHM Co., Inc, Lambertville, NJ, USA) into 50 mL of deionized water. Using an inert food resource allowed tight control of food availability; daily food ration was chosen based on previous experiments (Griffen & Drake 2008) to ensure population growth at the highest initial population size. Microcosms were kept at constant temperature (23 °C \pm 0.8 (s.d.)) and under constant light.

Pupating *Chaoborus* were replaced with larvae collected bi-weekly from a local pond and maintained with daily feeding of *D. magna* neonates. *Chaoborus* added to chambers were always starved for 24 h prior, to match the initial stocking conditions. Starting on day 16, *C. trivittatus* became rare in the pond, requiring a gradual shift to larvae of *C. punctipennis*. The largest individuals of *C. punctipennis* (7–8 mm) were smaller than the largest *C. trivittatus* (8–11 mm), but fed

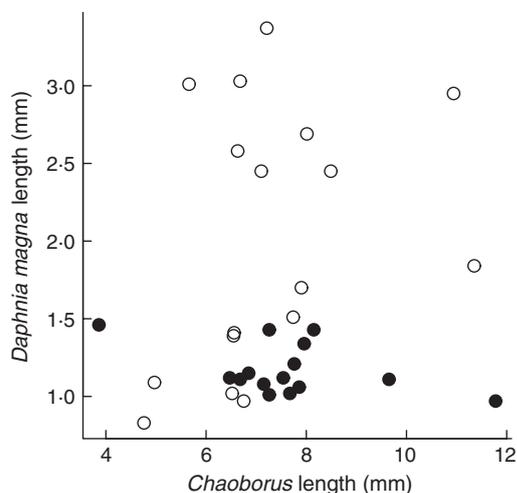


Fig. 1. *Daphnia magna* mortality based on body size and predator size. Solid circles = prey consumed, open circles = prey survived. One *D. magna* and one *Chaoborus* larvae were placed in 200 mL of synthetic hardwater medium and *D. magna* mortality was checked daily for 3 days.

on similar sized *D. magna* (< 1.5 mm or < 7 days old, Fig. 1). Consequently, switching predator species did not alter prey vulnerability, although the larger *C. trivittatus* may have consumed *D. magna* at a higher rate. This shift occurred after the time period relevant to the functional response and daily growth rate analyses presented below.

Daphnia magna populations were counted daily until day 40, then checked daily for extinction and counted weekly until the last extinction on day 123. Population size was estimated by averaging three counts taken with a hand tally counter. Two chambers (32 individuals, no predator and 32 individuals, predator) compromised by experimenter error were excluded from the functional response and growth rate analyses and treated as right-censored observations in survival analysis of extinction time data. After 90 days, populations began producing ephippia (resting eggs), coinciding with algal contamination affecting all remaining populations. Although in natural populations these eggs may have later hatched, we considered populations extinct when no *D. magna* remained in the water column (see Griffen & Drake 2008).

STATISTICAL ANALYSES

The shape of the functional response was assessed by logistic regression of the proportion of prey consumed on prey density, following Juliano (2001). The proportion of prey consumed was based on population size at day 7, as reproduction was first detected on day 8. The relationship between per capita growth rate ($\ln(N_x/N_0)$, 0.1 added to zeros; results are similar and statistically equivalent when constant is added to all values) and population density was tested using linear regression with predator presence as a covariate. This relationship was calculated at day 7 to characterize the effect of predation prior to reproduction, and again at day 14, which was chosen as the day before reproduction of the second generation (given the age at first reproduction was 7 days in this system). Using nearby dates provided similar results, but regression analyses on later days will have a decreasing signal of initial population size, as populations are influenced more by negative density dependence over much of their dynamics.

The effect of initial population size and predation on time to extinction was analysed using random survival forests (RSF) implemented in R (R 2.6.1 2007) (Ishwaran & Kogalur 2007). RSF extends

random forests to event-time analysis, avoiding restrictive assumptions of Cox proportional-hazards by averaging over a large number of binary decision trees, and allows for censored observations (Ishwaran *et al.* 2008). Variable importance was calculated as the increase in error when a variable is randomly permuted, and interactions were determined by comparing the additive importance of two variables to the increase in error when both variables are permuted together (Ishwaran 2007). Model prediction error is considered relative to a null expected error of 0.5 (random guessing), and is the average classification error for predicting which of two populations will go extinct first over all possible pairs of populations using Harrell's concordance index (Ishwaran *et al.* 2008). Proportion of populations extinct at the median extinction time was calculated to make qualitative comparisons to model predictions.

Results

CONCEPTUAL MODEL

The stochastic birth-death process with excess mortality from a predator with Type II functional response gives the sigmoid curve that is diagnostic of Allee effects, extending the concept of a predator-driven Allee effect to the stochastic case (Fig. 2). We note the reasonable agreement between the critical density given by eqn 2 and the apparent inflection point in the smoothed probability of extinction curve. The existence

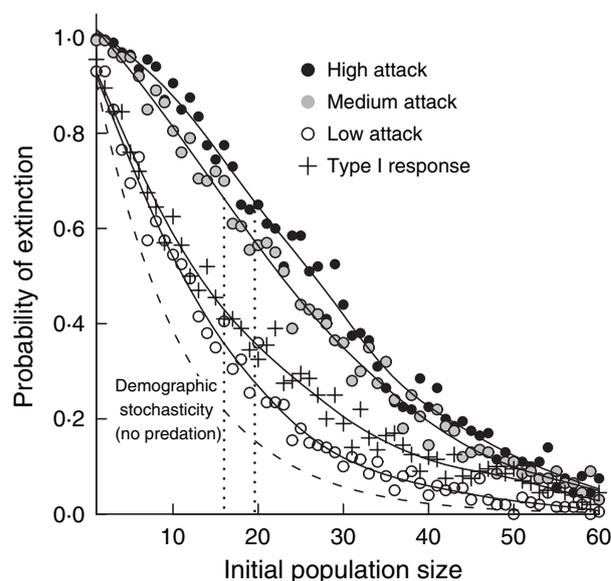


Fig. 2. Results of stochastic birth-death process simulations. Each parameterization was replicated 200 times at each initial population size and probability of extinction estimated from proportion of populations extant after 40 time steps. Circles are simulations with Type II functional response and attack rate $\alpha = 5$ ('high attack rate'; solid circles), $\alpha = 0.5$ ('medium attack rate'; grey circles) and $\alpha = 0.05$ ('low attack rate'; open circles). Crosses are simulation with Type I functional response with $\alpha = 0.05$. In all simulations $\beta = 1.1$ and $\mu = 1.0$ and handling time (T_h) = 0.5. Lines fit with smoothing splines, except for the deterministic expectation with no predator (---) which is given by $(\mu/\beta)^{N_0}$, the chance of ultimate extinction via demographic stochasticity. Dotted vertical lines show the deterministic critical population size at the upper equilibrium $N^* = 1/T_h \times (1/(\beta - \mu) - (1/\alpha))$ for $\alpha = 0.5$ and $\alpha = 5$.

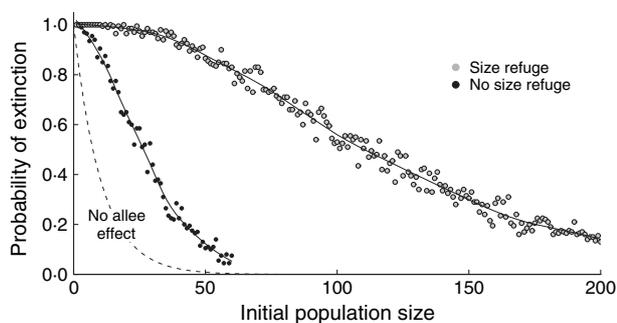


Fig. 3. Probability of extinction when prey reproduction and predation risk are stage (size) dependent. In the size dependent model (grey circles) juveniles matured at rate $\delta = 10$, only adults reproduced and juveniles were preferentially preyed upon 90% of the time. Simulations were replicated 200 times with $\beta = 1.1$, $\mu = 1.0$, attack rate (α) = 5 and handling time (T_h) = 0.5 (as in Fig. 2, also see Appendix S1, Supporting information). Both the general model without size dependence (solid circles) and the extended model including a size refuge for prey (grey circles) exhibit sigmoidal extinction curves. Lines fit with smoothing splines, except for the deterministic expectation with no predator (---) which is given by $(\mu/\beta)^{N_0}$, the chance of ultimate extinction via demographic stochasticity (as in Fig. 2).

of this critical density in the deterministic mean field model (eqn 1) depends on α and $\beta - \mu$ and exists in the positive quadrant if and only if $(\beta - \mu < \alpha)$. We conjecture that this phenomenon carries over to the stochastic case such that a sigmoidal probability of extinction curve (and, therefore, predator-driven Allee effect) occurs under the same conditions (Dennis 1989, Dennis 2002). Thus, as the ratio $(\beta - \mu)/\alpha$ increases, the probability of extinction collapses to the exponential decline of the simple birth-death process with no predation, the pattern expected as a result of demographic stochasticity (Fig. 2). The strength of the Allee effect is also affected by the ratio α/T_h (Fig. S2, Supporting information). Including a Type I functional response simply increases the overall mortality rate, causing a similar exponential decline with no inflection point (Fig. 2).

This picture is changed quantitatively, but not qualitatively, by size-selective predation. Most importantly, the model with size-selective predation retains the sigmoidal relationship between initial population size and extinction probability (Fig. 3). Given similar overall predation risk and the addition of both stage-specific reproduction and differential vulnerability to predators, extinction risk increased. This pattern obtained whether adults were more likely to survive attacks than juveniles or less likely than juveniles to be attacked (Appendix S1, Supporting information, Fig. S1, Supporting information). These results suggest a population with a size refuge is not necessarily at lower risk of extinction than a population without a size refuge.

FUNCTIONAL RESPONSE AND PER CAPITA GROWTH RATE

The proportion of *D. magna* consumed in the first 7 days decreased with initial population density (Fig. 4a) indicating

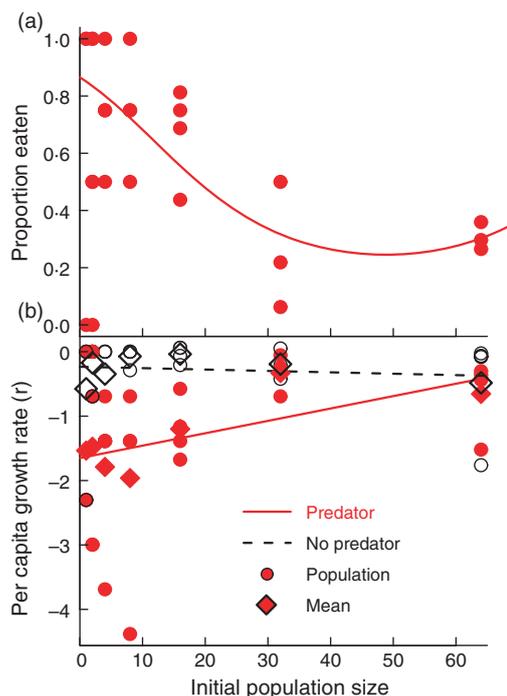


Fig. 4. Results from experimental populations. (a) Proportion *Daphnia magna* consumed by *Chaoborus trivittatus* by day 7 at each initial population size. Reproduction began on day 8. Negative slope is statistically significant (logistic regression, $P < 0.0002$) indicating Type II functional response (Juliano 2001). (b) Per capita growth rate due to predation ($\ln(N_{\text{day } 14}/N_{\text{day } 0})$, 0.1 added in case of zeros) for populations with (filled circles, solid line) and without *Chaoborus* (open circles, dotted line), mean values shown with larger symbols. Positive density dependence in presence of predation is statistically significant (overall model $R^2 = 0.29$, $P < 0.001$, effect of initial population size in presence of predator, $P = 0.019$).

a Type II functional response (Juliano 2001), resulting in a positive relationship between individual survival and population density. Due to high correlation between the parameters, α and T_h could not be simultaneously estimated in our study (Juliano 2001). Nevertheless, the decreased survival at low density resulted in a significant positive relationship between per capita growth rate and initial density of *D. magna* in the presence of *Chaoborus* (Fig. 4b), indicative of Allee effects. On day 7, the day before first reproduction, low density populations with predators had a substantially negative per capita growth rate, while higher densities were similar to predator-free populations, which had no relationship with initial density at low population sizes (Fig. 4b).

After a single generation, per capita growth rate decreased with initial population size and in the presence of predators (Table 1). Further, the interaction was significant and positive (Table 1), indicating that predator presence reversed the relationship between density and per capita growth rate causing a demographic Allee effect. As a result, per capita growth rate was low at high initial population size in all populations due to intraspecific competition, but was depressed at low initial population size when predators were present (Fig. 5a). Average growth rates were near or below zero at low initial

Table 1. Effect of initial population size and predation on per capita growth rate

Coefficients	Estimate	Error	P-value
Intercept	3.040	0.527	5.07e-07
Initial population	-0.058	0.019	0.004
Predator present	-2.945	0.746	< 0.001
Initial population × predator	0.0763	0.027	0.007

R-square = 0.26 *F*_{3,50} = 6.0 *P*-value = 0.001

Table 2. Effect of initial population size and predation on extinction

Variable	Mean importance ^a	95% CI ^b
Initial population	0.168	0.096–0.243
Initial population × predator	0.078	0.018–0.137
Predator	0.072	0.03–0.118
Random uniform	-0.006	-0.018 to 0.005
Random binary	-0.014	-0.039 to 0.014
Model error rate = 0.334		0.268–0.393

^aEstimated with a random survival forest (see Materials and methods).

^bFrom 999 bootstrap samples from a forest containing 10 000 trees.

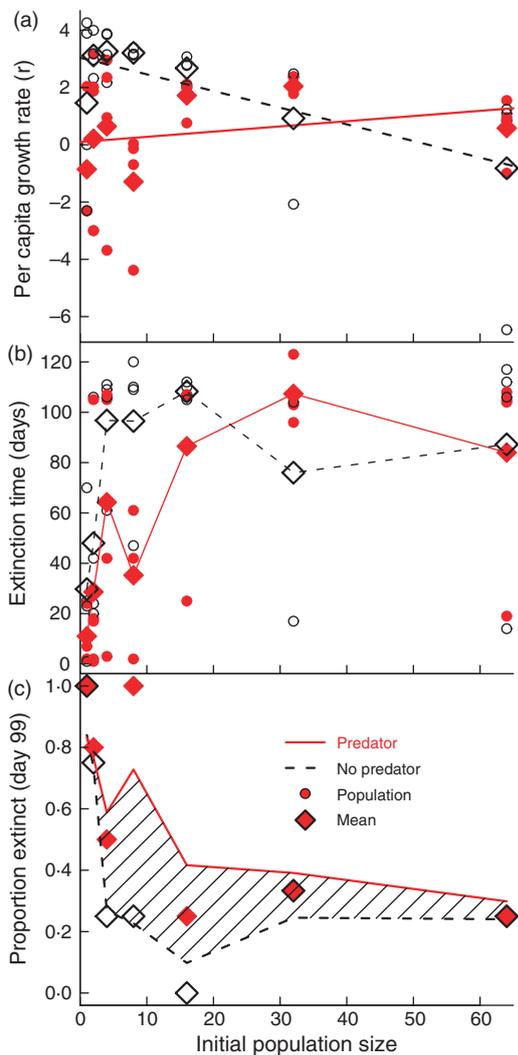


Fig. 5. (a) Per capita growth rate in 1st generation ($\ln(N_{\text{day } 14}/N_{\text{day } 0})$, 0.1 added in case of zeros) for populations with (filled circles, solid line) and without *Chaoborus* (open circles, dotted line), mean values shown with larger symbols. Regression lines are statistically significant (Table 1). (b) Time to extinction for populations with *Chaoborus* (filled circles) and without (open circles). Mean values at each initial population size are shown by larger symbols and connected with line segments. (c) proportion of populations extinct at the median time to extinction (99 days), comparable to Fig. 1. Symbols are observed data, lines are the probability of extinction predicted by the random survival forest with predators (solid line) and without predators (dotted line). The shaded area represents the difference in extinction between predator and non-predator groups.

density, but the regression model did not predict a critical density (intercept < 0) over the densities examined. The high variance at low densities precludes convincingly diagnosing either a weak or strong Allee effect based on the regression analysis.

EXTINCTION

Time to extinction depended on initial population size in both predator treatments and controls. Average time to extinction was lower in populations with predators than populations without predators for all populations with $N_0 < 32$ (Fig. 5b). Survival analysis showed both initial population size and predator presence to be significant predictors of extinction (Table 2) and that the effect of the interaction between initial population size and predation was of similar magnitude as the main effects (Table 2). Finally, overall probability of extinction was substantially greater when predators were present (Fig. 5c). The divergence of the relationships between density and extinction in the presence and absence of predation agreed with model predictions, exhibiting a shape consistent with exponential decline in the absence of predators, and a sigmoid-like decline with predators (Fig. 2). This can be seen in representative time series from two populations with low initial density (initial population size = 4) and extinction close to the median times to extinction with and without predators (42 days and 106 days respectively, Fig. S3, Supporting information).

Discussion

This paper reports an experimental demonstration of a predator-driven Allee effect in a simple, two-species system not subject to other sources of positive density dependence, such as mate limitation or cooperative interactions. As a result, low density populations had higher extinction rates in the presence of predators than in their absence and probability of extinction depended on initial population size, predator presence and their interaction, producing a pattern congruent with the predictions of a stochastic model. The detection of an Allee effect in extinction probability was paralleled by evidence for an Allee effect in per capita growth rate during the period of population establishment. Unlike previous

population-level experiments (Aukema & Raffa 2004), the component Allee effect in our system resulted in a demographic Allee effect with attendant consequences for population extinction.

The stochastic model predicted a sigmoid relationship between probability of extinction and initial population density in the presence of a predator with Type II functional response. This is the relationship expected for an Allee effect, with the inflection point corresponding to the critical density predicted in the deterministic case (Dennis 2002). While our experimental sample size and range of densities is limited, the qualitative agreement between observed extinction probability and model predictions for populations with and without predators supports the findings of the random forest survival analysis. In contrast to most Allee effect theory which has focused on general dynamics of deterministic models (e.g. Gascoigne & Lipcius 2004; Boukal, Sabelis & Berec 2007) our model underscores the importance of mechanistic underpinnings and stochasticity. The simulations show that the existence of a critical density due to a predator-driven Allee effect depends on the relative values of the intrinsic population growth rate, attack rate and, when present, handling time. When attack rate is slow relative to handling time, the effect of a Type II predator on extinction probability is indistinguishable from a Type I predator, while higher attack rates increase the critical density (Fig. 2, Fig. S2, Supporting information). The addition of a size refuge in prey retains qualitatively similar behaviour with increased complexity, as in the parameterization above (Fig. 3, Appendix S1, Supporting information) where extinction risk increases, perhaps because while adults are less likely to be preyed upon, the juvenile portion of the population is unable to reproduce, and the latter effect dominates.

The demographic Allee effect caused by predation that was evident in the extinction time distribution was also detectable in per capita growth rate. There was a positive relationship between density and per capita growth rate before and after first reproduction in the presence of the predator. At the end of the first generation this effect was statistically evident only as the interaction between density and predation. Another analysis (Angulo *et al.* 2007) found a similar result, in both cases high density populations showed negative density dependence independent of predation, making the comparison with a no predation control necessary to distinguish the Allee effect.

Other studies have suggested that a quadratic regression of growth rate on population density is a better test for a demographic Allee effect (Sibly *et al.* 2005). While a quadratic relationship does include the negative density dependence expected at high density, it assumes: (i) data is available across the entire range of densities and (ii) there is a symmetric relationship between density and per capita growth rate that is clearly absent from this and other data (Liebhold & Bascombe 2003, Kramer, Sarnelle & Knapp 2008). Detection of an Allee effect will often rely on more data at low density due to the higher variance (due to demographic

stochasticity) in these populations, and both the high variance and irregular spacing of densities are less than ideal for quadratic regression or the generalized additive models we explored as another nonlinear alternative (A.M. Kramer & J.M. Drake, unpublished data).

The experiment did not provide conclusive support for a strong Allee effect, although per capita growth rates were often negative at low density and the relationship between extinction probability and density appears sigmoid. Our experiment did not have the statistical power to simultaneously estimate attack rate and handling time from our prey consumption data (Juliano 2001), so we are unable to parameterize our stochastic model to try and predict a critical density and see if it fell within the range of densities tested. The distinction between weak and strong Allee effects is an important one (Boukal *et al.* 2007; Courchamp *et al.* 2008), but our results indicate detectable increases in extinction even when small sample size and high variance obscure the strength of the effect.

Our experimental results provide evidence that an Allee effect resulting in increased extinction at low population density can be caused solely by predation. While previous work on the Allee effect has emphasized mate limitation and cooperative behaviour, the mechanism explored here expands the pool of species potentially subject to Allee effects to include all species subject to a generalist predator with a Type II functional response (Gascoigne & Lipcius 2004). Speculating further that attack rate will be higher than handling time in many predatory-prey interactions; we suggest that predator-driven Allee effects, potentially strong, may indeed be common in nature. It follows that accurately assessing extinction risk in small populations and rare species may require understanding the characteristics not only of the species of conservation concern but also of their predators.

Acknowledgements

We thank four anonymous reviewers for suggestions on earlier versions of this manuscript. Funding for this project was provided by the University of Georgia Odum School of Ecology, a grant from the Great Lakes Protection Fund, and research grant # 0914347 from National Science Foundation, program BE-UF: Ecology of Infectious Disease.

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Received 9 April 2009; accepted 14 December 2009

Handling Editor: Andrew Beckerman

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Size-selective predation alternative formulation and parameterization.

Fig. S1. Comparison of size-selective predation models.

Fig. S2. Relative influence of attack rate and handling time on extinction probability.

Fig. S3. Time series of representative experimental populations with and without predators.

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