

Research



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Fear creates an Allee effect: experimental evidence from seasonal populations

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Allee effects driven by predation can play a strong role in the decline of small populations but are conventionally thought to occur when generalist predators target specific prey (i.e. type II functional response). However, aside from direct consumption, fear of predators could also increase vigilance and reduce time spent foraging as population size decreases, as has been observed in wild mammals living in social groups. To investigate the role of fear on fitness in relation to population density in a species with limited sociality, we exposed varying densities of *Drosophila melanogaster* to mantid predators either during an experimental breeding season or non-breeding season. The presence of mantids in either season decreased the reproductive performance of individuals but only at low breeding densities, providing evidence for an Allee effect. We then used our experimental results to parametrize a mathematical model to examine the population consequences of fear at low densities. Fear tended to destabilize population dynamics and increase the risk of extinction up to sevenfold. Our study provides unique experimental evidence that the indirect effects of the presence of predators can cause an Allee effect and has important consequences for our understanding of the dynamics of small populations.

1. Introduction

Given that many populations show strong negative density-dependence, animal extinction is somewhat paradoxical because individuals from depressed populations should have high fitness. Allee effects, or positive density-dependence, are phenomena that lead to positive relationships between population density and individual fitness and, therefore, can play an important role in driving small animal populations to extinction [1]. Classic examples of Allee effects have focused on intrinsic limitations at small population size, such as inbreeding depression and genetic bottlenecks, demographic stochasticity, environmental conditioning of habitat, cooperative foraging and mate limitation [2–6]. Although predators are often involved in animal extinctions, predation's role in creating Allee effects can be limited because population size (i.e. numerical response) of specialist predators should decline as prey population size declines while generalist predators may develop alternative search images and switch to other prey, with both phenomena leading to negative density-dependence of the prey [2]. Exceptions often involve specific conditions, such as social mammals or type II functional responses in unstructured habitats [7–11].

Whereas textbook summaries of the effect of predation focus on direct consumption of prey by predators, there is growing evidence that the fear of predators can be as important as direct consumption. When animals fear predators, they often spend more time being vigilant, less time foraging and less time in higher food-quality, but riskier, habitats [12–15]. Such behavioural responses to fear can lead to stress-related physiological changes and have a negative impact on body condition [16–18], which can then influence both reproductive success and survival [19–21], eventually influencing long-term population dynamics [22,23], and even ecosystem function [14,19,24,25]. The impacts of fear can also be transgenerational due to maternal effects impacting offspring development

[18,26–28]. Indeed, averaged across many studies, the population-level effect of fear on prey fitness can be equivalent to the effect of direct predator consumption [22].

Fear of predators could heighten Allee effects because individuals are more vigilant as density declines. Field studies of social mammals have shown that individual vigilance increases as group size declines, and that smaller groups are more likely to go extinct due to predation [29,30]. However, such an effect may not be limited to social mammals if fear compensates for negative density-dependence. For instance, if lower densities lead to fewer social interactions, then vigilance arising from fear of predators may become more important by resulting in de facto reduced densities with respect to social interactions. Thus, fear could create an Allee effect that increases the risk of extinction, and also potentially destabilizes dynamics, by decreasing the ability of populations to rebound through negative density-dependent processes.

To experimentally examine the effect of density on the fear response, we exposed *Drosophila* to the scent of a mantid predator either in a simulated breeding season, a simulated non-breeding season or neither, and then examined fecundity and offspring body mass at four different densities. Fear responses are typically multimodal, and the effect of fear from the mantid is likely due to a combination of vibrations and scent from the mantid, and the scent of dead flies defecated by the mantid. Previously, we demonstrated that exposing *Drosophila* to a mantid predator in the non-breeding season reduced fecundity the following breeding season and that mantid exposure in the breeding season caused offspring to develop faster and weigh less as adults, presumably because stressed mothers influenced offspring development [18]. Thus, the effects of fear in the non-breeding season carried over to impact fecundity the following breeding season and the effects of fear during development carried over to impact adult body mass. To understand the effect of density on fear responses, we examined the two endpoints highlighted by our previous study: fecundity and offspring body mass. We predicted that the carry-over effect response of fear on both fecundity and offspring body mass would be higher at smaller population sizes because individuals spend more time being vigilant. Given that the population parameters for our study population have previously been quantified in detail [31,32], we then modelled the impact of these effects on population stability and persistence.

2. Material and methods

Many animals have distinct stages in their annual cycle (seasons) that correspond with environmental variation, principally food availability. Here, we consider a system with two seasons defined by whether an animal is breeding or not breeding ([31,32]; see electronic supplementary material, Detailed Methods, figure S1), although the principles could be extended to more complex seasonality. Our system mimics several key elements of seasonality in the wild: (i) the breeding season is shorter than the non-breeding season; (ii) flies are not food-restricted during the non-breeding season at most densities, but females have no source of protein and no laying medium, and therefore do not lay eggs; and (iii) fecundity declines with time during the breeding season because late-laid eggs have low survival [18,33].

We used Chinese praying mantids, *Tenodera aridifolia sinensis* (hereafter ‘mantids’) as predators. Previous work showed that mantids can cause strong fear responses in the wild, with

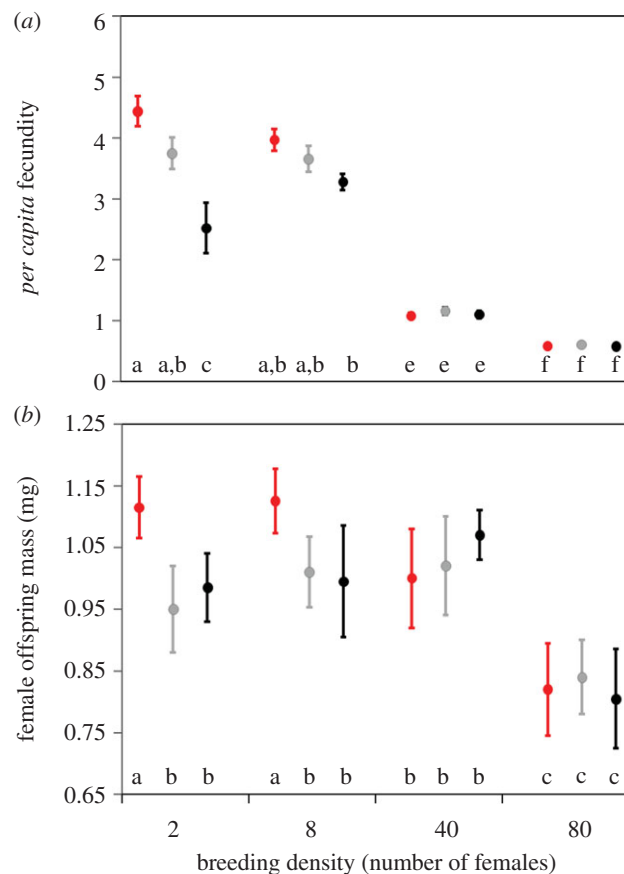


Figure 1. (a) Per capita fecundity and (b) female offspring mass as a function of breeding density (total population of males and females) following treatment without mantid scent (control, red), mantid scent during the breeding season (grey) or mantid scent during the non-breeding season (black). Treatments sharing the same letter were not statistically different from one another. (Online version in colour.)

herbivorous prey emigrating from areas that mantids are introduced [25,34]. We tested *Drosophila* with single first instar mantids that had been feeding on adult *Drosophila* for their entire lives prior to the start of the experiment. To control for age and body mass, we only used individual adult *Drosophila* between 1- and 3-days old from parents bred at low density. To obtain these offspring, we selected males and females and placed 16 individuals (50 : 50 sex ratio) in separate vials with fresh food for 24 h. We used only individuals that emerged between days 10 and 12 post-lay. We then combined these offspring and randomly grouped equal ratios of males and females into one of three ‘predator’ treatments: ‘control’ with no mantid, ‘non-breeding mantid’ with mantid present but not visible during the non-breeding season and ‘breeding mantid’ with mantid scent impregnated for 24 h prior to measurements. For each ‘predator’ treatment, we had four ‘density’ treatments ($n = 15$ replicates at each density and ‘predator’ treatment): 4, 16, 80 and 160 individuals (50 : 50 sex ratio).

All treatments began at the start of the non-breeding season and finished at the end of the breeding season, which we labelled as day 0. After 4 days in the non-breeding season, we moved the survivors to the breeding season, but controlled density (so that there was the same density in the breeding season and non-breeding season even though some individuals died during the non-breeding season), by combining all survivors from each treatment at the end of the non-breeding period and then placed the same density of flies (50 : 50 sex ratio) as was present in the non-breeding season in each breeding vial ($n = 9-14$ replicates at each density and ‘predator’ treatment during the breeding season).

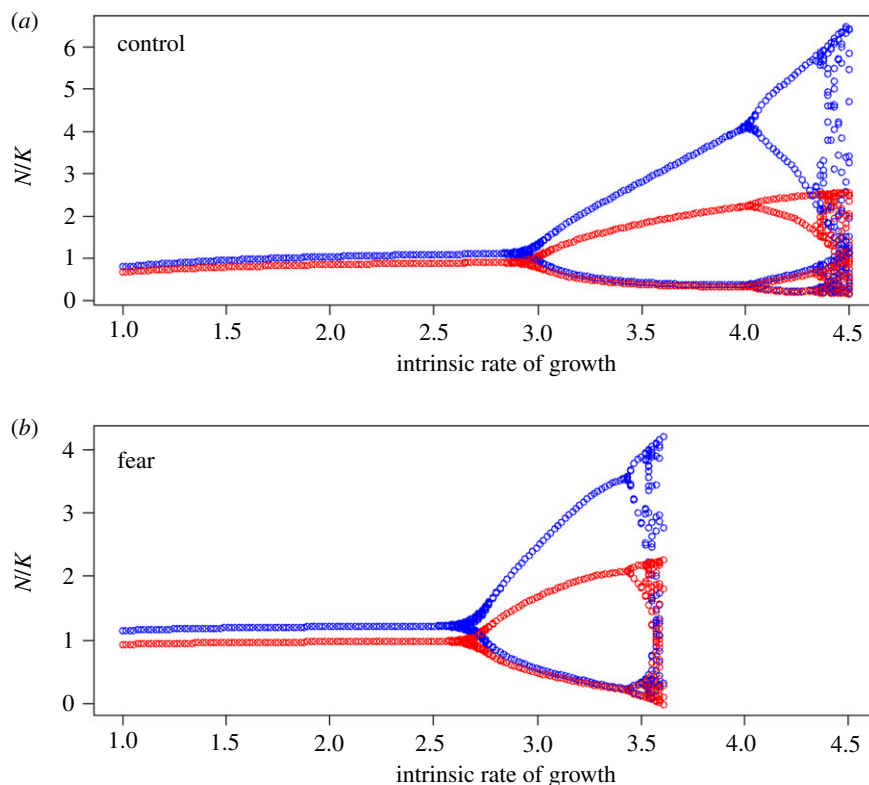


Figure 2. Bifurcation diagram of (a) bi-seasonal Ricker model with carry-over effect (from [31]) and (b) bi-seasonal Ricker model with carry-over effects in the presence of fear. The model is parametrized using the data presented in our paper. Both the non-breeding (red) and breeding (blue) seasons are shown. (Online version in colour.)

To investigate the effects of the ‘predator’ treatment and density on reproductive output, we counted the total number of offspring emerged, which we termed ‘fecundity’. Given that over 90% of eggs hatch, the number of offspring emerged is very similar, and highly correlated with, the number of eggs laid [18]. We also measured ‘female offspring mass’, which was the average mass of female offspring on the day juvenile flies emerged.

(a) Population model

To explore the population-level consequences of fear, we used a bi-seasonal population model constructed and validated by Betini *et al.* [31] on the same lines of flies we used in this study. The model describes the population-level responses within our seasonal experimental system via a bi-seasonal Ricker model. The population size at the end of the breeding season, X_t , for generation t is given by

$$X_t = Y_{t-1} e^{(r_{\max} + cX_{t-1})(1 - (Y_{t-1}/K_b))}$$

and the population size at the end of the non-breeding season, Y_t , is given by:

$$Y_t = X_t e^{r_{nb}(1 + (X_t/K_{nb}))},$$

where r_{\max} is the maximum intrinsic rate of growth in the breeding season, c a coefficient representing the carry-over effect associated with breeding density, K_b the carrying capacity in the breeding season, r_{nb} the intrinsic rate of growth in the non-breeding season and K_{nb} the carrying capacity in the non-breeding season. To construct the model, we assumed that the effect of reduced fecundity associated with fear in the non-breeding season would cause a proportional increase in c and decrease in r_{\max} (reduced offspring size; [18]), while the effect of reduced development time associated with fear in the breeding season was a proportional decrease in r_{\max} (reduced offspring size; [18]).

We present the results from 10 000 simulations with random noise multiplied to the same population models (sex ratio of 50 : 50) during both the breeding and non-breeding seasons

($2\sigma = \pm 80\%$, but with survival during non-breeding constrained not to be greater than 1) such that population size at the end of the non-breeding season and breeding season had a stochastic component. If the population dropped below one individual, then the population was considered extinct.

(b) Statistical analysis

To compare fecundity and development time among ‘predator’ treatments, densities and their interactions, we used general linear models. All analyses were conducted in R. v. 3.2.0 with statistical significance set at $\alpha = 0.05$.

3. Results

Fecundity varied with ‘predator’ treatment (general linear model: $F_{2,139} = 7.6$, $p = 0.0005$), density ($F_{1,139} = 344$, $p < 0.00001$) and the interaction between ‘predator’ treatment and density ($F_{2,139} = 3.85$, $p = 0.02$). Thus, fecundity declined with density and was lower in the non-breeding mantid treatment, but the effect of the non-breeding mantid treatment was only apparent at low densities (figure 1). Female offspring body mass varied with ‘predator’ treatment ($F_{2,139} = 7.51$, $p = 0.0008$), density ($F_{1,139} = 31.4$, $p < 0.00001$) and the interaction between ‘predator’ treatment and density ($F_{2,139} = 5.58$, $p = 0.005$). Thus, female offspring body mass declined with density and was lower in both experimental ‘predator’ treatments, but the effect of both ‘predator’ treatments was only apparent at low densities (figure 1). A relative Allee effect was present in both traits, with the impact of fear being greater at low densities, and trait levels declining or remaining stable at low densities compared with moderate densities.

Population models incorporating the effect of fear were less stable than models that did not incorporate fear (figure 2).

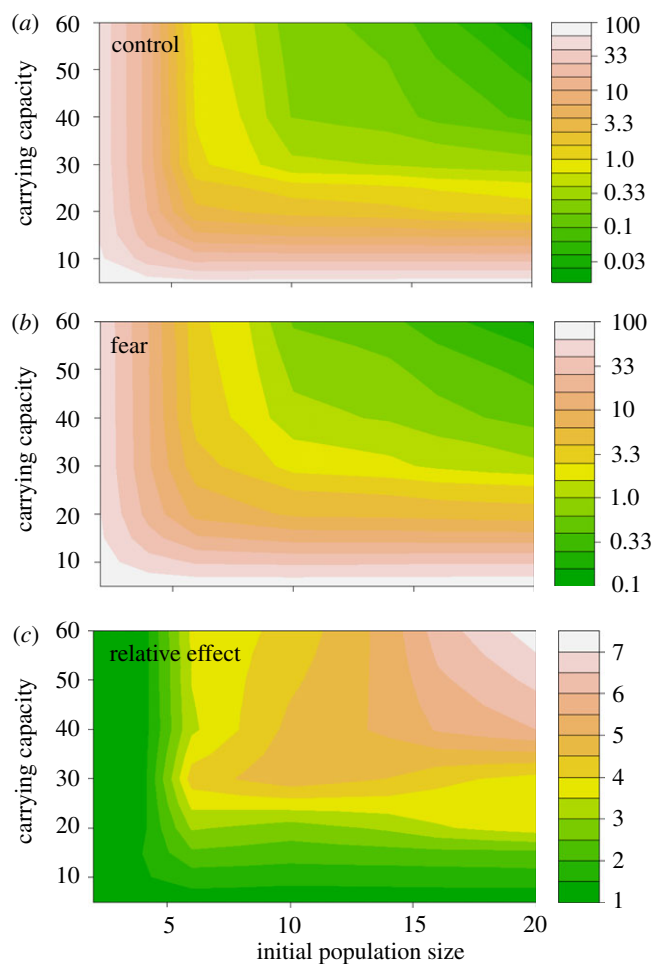


Figure 3. Percentage of modelled populations that go extinct within 10 generations starting with each initial population size and for a given carrying capacity, (a) without the non-consumptive effects of predators, and (b) with the non-consumptive effects of predators. (c) The ratio of the percentage of populations that go extinct within 10 generations with the non-consumptive effect of predators to the percentage without the non-consumptive effects of predators. (Online version in colour.)

Specifically, seasonal populations became unstable at an intrinsic rate of growth of about 3.6 when fear was incorporated into the model compared with 4.2 when fear was not incorporated. By contrast, seasonal populations with no carry-over effect or fear became unstable at an intrinsic rate of growth of 3.2. The probability of extinction decreased with carrying capacity and initial population size (figure 3). The probability of extinction at low carrying capacities and initial population sizes was higher for populations with fear than without fear (figure 3). The probability of extinction for an initial population size of 4 and a carrying capacity of 10 was approximately 48% with fear and approximately 33% without fear. By contrast, the probability of extinction for an initial population size of 20 and a carrying capacity of 60 was approximately 0.15% with fear and approximately 0.02% without fear. Thus, although the absolute difference in the probability of extinction with fear was highest at low initial population size and carrying capacity, the relative difference was highest at higher initial population sizes and carrying capacities (figure 3b).

4. Discussion

As we predicted, the effect of fear on fecundity and offspring growth was most pronounced at low densities. At low

densities, as previously shown [18], the scent of a mantid during the non-breeding season caused female flies to breed in poor condition, and lay fewer eggs that grew into smaller flies, while the scent of a mantid during the breeding season caused female flies to lay eggs that developed into smaller flies. At high densities, flies apparently did not experience the impact of fear either because flies were already at maximal levels of stress or because they spent less time being vigilant in the presence of many conspecifics. Regardless of the proximate mechanism, fear partly compensated for the effect of negative density-dependence creating a demographic Allee effect.

Our experimental system clearly demonstrated an Allee effect similar to those reported to occur in field studies of social mammals. For instance, lamb survival in bighorn sheep (*Ovis canadensis*) is positively correlated with population density because larger herds can better protect their offspring, but there is no overall relationship between population density and growth because of other confounding variables in the wild [35]. Mortality is higher in small suricate (*Suricata suricatta*) groups than large groups, but only in areas of high predation and, in those areas, all small suricate groups eventually go extinct [28]. Similarly, field studies have documented Allee effects associated with type II functional responses [7,36]. For example, predators overwhelm defences in small bird colonies [37], small native animal populations are eliminated by generalist, introduced predators [38,39] and fish stocks are diminished as commercial fisheries concentrate their resources on dwindling populations [40,41]. Finally, complex interactions among multiple prey have led to Allee effects in caribou [42]. Our study extends these earlier studies to provide clear experimental evidence that predators can create Allee effects beyond the narrow situations previously envisioned involving type II predation in unstructured habitats or social mammals [7–12,43].

Other studies demonstrated Allee effects in *Drosophila* based on factors intrinsic to the population rather than the effect of predators [44,45]. At low population size, aggregative pheromone levels, and consequently oviposition rates, by females are reduced [45]. The lower consequent larval densities are unable to temper fungal growth leading to reduced larvae survival [44]. Our work extends those ideas to systems that include predators and seasonality.

Fear tended to destabilize populations by decreasing the ability of small populations to rebound via negative density dependence. Indeed, the probability of extinction was higher for populations in the presence of fear than without fear. By contrast, density-mediated carry-over effects, which have been reported in the same experimental seasonal population used in this study, tended to stabilize populations [31]. Thus, one might expect that fear would increase population stability due to the enhanced carry-over effects from non-breeding to breeding and from mother to offspring. Indeed, even with fear, population stability was higher with carry-over effects than without carry-over effects. However, because those effects were only pronounced at low densities, leading to lower fecundity and population growth, the net effect of fear was to destabilize populations.

Our work may have direct practical implications. Invasive arthropod generalist predators, such as Chinese praying mantids, have disrupted many ecosystems worldwide, although their effects are often difficult to predict [46]. Indeed, arthropod generalist predators often exert strong top-down control on prey populations, primarily via fear rather than direct

predation, and often leading to trophic cascades [25,46–48]. Mantids are known to increase fear in prey populations, leading them to emigrate from areas with high mantid densities [25,34], and our work suggests that prey species with lowest densities may be most impacted. We suggest that the destabilizing and Allee effects associated with fear of those predators may be one reason why their impacts are unpredictable. Although our mantids only ate *Drosophila*, because we maintained a constant mantid density rather than presenting a numerical response typical of a specialist predator, our results may be more typical of a generalist predator whose abundance is maintained high by alternative prey even as one prey species declines.

The likelihood of extinction was highest in our seasonal experiments for small initial population size and small carrying capacities, which is unsurprising, given that many past extinctions have occurred when population size has been reduced (e.g. overhunting) or carrying capacity is inherently low (e.g. island species) [43]. We clearly show that reductions in carrying capacity (e.g. habitat loss) can leave populations vulnerable to stochastic events (e.g. climatic variability) that reduce population size, but that those effects are exacerbated in the presence of fear. Interestingly, the relative impact of fear was largest at relatively larger population sizes and carrying capacities because fear reduced the ability of density dependence to rescue those populations during crashes (figure 3). As such, fear is yet another example of multiple,

likely interacting, Allee effects that complicate population management [43,49].

Predators have caused the extinction of many wild animals and fear-associated Allee effects may have played a role in those extinctions [2,43,50]. In particular, fear is known to be associated with population declines in many wild systems. For instance, increasing populations of birds of prey have led to declines in waterbird populations primarily by causing waterbirds to reduce time spent foraging or abandon their offspring en masse, which are then eaten by other birds [51,52]. We suggest that such fear effects may become more pronounced as population size declines, as observed by Gilchrist [37], leading to reduced resilience in small populations and increased likelihood of extinction.

Data accessibility. Data appear in the electronic supplementary material.

Authors' contributions. K.H.E. wrote the manuscript, conducted the experiments and performed the analysis with assistance from G.S.B. and D.R.N. D.R.N. supervised the work and designed the study with K.H.E. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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