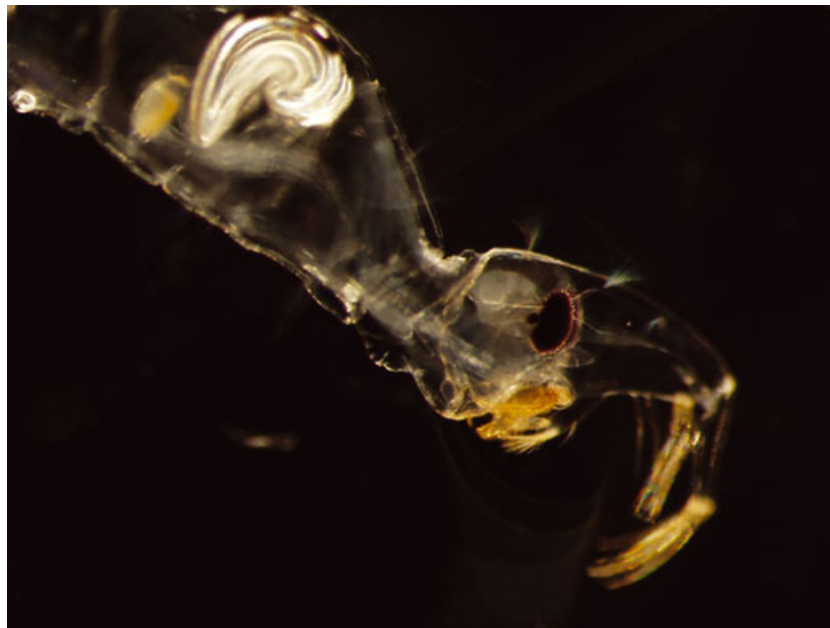


IN FOCUS

Safety in numbers: extinction arising from predator-driven Allee effects



Chaoborus punctipennis under dark field microscopy. *Chaoborus* preying on *Daphnia magna* cause lower *per capita* growth rate and higher extinction risk in small populations, providing experimental confirmation for a predator-driven Allee effect. Photo by Meghan Duffy.

A.M. Kramer & J.M. Drake (2010) Experimental demonstration of population extinction due to a predator-driven Allee effect. *Journal of Animal Ecology*, **79**, 633–639.

Experimental evidence of extinction via an Allee effect (AE) is a priority as more species become threatened by human activity. Kramer & Drake (2010) begin the International Year of Biodiversity with the important – but double-edged – demonstration that predators can induce an AE in their prey. The good news is that their experiments help bridge the knowledge gap between theoretical and empirical AEs. The bad news is that this predator-driven AE precipitates the prey extinction via a demographic AE. Although their findings will be sensitive to departures from their experimental protocol, this link between predation and population extinction could have important consequences for many prey species.

A demographic Allee effect (AE) describes a decrease in population growth rate at small population size or low density (Stephens, Sutherland & Freckleton 1999; Fig. 1a). Despite the increasing numbers of species coming under threat from human activity, evidence for demographic AEs is rare (Gregory *et al.* 2010). One of the (many) possible reasons for this lack of evidence is a lingering perception that such processes affect only social and cooperative species though intrinsic factors, such as the requirement for African wild dogs *Lycaon pictus* to hunt in groups to overpower large prey (Cour-

champ, Rasmussen & Macdonald 2002). Gascoigne & Lipcius (2004), however, showed that a predator – an extrinsic factor – could induce an AE in its prey if it maintained a type II (hyperbolic) functional response to changes in prey density. A type II functional response describes a decelerating predator feeding rate with increasing prey density that asymptotes at higher prey densities (Gascoigne & Lipcius 2004; Fig. 1b). Put plainly, higher numbers of individual prey translate to a lower likelihood that each individual will be eaten – thus there is safety in numbers. Conversely, individual prey in small and declining populations will suffer a heightened predation rate, and this has been observed repeatedly in natural populations. For example, Angulo *et al.* (2007)

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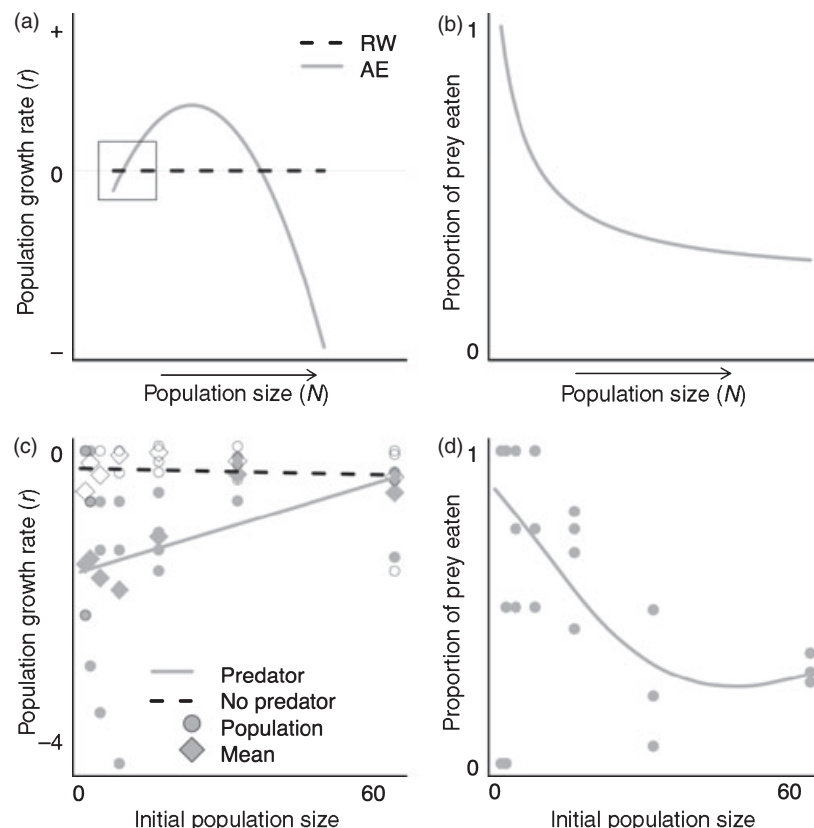


Fig. 1. (a) A plot to show the shape of a demographic Allee effect (AE) in population growth rate (r) in contrast to no growth or random walk (RW). Note how, in contrast to RW, r with an AE is low and negative at low population size (N ; see the inset box). (b) A plot to show a type II predator functional response in prey consumption rate (here shown as proportion of prey consumed to compliment Kramer & Drake (2010)). (c) The predator-driven demographic AE driven by (d) the type II functional response of *Chaoborus* prey consumption rate at experimental initial densities of *Daphnia*. Compare plots (a) to (c) and (b) to (d) in light of their similarities. Plots (c) and (d) were redrawn from Kramer & Drake (2010).

showed the existence of a demographic AE in the California Channel Island fox *Urocyon littoralis* and higher adult survival on islands where their predators – golden eagles *Aquila chrysaetos* – had been removed. Yet, to our knowledge, no clear demonstration existed to show that such a predator-driven AE could precipitate population extinction.

Kramer & Drake (2010) report that predatory midge larvae of the genus *Chaoborus* can induce a demographic AE in water flea *Daphnia magna* populations via a predator-driven AE, and that this predator-driven demographic AE can speed smaller prey populations to premature extinction. Although not the first evidence of a predator-driven demographic AE, Kramer & Drake (2010), by using a controlled laboratory experiment with replication, was able to demonstrate unambiguously this effect. As Kramer & Drake (2010) point out, other reported cases of predator-driven AEs might support alternative explanations. For example, the Island fox also exhibits reduced pup survival at smaller population sizes (Angulo *et al.* 2007). This is an example of a component AE that describes a decrease in a surrogate measure of fitness (e.g., reproduction, survival, etc.) at small population size or low density (Stephens *et al.* 1999). Under certain conditions, such component AEs can manifest as a demographic AE, and in the case of the Island fox, represented an alternative explanation to a predator-driven AE (Angulo *et al.* 2007). Of

course, the presence of a type II predator function response needs not translate to a predator-driven AE, if predation pressure is insufficient. Moreover, even if induced in a laboratory or an *in situ* field setting, a predator-driven AE might be too weak to manifest as a demographic AE, as is true of any component AE (Stephens *et al.* 1999).

Although not the first evidence of a predator-driven demographic AE, Kramer & Drake (2010) do present the first experimental demonstration that this process can precipitate population extinction. They developed a stochastic predator-driven AE model for their *Chaoborus*–*Daphnia* predator–prey system that predicted a sigmoid prey population extinction probability curve characteristic of a demographic AE (Dennis 1989). Armed with these predictions, they revealed a lower population growth rate (r) at low prey densities (Fig. 1c) driven by a type II functional response in *Chaoborus* predation on different *D. magna* densities (Fig. 1d). Indeed, this finding was strengthened by comparison with the control groups (no predators); control group r was comparatively unchanging across different prey densities, and was roughly the same as for experimental groups at highest prey densities. By comparing observed population extinction probabilities to predictions from their mechanistic model, Kramer & Drake (2010) established a clear link between a predator-driven AE and population extinction due to a demographic

AE. This represents the first experimental illustration of a predator-driven AE leading to population extinction. Sinclair *et al.* (1998) provide field examples of this link, such as the quokka *Setonix brachyurus* reintroductions in Australia whose failures were attributed to introduced fox *Vulpes vulpes* predation. These field examples, however, might support alternative explanations.

Experiments are not without their problems, and Kramer & Drake (2010) have their fair share. Apart from the logistical problems of contamination and a shortage of suitable predators (that they overcome appropriately), their findings are likely to be sensitive to the experimental conditions from which they are derived. For example, *Chaoborus* does not mount a numerical or aggregative response to changes in *D. magna* density. While this simplification permits the isolation of a predator-driven demographic AE, it might not easily generalize to any but the shortest of time-scales under field conditions. Interestingly, prey aggregation might be a necessary condition for a predator-driven Allee effect under field conditions (McLellan *et al.* 2010). Excessive variation in calculated r prevented them estimating the Allee threshold (A) beneath which r becomes negative and the population (usually) begins its descent to extinction (a 'strong' AE; Wang & Kot 2001). Angulo *et al.* (2007) also failed to isolate A but for a different reason. Female Island foxes showed higher reproduction at low density (presumably due to a release from competition) that partially offset the component and demographic AEs. This latter case highlights a larger issue in the detection of AEs, particularly demographic AEs; evolution should act against any mechanism that results in lower individual fitness. Consequently, species should be adapted either to counteract AEs or to avoid the population sizes at which they act (Courchamp, Berec & Gascoigne 2008).

The aforementioned reasons alone should illustrate the point that experiments do not always epitomize the complexities of nature, particularly when examining unstable systems (Stephens *et al.* 1999). To a large extent this problem of oversimplification can be overcome by performing experiments *in situ*. For example, Turchin & Kareiva (1989) manipulated both fireweed aphid *Aphis varians* and their predator – the common ladybird beetle *Hippodamia convergens* – densities to demonstrate the existence of a predator-driven AE. Admittedly, the scale and replication required to represent complex systems adequately might be inhibitive. If, however, we consider human interventions as manipulations, then species introductions and reintroductions present opportunities to study basic ecological processes (Shea & Chesson 2002). Indeed, such events have provided the setting for several predator-driven AE studies including the quokka and island fox (Sinclair *et al.* 1998; Angulo *et al.* 2007). Also, humans themselves might be regarded as part of the system – the predator. Human exploitation of natural populations might induce AEs including, for example, the highly publicized collapse and failing recovery of the cod fishery off Newfoundland, Canada (Rose & Kulka 1999).

Adding humans to the list of predators doubtless adds numerous examples to the list of predator-driven AEs;

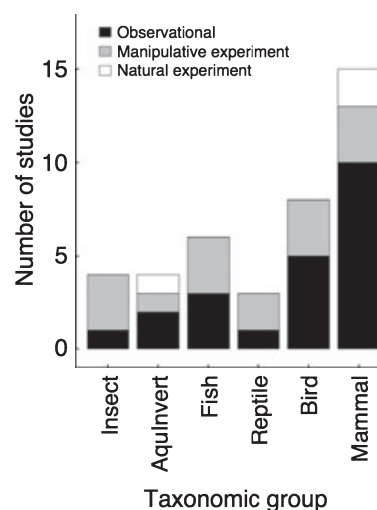


Fig. 2. A barplot to show the relative numbers of predator-driven Allee effect (AE) studies included in a recent review (Kramer *et al.* 2009) and book (Courchamp *et al.* 2008) on AEs. Studies are categorized by taxonomic group and type of study. Although not a comprehensive treatment of the predator-driven AE literature, there are several interesting observations. Most studies were on mammals and were observational. With the exception of one natural experiment in an aquatic invertebrate (AquInvert), natural experiments appear to be confined to mammals. Our definition of natural experiment includes species introductions and perhaps reflects a taxonomic bias in invasive species studies. Manipulative experiments are generally considered to give the best proof of predator-driven AEs, and there are similar numbers between insects and mammals. This might also reflect a bias because we considered a species reintroduction as a manipulation. Finally, two studies of insects, fish and reptiles, and one of AquInverts (Kramer & Drake 2010) were manipulative experiments done in laboratories. The references used to compile this graphic are presented in Appendix S1.

however, according to a recent literature review of the AE (Kramer *et al.* 2009) and book (Courchamp *et al.* 2008) there are relatively few studies published on the subject (Fig. 2). Furthermore, many of these are based on observations of single populations, and might not hold up to closer scrutiny. Two clear recommendations can be made here: first, we must consider the wider definitions of predator-driven AEs. Prey behaviours like the 'dilution effect' might be indicative of a predator-driven AE and have a long research history. Indeed, a crude search for the topical keywords '*dilution effect*' AND *predat** using the ISI Web of Science interface to the Science Citation Index Expanded from 1899 to present (performed 18/01/10; *indicates a wildcard representing a character string of any length) revealed some 73 references – approximately twice the number used in Fig. 2. Second, we launch a call for more carefully designed *in situ* field experiments, such as those by Turchin & Kareiva (1989), to demonstrate the existence of predator-driven demographic AEs despite nature's complexities.

Kramer & Drake (2010) merely (and modestly) hint at the implications of their findings, speculating a higher incidence of demographic AEs in populations of prey species subject to a type II functional response (a potentially large number of species). We, however, cannot resist the temptation to con-

sider briefly some untoward implications of predator-driven AEs using two examples chosen to highlight the complexities of considering multiple species interactions. First, removal of top predators can have cascading consequences when viewed in the context of food webs. For example, it seems that fishermen, by removing large predatory fish, freed the crown-of-thorns starfish *Acanthaster planci* from a weak predator-driven AE, which subsequently underwent a population boom with dire consequences for its reef-building coral prey (Dulvy, Freckleton & Polunin 2004). Second, while some anti-predator behaviours are effective to combat generalist predators, such behaviours might render the prey vulnerable to specialist predators. For example, Pacific herring *Clupea herangus pallasii* shoal in response to predation and humpback whales *Megaptera novaeangliae* use bubble netting to induce this behaviour before attacking the shoal from below, as if it were one single individual (Sharpe & Dill 1997).

Kramer & Drake (2010) have closed an important knowledge gap with the experimental demonstration of a predator-driven AE. These results show that despite more than half a century of research into the core processes of the AE, much remains to be studied. For example, and to close with a provocative question, we might now wonder whether the same principles driving predator-driven AEs could apply to species competing for limited resources, in what might become known as a competition-driven AE.

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Supporting Information

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

Appendix S1. A list of the predator-driven Allee effect studies that were used to compile Fig. 2.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

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