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Summary

1. In a population with Allee effects a positive relationship exists between fitness and population size or density. Allee effects may result in extinction thresholds and are therefore crucial in conservation and management. It has been shown theoretically that Allee effects can be driven by predation; however, there are few empirical data. Previous empirical work on Allee effects has emphasized that taxa with life-history characteristics such as co-operative breeding may be prone to such effects. Because predation is a general ecological mechanism, Allee effects may be more widespread than previously thought.

2. We used a series of simple heuristic models to develop a theoretical framework for understanding predation-driven Allee effects as a function of predator functional and aggregative responses.

3. Predators can create an Allee effect if they have a type I (linear) or type II (saturating) functional response without a type III (sigmoid) aggregative response, or vice versa. In addition, predation must be the main driver of prey dynamics, and prey must have little spatial or temporal refuge from predation.

4. We highlighted several, mainly unrecognized, examples of predation-driven Allee effects from the literature, the majority of which came from systems that had been perturbed by exploitation or introduced predators.

5. *Synthesis and applications*. Allee effects can arise from a general ecological process under a variety of different combinations of functional and aggregative responses. Allee effects may thus be present in a broad spectrum of different taxa with different types of life history, not only those taxa, such as broadcast spawners and co-operative breeders, on which empirical work has focused thus far. Conservation biologists and managers working with heavily exploited or threatened populations, or attempting reintroductions, should be aware of the possibility of a threshold population size or density below which extinction is likely. These thresholds can occur regardless of species life history, if predation is a major source of mortality and spatial and temporal predation refuges are limited.

Key-words: aggregative response, critical thresholds, functional response, local extinction, non-linear dynamics, positive density dependence

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Introduction

Allee effects (a positive relationship between fitness and population density or size) can create critical thresholds below which the population growth rate is negative and populations crash to extinction (Allee 1931; see reviews in Dennis 1989; Courchamp, Clutton-Brock & Grenfell 1999; Stephens & Sutherland 1999). Allee effects are critical for the management of endangered and exploited populations and for reintroductions

(Dennis 1989; Sinclair *et al.* 1998; Courchamp, Clutton-Brock & Grenfell 1999). Most empirical work on Allee effects has focused on species with a specific life-history trait that will reduce a component of fitness below a certain density. A well-known example is broadcast spawning in marine invertebrates with low adult dispersal, where there is a strong exponential relationship between local density or nearest neighbour distance and fertilization efficiency (Denny & Shibata 1989; Levitan, Sewell & Chia 1992; Levitan & Young 1995; Gascoigne & Lipcius 2004). Pollination in plants is to some extent an analogous system, where Allee effects have also been demonstrated (Lamont, Klinkhammer & Witkowski 1993; Groom 1998; Hackney & McGraw 2001). Reproductive

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Allee effects have also been shown empirically in co-operative breeders such as African wild dogs *Lycaon pictus*, where a critical pack size is required for successful reproduction (Courchamp & Macdonald 2001).

Empirical work on Allee effects has thus been mainly confined to taxa with a limited range of life-history characteristics. In this study we laid out a theoretical framework for Allee effects driven not by the specifics of species life history, but by a general ecological mechanism (predation). This means that Allee effects may occur in a wider range of taxa than has been considered by applied ecologists and conservation biologists to date.

Studies of Allee effects have also tended to focus on a given component of fitness (usually reproduction, as discussed above, but also survival; Calvert, Hedrick & Brower 1979; Clutton-Brock *et al.* 1999). Overall fitness is the net outcome of several density-dependent and density-independent components (fecundity, fertilization efficiency, larval or juvenile survival, growth rates, time to maturity, longevity, etc.) so overall fitness, and hence population growth rate, may not always react predictably to density-dependent changes in one component of fitness, such as fertilization efficiency. Hence, any particular component Allee effect (positive density dependence in one component of fitness, such as reproductive output) will not inevitably produce a demographic Allee effect (positive density dependence in the population growth rate; *sensu* Stephens, Sutherland & Freckleton 1999; for an example see Levitan 1991). Whether a component Allee effect creates a demographic Allee effect depends on the trade-offs between positive and negative density dependence due to various component effects. A component Allee effect will create a demographic Allee effect and drive a population to extinction only if that component of fitness has predominant control over population dynamics at the relevant population density. A demographic Allee effect is sometimes referred to as 'depensation', particularly in the fisheries literature.

Empirical studies of Allee effects have largely focused on positive density dependence in reproductive output, with mechanisms such as co-operative breeding, fertilization efficiency and mate finding (reviewed in Gascoigne & Lipcius 2004), and in some cases reproduction has become part of the definition of an Allee effect (Pulliam & Dunning 1997). The focus on specific reproductive traits that are likely to provide mechanisms for Allee effects has left many conservation biologists with the idea that Allee effects are generally confined to species with a limited range of life histories. However, although this is less well known, Allee effects in survival probability may also be caused by predation (Dennis & Patil 1984; Dennis 1989; Courchamp, Clutton-Brock & Grenfell 1999; Frank & Brickman 2001; Schreiber 2003). This is a more general ecological mechanism that may be applicable over a range of species with different life-history traits.

In a predator–prey relationship, predators react to prey density in three interrelated ways: (i) individual predators change their feeding rates in response to changes in prey density (the functional response); (ii) predators aggregate at patches of high prey density (the aggregative response); (iii) predator population size varies as a function of prey availability (the numerical response).

The first two act over shorter time scales (individual predator response time) than the third (predator population response time).

The predator functional response has been seen by modellers as a mechanism for creating an Allee effect, although it may not be identified as such (May 1977; Dennis & Patil 1984; Dennis 1989; Courchamp, Clutton-Brock & Grenfell 1999; Frank & Brickman 2001; Schreiber 2003). Conversely, it is usually overlooked as a mechanism by empiricists and conservation biologists (Pulliam & Dunning 1997). This is important because it means that applied ecologists, conservation biologists and managers generally have a narrow focus on Allee effects, as something relevant to a small range of taxa with specific life-history characteristics. Predation-driven Allee effects, however, are created by a general ecological mechanism and might therefore be relevant to any taxa that has been reduced to low population size or density.

In this study, we explored a theoretical framework for Allee effects driven by short time scale predator responses to prey (functional and aggregative responses). We addressed the following specific questions. (i) What combinations of functional and aggregative response types can create an Allee effect? (ii) Can certain types of functional or aggregative response mitigate Allee effects? (iii) What is the evidence for predation-driven Allee effects in the empirical literature? (iv) Can we predict the type of populations for which predation-driven Allee effects are likely to be a major conservation or management issue?

Methods

FUNCTIONAL RESPONSE MODEL

The functional response defines the rate of prey consumption, by a given number or density of predators, as a function of prey density (Holling 1959). The per capita functional response can be interpreted (given appropriate parameterization) as the probability of a prey individual being consumed by a predator as a function of prey density. A prey individual's probability of not being consumed (prey survival probability), for a given predator number or density, is thus (1 – the per capita functional response).

Predator–prey theory traditionally defines three types of functional response: linear (type I or Lotka–Volterra), hyperbolic (type II) and sigmoid (type III). Other types of functional response are possible; these characteristically alter predator–prey dynamics only at high density (Arditi 1982) or they combine aggregative and numerical responses (ratio-dependent functional responses; Arditi & Ginzburg 1989; Hanski 1991). The functional

response may also be defined in terms of the overall or mean functional response of a predator guild, which can also be measured and defined as type I, type II, type III, etc. (Seitz *et al.* 2001). For the purposes of this heuristic model it does not make any difference whether we regard the predators as one species or several, as long as their overall responses can be defined.

Type I (linear) functional response

In a type I functional response, prey consumption rate per predator initially increases linearly with prey density, before reaching a maximum. The type I functional response is considered a realistic model mainly for passive predators such as filter feeders and web-spinning spiders, although it may be more widespread (Arditi 1982).

We model a type I functional response as follows:

$$y = \alpha N \qquad \text{for } N \leq N_{\text{crit}}$$

$$y = \alpha N_{\text{crit}} \quad \text{for } N > N_{\text{crit}} \qquad \qquad \text{eqn 1}$$

where y = rate of prey consumption per predator, N = prey density, N_{crit} = prey density where predator consumption rate reaches a maximum, α = rate of consumption per unit prey density (Fig. 1a).

Corresponding prey survival probability for a given density of predators, as a result of predation with a type I functional response:

$$p = 1 - \gamma \qquad \text{for } N \leq N_{\text{crit}}$$

$$p = 1 - \frac{\gamma N_{\text{crit}}}{N} \quad \text{for } N > N_{\text{crit}} \quad \text{(Fig. 1b)} \qquad \text{eqn 2}$$

The coefficient above has been changed from α to γ to make it clear that this reinterpretation of the per capita functional response in terms of probabilities requires a parameterization of the equation such that such that $0 < p < 1$. This arrives naturally from the definition of the functional response: the functional response is usually defined as the rate of prey consumption per predator (Holling 1959). Therefore the per capita functional response is the prey consumption rate per predator per prey, which must be between 0 and 1. Because we are interested in the qualitative rather than the quantitative form of the relationships, we have subsumed all coefficients in the final equation into γ, which bounds the equation in the appropriate way.

Type II (hyperbolic) functional response

In a type II functional response, predator feeding rate rises hyperbolically to an asymptote as prey density increases. We model a type II functional response as follows (simplified from Holling 1959):

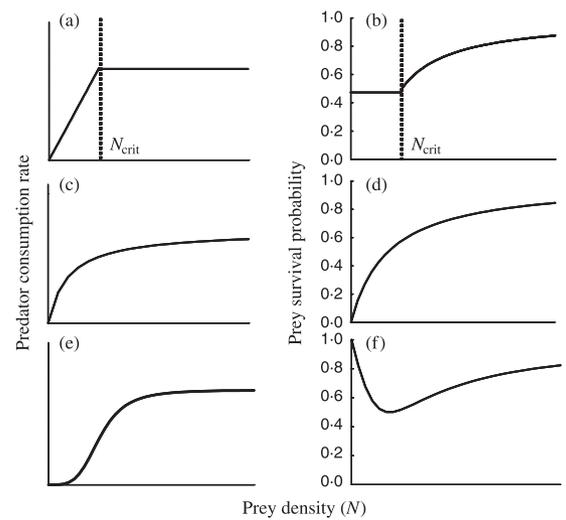$$y = \frac{\alpha N}{1 + \beta N} \quad \text{(Fig. 1c)} \qquad \text{eqn 3}$$

Fig. 1. The three major types of functional response, and the corresponding prey survival probability curve: type I functional response (a, b), type II functional response (c, d) and type III functional response (e, f). Graphs on the left are functional response curves, and show prey consumption rate per predator per unit time (*y*-axis) as a function of prey density (*x*-axis). Graphs on the right show probability of prey individuals escaping predation (*y*-axis) as a function of prey density (*x*-axis).

Corresponding prey survival probability for a given density of predators, as a result of predation with a type II functional response (with appropriate parameterization):

$$p = 1 - \frac{1}{1 + \gamma N} \quad \text{(Fig. 1d)} \qquad \text{eqn 4}$$

Type III (sigmoid) functional response

A type III functional response is similar to a type II at high prey densities. At medium and low prey densities, however, the relationship between predator consumption rate and prey density is different. For a type III response, the slope of the curve is at a maximum at intermediate prey density, rather than low prey density as in a type II response. A type III response can arise from 'prey switching', whereby at low density of prey species A, predators switch to feeding on prey species B.

We model a type III functional response as follows:

$$y = \frac{\alpha N^2}{1 + \beta N^2} \quad \text{(Fig. 1e)} \qquad \text{eqn 5}$$

Corresponding prey survival probability for a given density of predators, as a result of predation with a type III functional response:

$$p = 1 - \frac{N}{1 + \gamma N^2} \quad \text{(Fig. 1f)} \qquad \text{eqn 6}$$

FUNCTIONAL AND AGGREGATIVE RESPONSE MODEL

The functional response model above assumes a linear aggregative response, i.e. that predator numbers per prey are constant across the full range of prey density.

However, we can incorporate other aggregative responses into the model in an exactly analogous way to the functional response: (i) constant predator numbers (no aggregative response); (ii) constant predator to prey ratio, i.e. a linear (type I) aggregative response; (iii) asymptotic (type II) aggregative response; and (iv) sigmoid (type III) aggregative response. The total probability that a prey individual will be killed by a predator is the per capita functional response (the probability that an individual predator will kill that prey individual as a function of prey density) multiplied by the per capita aggregative response (the number of predators encountered by that prey individual as a function of prey density).

We focus on a type II functional response, which is typically the most common (Arditi 1982; Begon, Harper & Townsend 1996; Johnstone & Norris 2000; Seitz *et al.* 2001), and examine prey survival probability (*p*) with the various aggregative responses. We use δ as the coefficient for the aggregative response in the same way that we use γ as the coefficient of the functional response.

This leads to the following responses.
Constant predator numbers (no aggregative response):

$$p = 1 - \frac{1}{N(1 + \gamma N)} \qquad \text{eqn 7}$$

Linear aggregative response:

$$p = 1 - \frac{1}{1 + \gamma N} \qquad \text{eqn 8}$$

'type II' aggregative response:

$$p = 1 - \frac{1}{(1 + \delta N)(1 + \gamma N)} \qquad \text{eqn 9}$$

'type III' aggregative response:

$$p = 1 - \frac{N}{(1 + \delta N^2)(1 + \gamma N)} \qquad \text{eqn 10}$$

ADDING PREDATOR DENSITY TO THE FUNCTIONAL RESPONSE MODEL

We can extend the functional response model to look at prey survival probability as a function of both prey and predator density. Prey encounter probability (*p*(enc)) as a function of predator density can be modelled as a simple hyperbolic curve:

$$p(\text{enc}) = \frac{\delta P}{1 + \delta P} \qquad \text{eqn 11}$$

where *P* = predator density.

The per capita functional response (in this case a type II functional response) is the probability that an individual prey will be consumed if it encounters a predator as a function of prey density (*p*(con | enc)):

$$p(\text{con}|\text{enc}) = \frac{\gamma}{1 + \gamma N} \qquad \text{eqn 12}$$

where *N* = prey density.

The total probability of a prey individual being consumed by a predator is the product of the probability that the prey individual will encounter a predator and the probability that the prey will be consumed if it is encountered:

$$p(\text{con}) = p(\text{con} | \text{enc}) \times p(\text{enc}) \qquad \text{eqn 13}$$

With corresponding prey survival probability:

$$1 - p(\text{con}|\text{enc}) \times p(\text{enc}) = 1 - \frac{\delta \gamma P}{(1 + \delta P)(1 + \gamma N)} \qquad \text{eqn 14}$$

Results

FUNCTIONAL RESPONSE MODEL

To create an Allee effect, prey survival probability must be positively related to density at the lower end of the prey density scale, which is indicated by a positive slope in the relationship between prey survival probability and prey density. The type I functional response is positively density dependent above N_{crit} but density independent below N_{crit} (equation 2; Fig. 1b). A type I functional response could cause an Allee effect under these circumstances if the reduction in fitness at intermediate density is sufficient to create a negative population growth rate in the density independent part of the curve at lower density.

For a type II functional response, the slope of the curve is positive across the entire range of prey density, and the slope is steepest close to the origin. Hence (all else being equal), prey fitness due to predation is always positively density dependent with a type II functional response. Furthermore, fitness declines most strongly with density when density is low. Hence the type II functional response has the potential to create an Allee effect in prey population dynamics, and this Allee effect is likely to be stronger than that created by a type I functional response (equation 4; Fig. 1d).

A type III functional response, like a type I functional response, results in positive density dependence in prey fitness at high prey density but not at low prey density; in fact, the slope is negative at lower densities. A type III response can keep prey at a low stable equilibrium, corresponding to the minimum in the graph above (sometimes called a 'predator pit'). This functional response does not have the potential to create an Allee effect, and could potentially counteract an Allee effect in some other component of fitness (equation 6; Fig. 1f).

FUNCTIONAL AND AGGREGATIVE RESPONSE MODEL

The Allee effect generated by a type II functional response is eliminated by a type III aggregative response (equation 10; Fig. 2). However, with other types of functional response, or with constant predator density, the Allee effect is maintained (equations 7–9; Fig. 2). This also applies in reverse; a type II aggregative response can create an Allee effect that is mitigated by a type III functional response but maintained by other types of
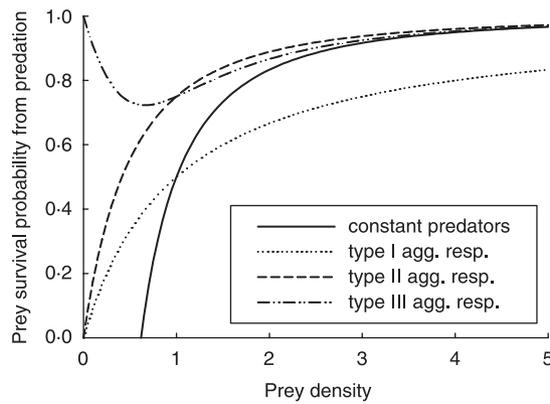
Fig. 2. Different types of aggregative response (agg. resp.) (constant predators = no aggregative response, or type I, type II or type III aggregative responses) combined with a type II functional response ($\delta = \gamma = 1$).

Fig. 3. Contours of equal prey survival probability as a function of prey numbers (N) and predator numbers (P), with a type II functional response and no aggregative response ($\delta = \gamma = 1$).

functional response. A type II functional response with constant predator numbers creates the strongest Allee effect, followed by a type II response with a type I aggregative response, followed by two type II responses. The effect of each combination of functional and aggregative response is shown in Table 1.

ADDING PREDATOR DENSITY TO THE FUNCTIONAL RESPONSE MODEL

When the functional response is of type II, prey survival probability depends mainly on predator density (P) at low prey density, and mainly on prey density (N) at high predator density (Fig. 3). The true relative importance of prey and predator density depends to some extent on the coefficients (here set to be equal), but this model implies that dynamics at low prey density will be dominated by changes in predator numbers rather than prey numbers, i.e. the aggregative rather than the functional response. Thus the shape and strength of the aggregative response is likely to be important in determining the strength of the predator-driven Allee effect.
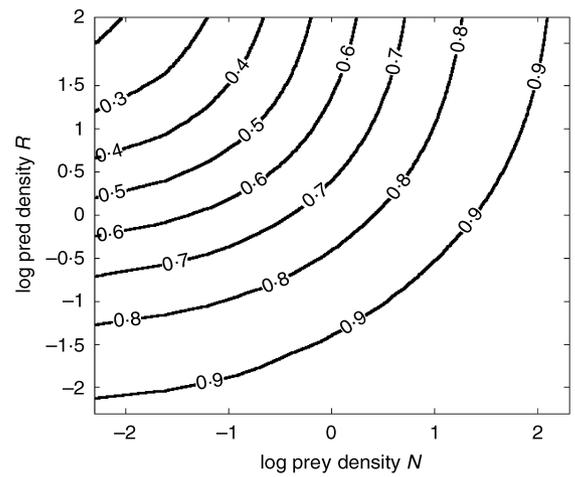
EMPIRICAL DATA

Predator-driven Allee effects are difficult to demonstrate in the field because clear evidence requires data on predation rates and prey dynamics across a range of prey population size; however, we did find several clear examples (Table 2). It is striking that Table 2 contains examples from a range of taxa, from different habitats and with different life histories, including mammals (marsupial and placental), birds, fish (marine, freshwater and anadramous), molluscs and echinoderms. It includes species that reproduce only once (migratory Pacific salmonids) vs. over many years (seabirds, cod *Gadus morhua*, many mammals), species that produce thousands or millions of eggs (fish, invertebrates) vs. one offspring per year (seabirds, quokka *Setonix brachyurus*, rock wallabies *Petrogale lateralis*), species with prolonged parental care (quokka, up to 40 weeks) vs. species with none (most fish, invertebrates), species with complex social structures (quokka, meerkat *Suricatta suricatta*) vs. species with none (invertebrates) and

Table 1. Summary of modelling results: outcome of combinations of functional and aggregative responses and circumstances in which they might occur

Functional response	Aggregative response	Allee effect?	Circumstances
Type I	Not type III	Yes: weak	Passive predators (filter feeders, web-spinning spiders)
Type II	Not type III	Yes	Predators aggregate to high prey density but do not avoid patches of low prey density or switch to alternative prey
Type III	Any	No	Predators switch to alternative prey at low prey density
Not type III	None	Yes: strong	Predators do not switch to alternative prey and do not alter their density in response to prey density (generalist or sessile predators)
Not type III	Type I	Yes: weak	??No information about type I aggregative response; probably not very likely
Not type III	Type II	Yes	Predators aggregate to high prey density but do not avoid patches of low prey density or switch to alternative prey
Any	Type III	No	Predators aggregate to high prey density and avoid patches of low prey density; less likely for territorial or agonistic predators

Table 2. Empirical evidence for a predator-driven Allee effect. Our criteria were (i) that prey in small/sparse populations have higher mortality than those in large/dense populations due to predation (component Allee effect), or (ii) that predation causes a lower population growth rate or higher extinction risk for small/sparse populations than for large/dense ones (demographic Allee effect)

Prey species	Predator species	Outcome and type of Allee effect (demographic vs. component)	Reference
Quokka *Setonix brachyurus*	Introduced foxes *Vulpes vulpes* and cats *Felis catus*	Critical population size of 100–150 animals below which population goes extinct (demographic Allee effect)	Sinclair *et al.* (1998)
Black footed rock wallabies *Petrogale lateralis*	Introduced foxes	Critical population size of 5–10 animals below which population goes extinct (demographic Allee effect)	Sinclair *et al.* (1998)
Eastern barred bandicoot *Perameles gunnii*	Introduced foxes and cats	Accelerating population decline due to predation (demographic Allee effect)	Sinclair *et al.* (1998)
Hutton's and sooty shearwaters *Puffinus huttoni*, *Puffinus griseus*	Introduced pigs *Sus scrofa* and stoats *Mustela erminea*	Small colonies in decline due to predation; large colonies stable. Critical threshold of *c.* 600 pairs (demographic Allee effect)	Cuthbert (2002)
Thick-billed murre *Uria lomvia*	Gulls	Small and/or sparse colonies declining due to gull predation; large dense colonies stable (demographic Allee effect)	Gilchrist (1999)
Migrating salmonids	Mergansers *Mergus merganser*	Higher proportion of salmon lost to predation when population is smaller (component Allee effect in survival).	Wood (1987)
Cod *Gadus morhua*	Commercial fishing	Stock collapse because higher proportion of the population caught per unit effort as population declined (demographic Allee effect)	Rose & Kulka (1999)
Rainbow trout *Oncorhynchus mykiss*, walleye *Stizostedion vitreum*, pike *Esox lucius*, lake trout *Salvelinus namycush*	Recreational fishing	Sequential stock collapse because higher proportion of the population caught per unit effort as population declined (demographic Allee effect)	Post *et al.* (2002)
Soft-shelled clam *Mya arenaria*	Blue crab *Callinectes sapidus*	Type II functional response in mud habitats leads to seasonal local extinction, while type III functional response in sand allows persistence (demographic Allee effect)	Eggleston, Lipcius & Hines (1992), Seitz *et al.* (2001)
Crown-of-thorns starfish *Acanthaster planci*	Coral reef fishes Balistidae, Labridae, Lethrinidae	Starfish have negative population growth rate at low population size and positive population growth rate at high population size; threshold *c.* 250 km^{-2} of reef. Population size negatively correlated to density of predatory fish (demographic Allee effect)	Dulvy, Freckleton & Polunin (2004)
Meerkat *Suricata suricatta*	Jackal *Canis mesomelas*, eagles *Polemaetus bellicosus* and *Aquila rapax* and others	Juvenile survival lower in small groups than large groups in areas with high predator densities but lower in large groups than small groups in areas with low predator densities (component Allee effect in juvenile survival).	Clutton-Brock *et al.* (1999)

grazers/detritivores (quokka, rock wallaby, clam) vs. top predators (cod, most of the lake fish species, seabirds).

From an applied standpoint it is extremely significant that human intervention has played a dominant role in the ecosystem, such that prey population size has been reduced and the stabilizing effect of high prey density has been removed. In the first three examples (endangered Australian marsupials; Sinclair *et al.* 1998), hunting pressure has driven prey populations to such low levels that they can easily be driven to local extinction by introduced predators, and there is a critical population size threshold for successful reintroduction. Hunting also reduced the size and density of thick-billed murre *Uria lomvia* colonies (Gilchrist 1999), rendering them vulnerable to gull predation. Many shearwater (*Puffinus huttoni*, *Puffinus griseus*) colonies in New Zealand were reduced in size by feral pigs *Sus scrofa*, such that the smaller and sparser colonies are now vulnerable to predation by stoats *Mustela erminea* (Cuthbert 2002). In two other examples, cod *Gadus morhua* and Canadian lake fish (rainbow trout *Oncorhynchus mykiss*, walleye *Stizostedion vitreum*, pike *Esox lucius* and lake trout *Salvelinus namycush*), humans are the predators creating the Allee effect (Rose & Kulka 1999; Post *et al.* 2002). In two other examples, it is predator numbers that have been depleted by humans. Crown-of-thorns starfish *Acanthaster planci* are maintained at constant low population density in the presence of fish predators but can outbreak to high population densities where predators have been depleted by humans (Dulvy, Freckleton & Polunin 2004). Juvenile survival of the meerkat *Suricata suricatta* is lower in small groups than in large groups in a national park, but lower in large groups than in small groups in nearby ranchland where predators are less dense (Clutton-Brock *et al.* 1999). Finally, in the two examples where human intervention is not important (migrating salmonids, soft-shelled clam *Mya arenaria*), the overall system is stable despite Allee effects.

Discussion

FUNCTIONAL AND AGGREGATIVE RESPONSES AND THE ALLEE EFFECT

The strongest Allee effect arises from a type II functional response with either no or a type II aggregative response (Table 1). Predator–prey models incorporating a type II functional response have unstable prey dynamics (May 1974; Hassell 1978) and can cause critical population size effects in prey (Dennis & Patil 1984; Sinclair *et al.* 1998; Cantrell, Cosner & Fagan 2001). Fisheries scientists have also considered the 'functional' responses of fishermen in terms of changes in effort with changes in fish stock size, and shown that a type II 'functional response' of fishing effort with declining stock size can result in critical thresholds for stock collapse (Hilborn & Walters 1992).

The association between functional response and Allee effects in prey has not been made to date in empirical studies, the predator–prey literature and general ecological texts. From a management and conservation perspective, it is critical to realize that predation has the potential to create an Allee effect in prey dynamics, without recourse to specific traits in the prey life history such as co-operative breeding or broadcast spawning.

Given the importance of predator density at low prey density (Fig. 3), the form of the aggregative response is likely to be very important in determining the presence and strength of a predator-driven Allee effect. Unfortunately, it is rarely quantified in empirical studies. A type III aggregative response, which would mitigate the Allee effect, would result when predators actively avoid areas of low prey density as well as actively seeking out areas of high prey density, and would be less likely where predators interfere with each other, are territorial or are agonistic (Roger & Hassell 1974; Rohner & Krebs 1998; Clark *et al.* 1999).

MODEL LIMITATIONS

Our model is simplified in that it does not incorporate a numerical response for predators separate from the aggregative response, since it acts over a longer time period and would thus require a more complicated model. We are looking at short-term Allee effects, which might in the long term be mitigated (or exacerbated) by a predator numerical response (among other things).

The conclusions from this model correspond well to those from more specific predator–prey models. In a Lotka–Volterra predator–prey system (linear functional response), aggregation is generally destabilizing unless it is accelerating, i.e. there are disproportionate numbers of predators in dense patches (Murdoch & Stewart-Oaten 1989), a type III aggregative response. Overall, predator–prey modellers have come to varying conclusions about the stabilizing effect of predator aggregation in model systems (Murdoch 1994), not surprising as the form of the response (i.e. the specifics of a given model) is critical to prey dynamics.

Despite its simplicity, the model gives a useful overview of where predator-driven Allee effects are likely to occur. In reality, the shape and strength of responses are variable in space and time (Hanski 1991; Morgan, Brown & Thorson 1997; Fauchald, Erikstad & Skarsfjord 2000; Johnstone & Norris 2000) and are difficult to measure. This model is useful in highlighting the role and consequences of the various responses.

PREY SPATIAL STRUCTURE

Prey can have three types of distribution: random, uniform and clumped. For a random distribution, functional and aggregative responses are both relevant. As the distribution becomes more uniform, there is less scope for an aggregative response, so a functional response-driven Allee effect potentially becomes more important. As the distribution becomes more clumped, a higher proportion of prey is living at high density, so

the functional response becomes less relevant and the aggregative response more important. For extremely aggregated distributions (such as schooling fish), predators can respond to prey population size or density both within aggregations and between aggregations, although the time scale of predator response may be much shorter within aggregations than between, hence this model is more relevant to predator movements within aggregations.

The literature on the effect of spatial heterogeneity on predator–prey relationships is substantial (Hassell 1984; Kareiva 1987; Taylor 1990; Hawkins, Thomas & Hochberg 1993; Murdoch 1994; Cosner *et al*. 1999; McCauley *et al*. 2000). In general, spatial heterogeneity in predator or prey distribution is stabilizing through the existence of refuge groups, although there are exceptions (Kareiva 1987).

Dispersal between subpopulations also reduces the likelihood of a demographic Allee effect (Taylor 1990; McCauley *et al*. 2000; Frank & Brickman 2000, 2001; but see also Murdoch *et al*. 1996). Even a small amount of connectivity between subpopulations may be sufficient to reduce extinction risk for each subpopulation significantly (Hill, Hastings & Botsford 2002), and habitat fragmentation that isolates small subpopulations can create a predator-driven Allee effect in model systems (Cantrell, Cosner & Fagan 2001).

EMPIRICAL EVIDENCE FOR PREDATOR-DRIVEN ALLEE EFFECTS

How likely is a predator-driven Allee effect in natural systems? The type II functional response is the most common (Arditi 1982; Begon, Harper & Townsend 1996; Johnstone & Norris 2000; Seitz *et al*. 2001); this is the case for both generalist and specialist predators (Murdoch & Oaten 1975; Sinclair *et al*. 1998). Specialist predators are most likely to have type III aggregative and numerical responses, but may not (Johnstone & Norris 2000). However, generalist predators seem the most likely candidates for creating Allee effects in prey, since they are the least likely to respond strongly to prey density over both short (aggregative response) and long (numerical response) time scales. In fact, generalist predators, or even predators with two main prey species, need not show any numerical or aggregative response to a given prey species (Cappuccino 1987; Sinclair *et al*. 1998).

In addition, prey as well as predator life history plays a role in determining the functional response. Some predator avoidance strategies, such as crypsis and refuges, are more effective at lower densities, yielding a type III functional response. Prey species with passive, non-density-dependent predation avoidance strategies, such as armouring, spines or aposematic colouring, are likely to yield a type II predator functional response (Cappuccino 1987; Jeschke & Tollrian 2000; Seitz *et al*. 2001). Such prey species use weight of numbers as an anti-predator strategy (the dilution effect) and this makes them theoretically vulnerable to Allee effects.

PREDATOR-DRIVEN ALLEE EFFECTS AND ECOSYSTEM RESPONSE

Predator-driven Allee effects may provide a useful tool in clarifying ecosystem-level responses to anthropogenic disturbance. Ecosystems can be regarded (simplistically) as a series of interconnected predator–prey relationships with different types of stabilizing factors. A predator–prey modelling framework may be valid even in systems that seem much more complicated (Murdoch *et al*. 2002). Ecosystems as diverse as rangelands, lakes and coral reefs have shown abrupt transitions to alternative stable states, with consumer dynamics as an important mediating factor (Noy-Meir 1975; Scheffer *et al*. 2001). Allee effects predict thresholds and non-linear population dynamics, and may provide a conceptual link between population, predator–prey and ecosystem dynamics.

SYNTHESIS AND APPLICATIONS

Conservation biologists and managers spend much of their time dealing with populations that are small or sparse, having been depleted by human activity, or with populations in fragmented habitats, or with attempts at reintroduction. In all these population types it is crucial to be aware that there is the potential for critical extinction thresholds in population size or density, and that these thresholds can occur in a wide range of taxa with different life histories. We present examples of predation-driven Allee effects in mammals (four examples), seabirds (two), fish (three) and marine invertebrates (two). Predator species include mammals (non-human) (five), birds (three), fish (one), invertebrates (one) and humans (two), mainly in systems where prey populations have been reduced for other reasons (habitat loss, exploitation, etc.). Managers and conservationists need to be aware of the potential for predation-driven Allee effects if (i) predation is a major source of mortality, (ii) prey have little spatial or temporal refuge from predation and (iii) predators are generalists and/or are territorial or agonistic. Precautionary management of such populations would involve taking Allee effects into account, particularly as Allee effects are not always apparent in the dynamics of spatially structured populations until collapse has occurred (Frank & Brickman 2000, 2001). From the perspective of conservation science, there is a large body of theory on positive density dependence and stability in ecological interactions that has so far not been integrated into work on Allee effects, but would be of immense practical use in the conservation and management of endangered species.

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