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## Effets Allee démographiques : évidence empirique et détection

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# **Demographic Allee effects: empirical evidence and detection**

**Stephen David Gregory**



## Abstract

A demographic Allee effect describes decreased population growth rate at reduced population size or density. They act to accelerate decline in declining populations, such as those reduced by habitat loss or overexploitation, and decelerate spread in increasing populations, such as those recovering from a reduced size or an introduced species. Demographic Allee effects are underpinned by one or more component Allee effects that describe the same dynamics as the demographic Allee effect but affecting surrogates of individual fitness, such as reproduction or survival, rather than population growth rate. The number of species and mechanisms revealing component Allee effects has been increasing exponentially. In contrast, the number of species and mechanisms revealing demographic Allee effects remains very few. Chapter two of this thesis reviews the concepts of component and demographic Allee effects with special reference to the vanishing chance of finding a mate at a reduced population size - a mate-finding Allee effect.

Given the abundance of component Allee effects and increasing numbers of threatened and invasive populations, observations of demographic Allee effects ought to be increasing too. Over 15 years of meta-analytical studies to quantify their commonness have, however, revealed but a few, questionable demographic Allee effects observations. There are, however, a couple of exceptions to this conclusion. Notably, a survey of fisheries experts suggested that demographic Allee effects affected almost half of a large sample of fish stocks. Chapter three of this thesis examines the evidence for demographic Allee effects in 1198 species' natural populations. This chapter was motivated by an expectation of a high incidence of demographic Allee effects and to assess the methods used to detect them. This expectation was, however, unfulfilled - approximately one percent of the 1198 species exhibited a demographic Allee effect and this result was sensitive to measurement error and other sources of variation.

There are many possible reasons why a component Allee effect might not be seen to manifest as a demographic Allee effect including the fitness benefits of reduced competition at reduced population size. Assuming the existence of demographic Allee effect, however, detecting it using conventional statistical methods might be complicated by the high variation in the population size required for it to reach the reduced size where the demographic Allee effect acts. Furthermore, this variation is likely to be distorted and exaggerated by measurement and observer error, deterministic trends, climatic fluctuations, interspecific interactions, and migration. Detection of a high order non-linear population dynamic, like a demographic Allee effect, from such high variation time series is woeful. Chapter four is devoted to demonstrating and then overcoming this conundrum. In it, I build on existing methods to develop a statistical procedure to better detect demographic Allee effects, thereby paving the way to better understand and predict them.

As might be expected, theory predicts that social species - species that depend on cooperative conspecifics to breed, feed and succeed - will be prone to demographic Allee effects. If their population declines below a specific number of individuals, then the remaining individuals cannot survive and must flee or perish. Using the statistical procedure developed in chapter four, in chapter five I show that demographic Allee effects are more likely in UK bats. Although possibly an artefact of the methods used to quantify them, I show that UK bats - social animals that gather in single-sex colonies to breed - exhibit a high incidence of demographic Allee effects. Almost half of the species examined revealed demographic Allee effects compared to their near absence in the 1198 random populations. Based on this finding, I predict that other group-forming social species will be prone to demographic Allee effects. This prediction remains to be tested.

Throughout the thesis, I try to use a few simple and engaging examples, including Atlantic cod and Kalahari meerkats, to illustrate some of the subtleties and complexities encountered while studying Allee effects, and particularly demographic Allee effects.

## **Declaration**

Une thèse faite soumise à l'Université Paris Sud XI le March 23, 2010 selon les régulations d'obtenir un doctorat. Je déclare que cette thèse est une œuvre personnelle.

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# **Chapter 1**

## **General introduction**

## 1.1 What is in a thesis introduction?

Before writing this introduction, I read a large number of introductions from theses in my field. My hope was to find some inspiration. Instead, all I found served to discourage me. It was not that the introductions were bad or uninformative, but rather they failed to tackle what I consider to be the question central to the introduction: *why did I do a thesis on this subject?* or more simply *why did I do this thesis?*

Of course, a thesis introduction should provide more than just an answer to this question. It should also provide (i) necessary definitions, (ii) a context for the thesis and (iii) a statement of the problem addressed by the thesis. Below, I address each of these sections in turn. Importantly, I will then also attempt to answer the question (iv) *why did I do this thesis?*

## 1.2 What is a demographic Allee effect?

There are two types of Allee effects: (1) a component Allee effect, and (2) a demographic Allee effect (Stephens et al. 1999). Both types of Allee effects affect reduced populations - that is populations that are smaller than they would be without human interference such as hunting or habitat destruction (Barry W. Brook et al. 2008). For example, cod populations worldwide have been overfished and their populations are much smaller today than they were in the past (Myers et al. 1997). This is clearly illustrated using the Atlantic cod *Gadus morhua* population off the coast of Newfoundland in Canada (see Figure 1.1). For 100 years between 1850 and 1950, small fishing boats were catching between 100 and 250 thousand tons of cod per year. Then after 1950 cod were fished using larger bottom-trawling boats. These bottom-trawlers were very effective at capturing cod and by the 1970's more than 700 thousand tons of cod were being caught - almost three times the size of landings only 30 years before. Perhaps unsurprisingly then, the cod population declined throughout the 1980s until in 1992 when, despite government and international protection, the Newfoundland cod population all but disappeared (Myers et al. 1997).

It has been suggested that the Newfoundland cod population suffered from a component and demographic Allee effect (Anderson and Rose 2001). A component Allee effect describes how when the population is reduced, like that of the Newfoundland cod in the 1970s, individuals might have difficulties accomplishing normal tasks, such as finding a sexual partner with whom to reproduce. It follows that as the population gets smaller, so the chance of each individual finding a sexual partner decreases, giving rise to a component Allee effect (Figure 1.2a). Component Allee effects can arise due to myriad mechanisms and as such can affect a range of 'fitness' components including reproduction, survival and even surrogate measures of these 'fitness' components such as weight gain (Stephens et al. 1999). A demographic Allee effect describes how the component Allee effect can cause changes in the size of the population. Sometimes, and as has been suggested for the Newfoundland cod, the decreased chance of finding a sexual partner with decreasing population size (the component Allee effect) results in fewer young being born because some of the individuals do not find a sexual partner. This means the population will be smaller in the following year, which again results in even fewer young being born. This results in the population declining at an accelerating rate each year, and this characterises a demographic Allee effect (Figure 1.2b). In cases when the population declines below a critical threshold size, known as the Allee threshold, the demographic Allee effect should drive the population to extinction in what has been termed an extinction vortex (Figure 1.3).

So, in the Newfoundland cod example, a possible component Allee effect in reproduction

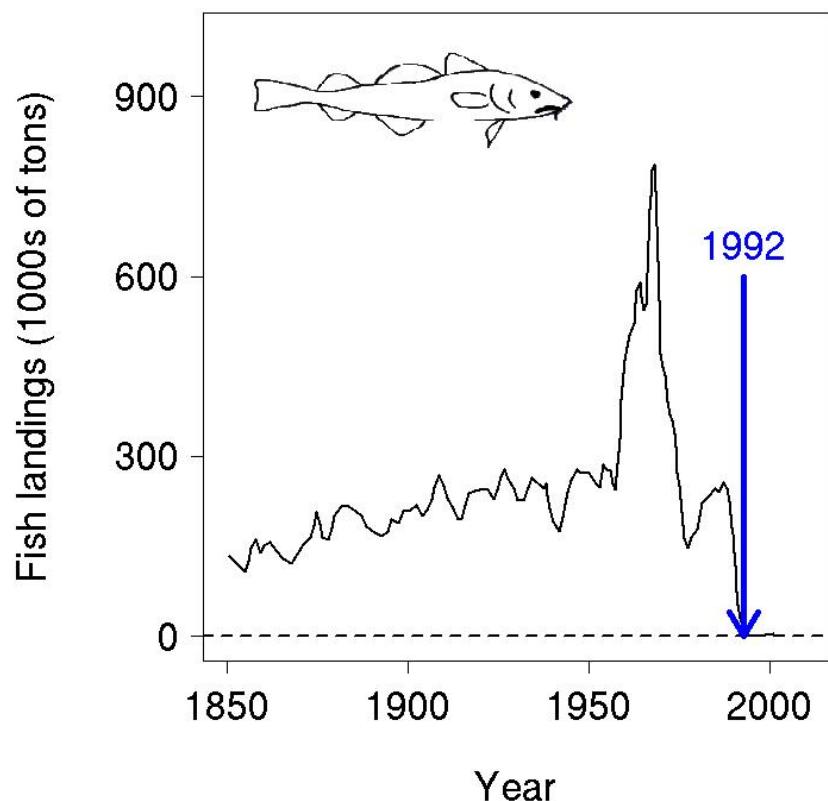


Figure 1.1: Newfoundland cod population decline: it appears that cod were fished sustainably until the late 1950s when bottom-trawlers increased cod landings. Increased landings correspond to a reduced population, and despite international restrictions including a moratorium, the population crashed in 1992 and the fishery was closed.

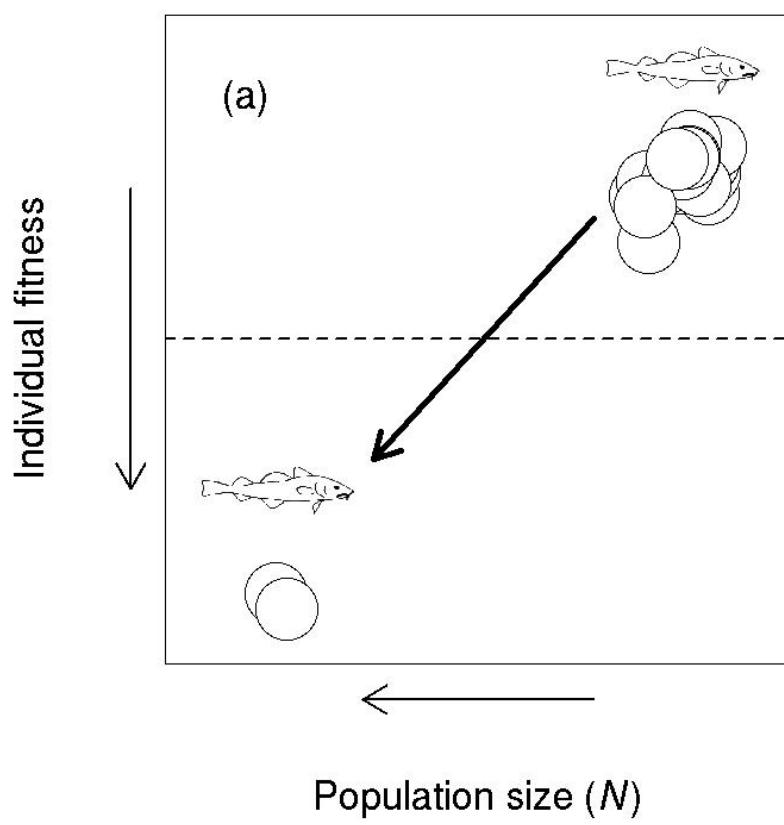


Figure 1.2: (a) A plot illustrating a component Allee effect in Newfoundland cod. The ‘fitness’ of each individual - here illustrated as the number of eggs produced per individual - decreases with decreasing population size.

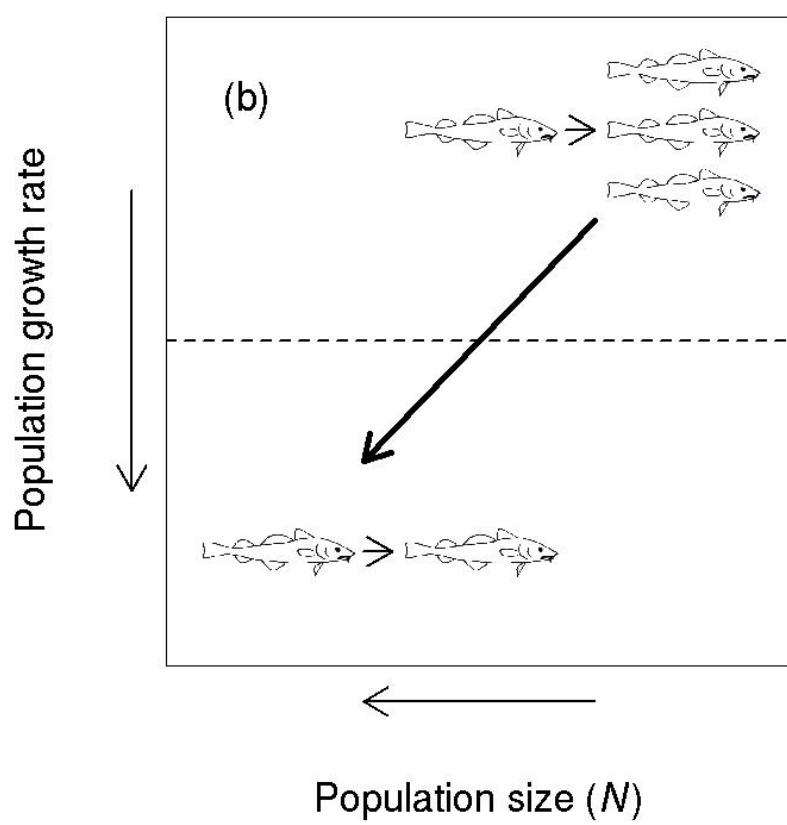


Figure 1.2: (b) A plot illustrating a demographic Allee effect in Newfoundland cod. The population growth rate - i.e., the number of reproducing adults produced per individual - decreases with decreasing population size.

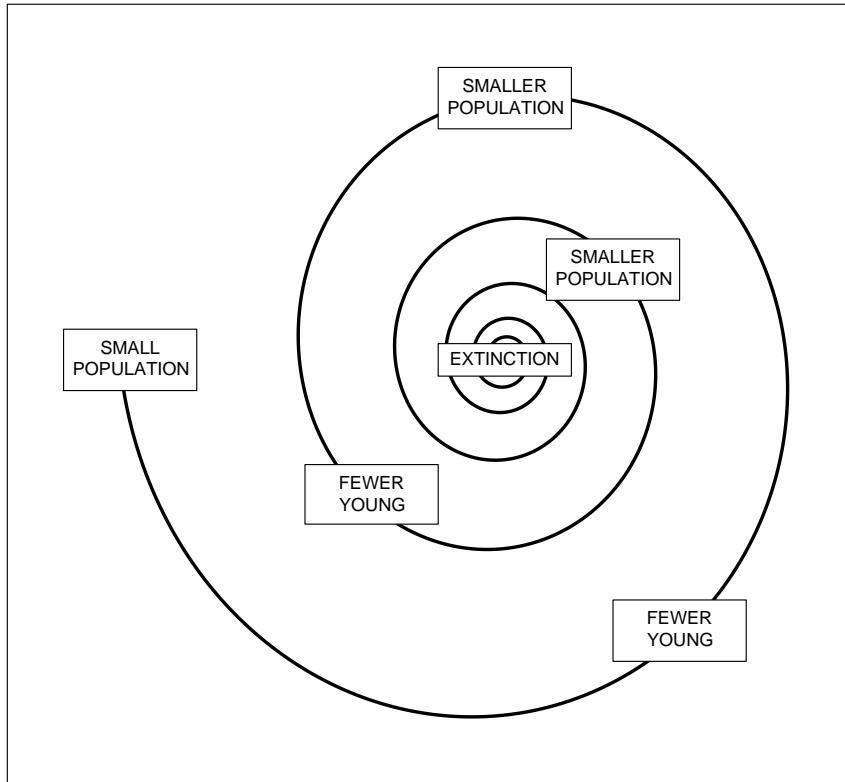


Figure 1.3: An illustration of how decreased reproduction in a small population can cause the population to become progressively smaller at an accelerating rate, until the population finally reaches extinction. This describes a demographic Allee effect, and the accelerated decline to extinction has been termed an “extinction vortex”.

could have led to a demographic Allee effect that caused the population to disappear (in this case the population did not go extinct but was scarcely detectable for a number of years; Anderson and Rose 2001). The co-occurrence of a component and demographic Allee effect would be no coincidence; whenever we observe a demographic Allee effect, we know that there must be a component Allee effect driving it (Stephens et al. 1999). Interestingly, more than one component Allee effect may underpin a demographic Allee effect (Berec et al. 2007), and this might be the case for cod. For example, Rowe et al. (2004) showed that reduced cod populations have reduced *per capita* reproductive output. Swain and Sinclair (2000) and Walters and Kitchell (2001) suggested that reduced numbers of adult cod would allow their prey fish populations to increase, which would then predate high numbers of cod eggs in a feedback loop known as the cultivation.

## 1.3 How common are demographic Allee effects?

Although a component Allee effect must underpin a demographic Allee effect, the reverse is not always true (Stephens et al. 1999). Scientists have observed component Allee effects in many species of animals and plants (see Kramer et al. 2009 for a review). Convincing observations of demographic Allee effects are, on the other hand, uncommon. Indeed, there have been several investigations attempting to isolate a demographic Allee effect (known as depensation in the fisheries literature) in cod yet there is still debate as to whether cod have suffered a demographic Allee effect (Shelton and Healey 1999). Perhaps the single most convincing evidence supporting this hypothesis is that the population has not, to this day, shown signs consistent with recovery (Lilly et al. 2008). Based on the belief that the cod population did not have a demographic Allee effect, several authors predicted that the population would double in size every 3 years (Myers et al. 1997) or 5-6 years (Hutchings 1999). A failure to recover from a reduced population size is consistent with the existence of a demographic Allee effect (Fu et al. 2001).

There are many possible explanations why we might infrequently observe demographic Allee effects and these can be usefully placed into three categories: (1) detection, (2) manifestation, and (3) observation. Various statistical tests have been used to search for evidence of demographic Allee effects as illustrated by the two following examples. (Walters and Kitchell 2001) asked three independent scientists to examine stock-recruitment curves and cast a vote for or against evidence of depensation. At the other extreme, (Liermann and Hilborn 1997) reanalyzed the stock-recruitment datasets of Myers et al. (1995) using a Ricker model reparameterized to ensure the depensation parameter had an unequivocal biological meaning. Their model was non-linear (but able to take a linear form) and they estimated the model parameters using a semi-Bayesian approach. Moreover, Liermann and Hilborn (1997) compared their depensation model to an equivalent model without the depensation parameter. Interestingly, Walters and Kitchell (2001) recorded high support for depensation while Liermann and Hilborn (1997) were unable to confirm or refute depensation in the species they analysed.

Given the variety of statistical approaches that have been deployed to detect demographic Allee effects, the emerging consensus is that they are uncommon (Courchamp et al. 2008, Kramer et al. 2009). Many researchers have speculated at reasons for this. Among other problems, they have noted that (i) short and highly variable datasets might not provide sufficient information to estimate Allee parameters, (ii) the datasets might not represent closed populations, (iii) the datasets might not span the spectrum of population sizes required to observe a demographic Allee effect, (iv) Allee effect models require estimation of at least one additional parameter (epitomising the Allee effect) compared to simpler population growth models, and (v) various factors complicating the detection of other population growth dynamics, such as trending and measurement error, will also affect our ability to detect demographic Allee effects. Whether any one or a combination of these factors can explain the apparent scarcity of evidence for demographic Allee effects remains unanswered.

Besides the long list of potential factors inhibiting the detection of demographic Allee effects, there is another explanation for their apparent scarcity - lack of manifestation. A component Allee effect might not manifest as a demographic Allee effect simply because there is a corresponding increase in some other component(s) of ‘fitness’ that offsets the component Allee effect (Stephens et al. 1999). For example, an overexploited cod population suffering from a component Allee effect in reproduction due to a scarcity of suitable mates (a mate-finding Allee effect) might never suffer a demographic Allee effect because the reduced population size encourages immigration of adult cod (Hutchinson et al. 2003).

The emergence of mechanisms that increase individual ‘fitness’ at reduced population sizes

and offset component Allee effects highlights an important point affecting the evidence for demographic Allee effects - we rarely observe populations around the sizes at which they act. Since component Allee effects affect individual ‘fitness’ they are subject to natural selection, and so organisms vulnerable to Allee effects ought to have evolved mechanisms either to counterbalance them or avoid population sizes or densities at which they act (Courchamp et al. 2008). Returning briefly to our cod example: Olsen et al. (2004) showed how, prior to their population collapse, cod were maturing younger suggesting that they were evolving to avoid small population sizes. Allee effects are, therefore, unstable dynamical states defined by the existence of an unstable threshold population size called the Allee threshold: populations near the Allee threshold will either quickly increase to their stable positive threshold (known as the carrying capacity) or quickly decline to extinction (Courchamp et al. 1999). For this reason Allee effects - both component and demographic - are theoretically more likely to be observed in populations that have been recently reduced and have recovered or gone extinct (i.e., NOT small or sparse populations *per se*).

## **1.4 Why are demographic Allee effects important?**

Demographic Allee effects are naturally uncommon because natural selection should drive evolution of mechanisms to prevent populations reaching the sizes at which they act. Furthermore, even if they are present, they are likely to be difficult to detect. So why then are demographic Allee effects important?

As already alluded to, demographic Allee effects are defined by an accelerating rate of population decline at reduced population size (or conversely an increase in population growth in a population at reduced size as might occur during a species introduction; see below). The key to understanding the importance of demographic Allee effects is in the word used to describe the population state at which they act: reduced. Many organisms cooperate for many reasons including to hunt food, to protect against predators, and to rear offspring. When their population is reduced to a small size there might be too few individuals to cooperate effectively with a corresponding decline in individual ‘fitness’, and a possible demographic Allee effect (Stephens and Sutherland 1999). Warder Clyde Allee (1885 - 1955) was the first to describe this possibility using the term “proto-cooperation” (Allee et al. 1949). Interestingly, he was a Quaker and Quakers, known as the Religious Society of Friends, express their beliefs as individuals but unite to take group decisions ([http://en.wikipedia.org/wiki/Religious\\_Society\\_of\\_Friends](http://en.wikipedia.org/wiki/Religious_Society_of_Friends)). Perhaps Allee’s belief in action ‘for the greater good’ drove him to describe proto-cooperation as a precursor to human cooperation?

Demographic Allee effects affect populations that are reduced in size. They therefore act independently of the factor that drives the population decline. Consequently, demographic Allee effects can affect any species that cooperates - even at a rudimentary level such as cooperating to sexually reproduce or gathering selfishly to reduce individual predation risk - and whose population is being reduced by any factor. Clearly, a demographic Allee effect is a prime suspect in the sudden collapse of the Newfoundland cod population. Unfortunately, the drivers of biodiversity loss rarely work singularly (Barry W. Brook et al. 2008) as, once again, can be illustrated using our cod example. Rose (2004) showed how changes in cod stocks were best described using a combination of exploitation and climate changes. Unfortunately, cod populations are not the only populations to come under threat from anthropogenic activity - there are more species at threat from anthropogenic activity today than ever Vitousek et al. (1997). Thus there is also a greater urgency than ever to try to understand where and when component Allee effects might manifest as demographic Allee effects.

## 1.5 Beyond cod

Until this point in the introduction, I have tried to illustrate the demographic Allee effect using only the Atlantic cod as an example. It should be clear, however, that component Allee effects, and therefore demographic Allee effects, can affect a much wider range of species. Kramer et al. (2009) recently reviewed studies published on Allee effects. In summary, they show that component Allee effects have been isolated in all major taxonomic groups except reptiles, and can act via a wide range of potential mechanisms. In addition, they review the support for demographic Allee effects emerging from meta-analyses and suggest that they are uncommon. Disregarding the potential bias that a failure to isolate a demographic Allee effect is a less desirable, and therefore less publishable, finding (so called ‘publication bias’), Kramer et al. (2009) suggest that terrestrial invertebrates and mammals show the highest incidence of demographic Allee effects. There is, however, the lingering issue of whether studies of demographic Allee effects are themselves taxonomically biased (Courchamp et al. 2008).

By constraining my explanation of the demographic Allee effect to the Atlantic cod example, I have emphasised a single perspective to view an Allee effect: as a decrease in individual fitness or population growth with decreasing population size. There exists a flip-side to this perspective: an Allee effect can also describe an increase in individual fitness or population growth rate with increasing population size (Stephens and Sutherland 1999). From this perspective an Allee effect is best thought of as intraspecific cooperation and should serve to further emphasise the diverse range of species and situations to which an Allee effect is relevant. Taylor and Hastings (2005) reviewed the role of Allee effects in biological invasions, or the human-assisted movement of species across gene-flow barriers. They highlighted studies showing how Allee effects can prevent species establishment if the propagule size (number of reproductive units) is too small. Allee effects can also dampen or halt the spread of an established alien species when there are too few individuals to colonise new areas. Of course, the idea that an increase in individual fitness or population growth rate with increasing size is only relevant to alien species is misleading. Social species all rely on the presence of conspecifics to participate in cooperative or social behaviours including breeding, predator defense, or thermoregulation, to name but a few cooperative behaviours (Stephens and Sutherland 1999).

While a thesis introduction is a good setting for a thorough treatment of the species and mechanisms giving rise to component and demographic Allee effects, this aim overlaps with the aim of the second thesis chapter: to provide an example-rich review of the Allee effect concept. Readers keen to discover more examples of Allee effects are encouraged to read on. On the other hand, the second thesis chapter only reviews Allee effect examples arising due to a single mechanism - a mate-finding Allee effect. Although I could provide a review of the mechanisms giving rise to Allee effects in this introduction, it would be a large undertaking and would merely constitute an update to a recent monograph by Courchamp et al. (2008). Readers wishing to read an extensive review of the mechanisms underpinning demographic Allee effects are therefore directed to Courchamp et al. (2008). Nevertheless, I hope that all readers will continue to read this thesis as it is littered with many interesting mechanisms and examples.

Table 1.1: A table listing all known meta-analytical studies that aimed to quantify empirical support ('Support') for demographic Allee effects across multiple species. Support is graded as 'Yes' if a non-negligible proportion of the cases analysed showed evidence of demographic Allee effects.

| Taxonomic group | Study citation              | Support | Details  |
|-----------------|-----------------------------|---------|--|
| Fish            | Myers et al. (1995)         | No      | Support in 3/128 exploited populations             |
| Birds           | Sæther et al. (1996)        | No      | No support in 11 small populations                 |
| Fish            | Liermann and Hilborn (1997) | ?       | Weak Bayesian support in 4 fish taxa               |
| Seals           | Gerber and Hilborn (2001)   | No      | No support in 25 reduced populations               |
| Fish            | Walters and Kitchell (2001) | Yes     | Support in $\approx$ 112/330 exploited populations |
| Salmon          | Barrowman et al. (2003)     | No      | No support unless $\geq$ 1 females/km of river     |
| Plants          | Reed (2005)                 | Yes     | Support in 'fitness' of 11 populations             |
| Various         | Sibly et al. (2005)         | No      | Quadratic support in 20/3269 series                |

## 1.6 Problem statement

"The importance of identifying component Allee effects is usually that their existence indicates the potential for existence of a demographic Allee effect, which is far less easily demonstrated."

Stephen, Sutherland & Freckleton (1999)

At least eight attempts have been made over the last two decades to quantify the empirical support for demographic Allee effects over multiple species (Table 1.1). Overall, the findings suggest that demographic Allee effects are uncommon, even in exploited and severely perturbed populations. With the exception of Sibly et al. (2005), all of these studies have focused on specific taxon or groups of organisms. Sibly et al. (2006) analyzed populations from many different taxa but used many populations per species that might have biased their results to over-represent well-studied species. Furthermore, with the exception of Walters and Kitchell (2001), all of these studies have used model-fitting meta-analytical approaches to detecting demographic Allee effects using single population time series. Walters and Kitchell (2001) used subjective and irreproducible expert opinions to identify evidence for demographic Allee effects. Results from fitting models to single population time series will, however, be highly sensitive to the quality and characteristics of the time series.

Despite the prevailing consensus that demographic Allee effects are uncommon, both the evidence for component Allee effects and the number of populations declining due to anthropogenic activity are increasing. These two conditions are conducive of demographic Allee effect manifestation and deserve a reappraisal of the evidence for demographic Allee effects. According to the taxonomic scope and potential pitfalls in the methods used in the studies listed in Table 1.1, assessment of the empirical evidence for demographic Allee effects would benefit from an unbiased multi-species meta-analysis of natural populations from a range of taxa and an associated analysis of the problems with fitting models to single time series. Subsequently, the search for empirical support for demographic Allee effects would benefit from development of a statistical procedure to overcome the problems associated with model-fitting to single time series, and verification that the new statistical procedure was useful.

## 1.7 Thesis aim and objectives

The principle aim of this thesis was to ascertain the commonness of demographic Allee effects and whether the methods we use to detect them might influence our answer to this question. The key objectives were to: (i) Review the concept and empirical evidence for Allee effects and use this as a platform to speculate about the commonness of demographic Allee effects in natural populations. (ii) Examine a large sample of taxonomically diverse populations for empirical support for demographic Allee effects and identify possible biases in the data and methods used to detect them. (iii) Highlight the biases of commonly used model-fitting methods for detecting demographic Allee effects in natural populations and propose an alternative method. And (iv) Use the newly developed method to seek evidence of demographic Allee effects in a group of social species.

Each objective has been tackled in a separate chapter, as indicated below, and the degree to which we achieved the overall aim of the thesis is evaluated in the discussion.

## 1.8 Thesis structure and papers

Excluding this introduction, the thesis chapters were written as articles for submission to peer-reviewed international science journals. Consequently, they are all written in English in the form of a scientific article (i.e., Abstract, Introduction, Methods, etc.) and are accompanied by their references and appendices. The chapters are as follows:

- I: Gascoigne, J., Berec, L., **Gregory, S.**, and Courchamp, F. (2009) Dangerously few liaisons: a review of mate-finding Allee effects, *Population Ecology*, **51**:355-372
- II: **Gregory, S.D.**, Bradshaw, C.J.A., Brook, B.W., Courchamp, F. (2010) Limited evidence for the demographic Allee effect from numerous species across taxa, *Ecology*
- III: **Gregory, S.D.**, Sutherland, W.J., Haysom, K.A., Courchamp, F. (*in prep*) Population variability and the demographic Allee effect *Methods in Ecology and Evolution*
- IV: **Gregory, S.D.**, Haysom, K.A., Briggs, P.A., Courchamp, F. (*submitted*) Examining evidence for demographic Allee effects in nine UK bat species, *Journal of Applied Ecology*

The thesis ends with a general discussion, a part of which was an invited ‘Focus’ article published as:

- V: **Gregory, S.D.**, Courchamp, F. (2010) Safety in numbers: extinction arising from predator-driven Allee effects, *Journal of Animal Ecology*

## 1.9 Why did I do this thesis?

Finally, it remains for me to address the question: *why did I do a thesis on this subject?* or more simply *why did I do this thesis?*

For me, the answer to this question is very simple. I study ecology because I want my work to be used in the preservation of biodiversity. I believe all ecology should be applied ecology, i.e., all ecological studies should have an explicit applied aspect or advance our understanding of ecology to better apply our knowledge to the preservation of biodiversity, through conservation and management. I believe that I can make a substantial contribution to the field of demographic

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Allee effects that can be applied to the management of threatened plant and animal populations. My reason for wanting to do this thesis is therefore to improve our ability to detect demographic Allee effects to facilitate the management of threatened and invasive populations of plants and animals. I will assess whether I achieved this personal aim in the thesis discussion.

But, why, if I want to help preserve biodiversity did I not chose to study one of the big drivers of biodiversity loss, such as habitat destruction, climate change, or overexploitation? Why did I study demographic Allee effects? In 1989, Jared Diamond defined the Evil Quartet as the four biggest drivers of biodiversity loss (Diamond 1989). These were overexploitation, habitat destruction, invasive species and extinction cascades. Today, there is good reason to extend this definition to include climate change (Barry W. Brook et al. 2008). Although demographic Allee effects are not drivers of biodiversity loss per se, they can catalyse the extinction of populations reduced in size by any of these big drivers of biodiversity loss. Furthermore, by catalyzing extinctions, they can cause extinction cascades. Consequently, understanding how to detect and to predict when and where demographic Allee effects will occur would make an important contribution to our endeavor to preserve biodiversity.

## **References**

- Allee, W. C., O. Emerson, T. Park, and K. Schmidt. 1949. Principles of animal ecology. Philadelphia, PA: Saunders.
- Anderson, J. T., and G. A. Rose. 2001. offshore spawning and year-class strength of northern cod (2J3KL) during the fishing moratorium, 1994-1996. Canadian Journal of Fisheries and Aquatic Sciences **58**:1386–1394.
- Barrowman, N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. Ecological Applications **13**:784–793.
- Barry W. Brook, Navjot S. Sodhi, and Corey J.A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution **23**:453–460.
- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. Trends In Ecology & Evolution **22**:185–191.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. Trends In Ecology & Evolution **14**:405–410.
- Diamond, J., 1989. Overview of recent extinctions. Pages 37–41 in Conservation for the twenty-first century. Oxford University Press.
- Fu, C. H., R. Mohn, and L. P. Fanning. 2001. Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. Canadian Journal of Fisheries and Aquatic Sciences **58**:1613–1623.
- Gerber, L. R., and R. Hilborn. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. Mammal Review **31**:131–150.

- Hutchings, J. 1999. Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. Canadian Journal of Fisheries and Aquatic Sciences **56**:1612–1623.
- Hutchinson, W. F., C. van Oosterhout, S. I. Rogers, and G. R. Carvalho. 2003. Temporal analysis of archived samples indicates marked genetic changes in declining North Sea cod (*Gadus morhua*). Proceedings of The Royal Society of London Series B-Biological Sciences **270**:2125–2132.
- Kramer, a., B. Dennis, a. Liebhold, and J. Drake. 2009. The evidence for Allee effects. Population Ecology **51**:341–354.
- Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierachic Bayesian meta-analysis. Canadian Journal of Fisheries and Aquatic Sciences **54**:1976–1984.
- Lilly, G., K. Wieland, B. Rothschild, S. Sundby, K. Drinkwater, K. Brander, G. Ottersen, J. Carscadden, G. Stenson, G. Chouinard, D. Swain, N. Daan, K. Enberg, M. Hammill, A. Rosing-Asvid, H. Svedäng, and A. Vázquez, 2008. Decline and Recovery of Atlantic Cod (*Gadus morhua*) Stocks throughout the North Atlantic. Pages 39–66 in G. Kruse, K. Drinkwater, J. Ianelli, J. Link, D. Stram, V. Wespestad, and D. Woodby, editors. Resiliency of Gadid Stocks to Fishing and Climate Change. Alaska Sea Grant, University of Alaska, Fairbanks.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenburg. 1995. Population-dynamics of exploited fish stocks at low population-levels. Science **269**:1106–1108.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications **7**:91–106.
- Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature **428**:932–935.
- Reed, D. H. 2005. Relationship between population size and fitness. Conservation Biology **19**:563–568.
- Rose, G. A. 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. Canadian Journal of Fisheries and Aquatic Sciences **61**:1553–1557.
- Rowe, S., J. A. Hutchings, D. Bekkevold, and A. Rakitin. 2004. Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). Ices Journal of Marine Science **61**:1144–1150.
- Sæther, B. E., T. H. Ringsby, and E. Roskaft. 1996. Life history variation, population processes and priorities in species conservation: Towards a reunion of research paradigms. Oikos **77**:217–226.
- Shelton, P. A., and B. P. Healey. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? Canadian Journal of Fisheries and Aquatic Sciences **56**:1521–1524.

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- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the Regulation of Populations of Mammals, Birds, Fish, and Insects. *Science* **309**:607–610.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2006. Response to Comments on "On the Regulation of Populations of Mammals, Birds, Fish, and Insects". *Science* **311**:1100d–.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends In Ecology & Evolution* **14**:401–405.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185–190.
- Swain, D. P., and A. F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:1321–1325.
- Taylor, C. M., and A. Hastings. 2005. Allee effects in biological invasions. *Ecology Letters* **8**:895–908.
- Vitousek, P., H. Mooney, J. Lubchenco, and J. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:39–50.

## Introduction Générale

### Qu'est-ce qu'il y a dans une introduction de thèse?

Avant d'écrire cette introduction, j'ai lu un grand nombre d'introductions de thèses dans mon domaine. Je cherchais l'inspiration mais tout ce que je trouve servi à me décourager. Ce n'est pas que ils ont été mal ou peu instructifs, mais c'est plutôt qu'ils n'ont pas considéré la question centrale d'une introduction de thèse: pourquoi ai-je fait une thèse sur ce sujet? Ou, plus simplement, pourquoi j'ai fait cette thèse?

Bien sûr, une introduction de thèse doit fournir plus qu'une réponse à cette question. Il devrait également prévoir (i) les définitions nécessaires, (ii) un cadre pour la thèse et (iii) une déclaration du problème posé par la thèse. Ci-dessous, je m'adresse à chacune de ces sections, à son tour. Surtout, je vais donc aussi essayer de répondre à la question (iv) pourquoi j'ai fait cette thèse?

### Qu'est-ce qu'un effet démographique Allee?

Il existe deux types d'effets Allee: (1) un effet Allee composante, et (2) un effet Allee démographique (Stephens1999a). Tous les deux affectent les populations qui sont réduites à cause des interventions humaines, comme la chasse ou la destruction d'habitat (Brook2008). Par exemple, les populations mondiales de morue ont été surexploités et, aujourd'hui, leurs populations sont plus petites que jamais (Myers1997). Ceci est clairement illustré à l'aide de la population de morue de l'Atlantique *Gadus morhua* de Newfoundland au Canada (voir Figure codcollapse). Depuis 100 ans, entre 1850 et 1950, petits bateaux artisanaux ont pêché entre 100 et 250 mille tonnes de morue annuellement. Après 1950, la morue ont été pêchées en utilisant de plus grands bateaux industriels. Ces bateaux industriels ont été très efficaces à la capture de morue et, à partir de l'année 1970, plus de 700 mille tonnes de morue ont été capturés - presque trois fois la montant de morue pêché 30 ans auparavant. Sans surprise, la population de morue ont diminué après 1980, lorsque, malgré un moratoire gouvernemental et de la protection internationale, la population de morue de Newfoundland disparaît en 1992 (Myers1997).

« Voir FIGURE 1.1 »

Figure 1.1. Le déclin de la population de morue de Newfoundland: il semble que la morue ont été pêchées de manière durable jusqu'à la fin des années 1950 lorsque la pêche industrielle à augmenter la montant de morue pêchée. Comme la montant de morue pêchée ont augmenté la population à diminuer, et malgré les restrictions internationales, y compris un moratoire, la population s'est écrasé en 1992 et la pêche a été fermée.

Il a été suggéré que la population de morue de Newfoundland a souffert d'un effet Allee composante et démographique (Anderson2001). Un effet Allee composante décrit la situation lorsqu'une population est réduite, comme celle de la morue de Newfoundland, les individus pourraient avoir des difficultés d'accomplir des comportements normaux, comme la recherche d'un partenaire sexuel pour se reproduire. Par conséquent, la population devient plus petite et la chance de chaque individu de trouver un partenaire sexuel diminue - un effet Allee composante (Figure 1.2a). Les effets Allee composants peuvent manifester en raison de mécanismes divers et peuvent affecter plusieurs composants de « fitness », y compris la reproduction, la survie et même des mesures de substitution de ces composants de «fitness» comme le gain de poids (Stephens1999a). Un effet Allee démographique décrit la situation lorsque l'effet Allee composante entraîner des changements dans la taille de la population. Parfois, et comme a été suggéré pour la morue de Newfoundland, la chance diminuée de trouver un partenaire sexuel avec une diminution de taille de la population (l'effet Allee composante) peut causer moins de morues juvéniles d'être né. Par conséquent, la population sera plus petite dans l'année suivante et encore moins de morues juvéniles seraient né, et la population diminuerait à un rythme accéléré chaque année, ce qui caractérise un effet démographique Allee (Figure 1.2b). Dans le cas où la population diminuerait en dessous d'une taille

de population critique (le seuil Allee), l'effet démographique Allee devrait conduire à l'extinction de la population dans ce qu'on a appelé une spirale d'extinction (Figure 1.3).

« Voir FIGURE 1.2a »

Figure 1.2 (a). Un graphique illustrant un effet Allee composante chez la morue de Newfoundland. La « fitness » de chaque individu - illustré ici comme le nombre d'œufs produits par individu - diminue avec la taille de la population.

« Voir FIGURE 1.2b »

Figure 1.2 (b). Un graphique illustrant un effet Allee démographique chez la morue de Newfoundland. Le taux de croissance de la population - illustré ici comme le nombre d'adultes reproducteurs produits par individu - diminue avec la taille de la population.

Il semble que, dans l'exemple la morue de Newfoundland, un effet Allee composante dans la reproduction aurait pu conduire à un effet Allee démographique qui a causé la population à disparaître (dans ce cas la population ne s'est pas éteinte, mais était à peine détectable pour un certain nombre d'années; Anderson2001). L'existence d'un effet Allee composant avec un effet Allee démographique ne serait pas un hasard; chaque fois que nous observons un effet Allee démographique, nous savons qu'il doit y avoir un effet Allee composant (Stephens1999a). En fait, il est possible qu'un effet Allee démographique pourrait être une manifestation de plusieurs effets Allee composantes (Berec2007), et ce pourrait être le cas pour la morue. Par exemple, Rowe2004 a montré que les populations de morue réduite ont une production reproductive individuelle réduite. Swain2000 et Walters2001 suggéraient que la réduction des morues adultes pourrait permettre à leurs populations de poissons proie à augmenter, ce qui mangerait un nombre d'œufs de morue élevé.

« Voir FIGURE 1.3 »

Figure 1.3. Un graphique illustrant la façon dont la reproduction diminuée dans une petite population peut entraîner la population à devenir progressivement plus petite à un rythme accéléré, jusqu'à son extinction. Cette dynamique décrit un effet Allee démographique par une spirale d'extinction.

### **Les effets Allee démographiques - sont-elles fréquent?**

Bien qu'un effet Allee composante doive sous-tendre un effet démographique Allee, l'inverse n'est pas toujours vrai (Stephens1999a). Les scientifiques ont observé des effets Allee composantes chez de nombreuses espèces d'animaux et de plantes (voir Kramer2009 pour une revue). Les observations convaincantes des effets Allee démographiques sont, en revanche, rares. En effet, il y a eu plusieurs études qui ont essayé d'isoler un effet démographique Allee (connu sous le nom « depensation » dans la littérature de pêche) de la morue mais il y a toujours des doutes que la morue a montré un effet Allee démographiques (Shelton1999). Peut-être l'évidence plus convaincante pour cette hypothèse est que la population n'a pas, à ce jour, récupéré (Lily2008). Si la population de morue n'avait pas un effet démographique Allee, puis elle devrait doubler de taille tous les 3 ans (Myers1997) ou 5-6 ans (Hutchings1999). La taille réduite de la population de morue est compatible avec l'existence d'un effet Allee démographique (Fu2001).

Il existe de nombreuses explications possibles pour lesquelles nous n'observons que rarement les effets Allee démographiques et ceux-ci peuvent être regroupés en trois catégories: (1) détection (2), manifestation, et (3) observation. Plusieurs tests statistiques ont été utilisés à la recherche des effets Allee démographiques, comme l'illustrent les deux exemples suivants. Walters2001 a demandé à trois scientifiques indépendants d'examiner les courbes de reproduction des poissons et de voter pour ou contre la présence de « depensation ». À l'autre extrême, Liermann1997 réanalysé la base de données de Myers1995 à l'aide d'un modèle Ricker reparamétrisés pour que le paramètre « depensation » avait un sens biologique. Leur modèle était non linéaire et ils ont estimé les paramètres du modèle en utilisant une analyse semi-bayésienne. En plus, Liermann1997 a comparé

leur modèle « depensation » à un modèle équivalent mais sans le paramètre « depensation ». Walters2001 trouvait une évidence élevée pour « depensation » mais Liermann1997 ont été incapables de confirmer ou d'infirmer « depensation » chez les espèces qu'ils ont analysé.

Une grande diversité des approches statistiques a été déployée pour détecter les effets Allee démographiques, mais il y a toujours un consensus qu'ils sont rares (Courchamp2008, Kramer2009). De nombreux chercheurs ont spéculé sur les raisons pour cela. Ils ont constaté que: (i) les séries temporelles courtes et variables ne pourraient pas fournir suffisamment d'informations pour estimer les paramètres statistiques, (ii) les séries temporelles ne représentent pas les populations fermées, (iii) les séries temporelles ne auraient que rarement tout le spectre des tailles de population nécessaire d'observer un effet Allee démographique, (iv) les modèles de l'effet Allee nécessitent au moins un paramètre supplémentaire (représentant l'effet Allee) par rapport aux modèles plus simples, et (v) d'autres facteurs, comme les tendances temporelles et l'erreur de mesure, qui compliquent la détection d'autres dynamiques de populations compliquent également notre capacité à détecter les effets Allee démographiques. Que ce soit un ou une combinaison de ces facteurs peut expliquer la rareté des effets Allee démographique reste sans réponse.

Outre la liste longue des facteurs potentiels qui inhibent la détection des effets Allee démographiques, il y a une autre explication pour leur rareté - ils ne se manifestent que rarement. Un effet Allee composante pourrait ne pas se manifester par un effet démographique Allee simplement parce qu'il y a une augmentation correspondante et compensant dans un autre composant (s) de «fitness» (Stephens1999a). Par exemple, une population de morue qui souffre d'un effet Allee composante dans la reproduction à cause d'une difficulté à trouver une partenaire sexuelle peut ne jamais souffrir un effet Allee démographique parce que la taille réduite de la population encourage l'immigration de morues adultes Hutchinson2003.

L'existence de mécanismes qui servent d'augmenter la « fitness » individuelle à les tailles de population réduite et, par conséquence, compenser les effets Allee souligne un point important affectant l'évidence des effets Allee démographique - il est rare d'observer des populations autour de la taille où il se manifeste l'effet Allee. Les effets Allee composante affectent la « fitness » individuelle, alors ils sont susceptible à la sélection naturelle. En conséquence, les organismes vulnérables aux Allee effets auraient du développé des mécanismes pour compenser ou d'éviter les tailles de population (Courchamp2008). Revenant à notre exemple de morue: Olsen2004 a montré que avant l'effondrement de leur population, les morue petites ont développé plus tôt que dans les années précédentes, ce qui suggère qu'ils étaient en évolution afin d'éviter la taille des populations de petite taille. Les effets Allee sont donc caractérisés par un état dynamique et instable défini par l'existence d'un seuil de taille de la population instable appelé le « seuil Allee »: les populations proches du seuil Allee se soit d'accroître rapidement à leur seuil positif et stable (appelé la « capacité de charge ») ou de baisse rapidement à l'extinction (Courchamp1999). Pour cette raison, les effets Allee - composante et démographique - sont théoriquement plus susceptibles d'être observé dans les populations qui ont été récemment réduites et récupérées ou disparues.

### **Pourquoi sont-ils importants les effets Allee démographiques?**

Les effets Allee démographiques devraient être rares parce que la sélection naturelle devrait conduire l'évolution des mécanismes visant à empêcher les populations d'atteindre la taille à laquelle ils agissent. Même si ils sont présents, les effets Allee démographiques sont susceptibles d'être difficiles à détecter. Alors pourquoi sont-ils importants les effets Allee démographiques?

Comme nous avons vu, les effets Allee démographiques sont définis par une accélération du taux de décroissance de la population à les tailles de population réduites (ou inversement une augmentation de la croissance démographique dans une population à taille réduite qui pourrait se produire lors d'une introduction d'espèces; voir ci-dessous). La clé pour comprendre l'importance des effets Allee

démographiques est le mot utilisé pour décrire l'état de la population affectée: réduite. De nombreux organismes coopèrent pour des raisons nombreuses, y compris la chasse et pour se protéger contre les prédateurs. Lorsque leur population est réduite à une petite taille, il peut y avoir trop peu d'individus de coopérer efficacement avec une baisse correspondante dans la «fitness», et peut-être un effet Allee démographique (Stephens1999). Warder Clyde Allee (1885 - 1955) a été le premier à décrire cette possibilité en utilisant le terme « proto-coopération » (Allee1949). Il était un Quaker et les Quakers, connu sous le nom de la Société religieuse des Amis, expriment leurs convictions individuellement, mais se réunissent pour prendre des décisions de groupe ([http://en.wikipedia.org/wiki/Religious\\_Society\\_of\\_Friends](http://en.wikipedia.org/wiki/Religious_Society_of_Friends)). Peut-être sa croyance dans l'action de groupe l'a conduit à décrire « proto-coopération » comme un précurseur à la coopération de l'homme?

Les effets Allee démographiques touchent les populations qui sont de taille réduite. Alors, ils affectent les populations indépendamment des facteurs qui a causé le déclin de la population. Par conséquent, les effets Allee démographiques peuvent affecter n'importe quelles espèces qui coopèrent - même à un niveau rudimentaire, comme une coopération pour se reproduire sexuellement - et dont sa population est réduite. De toute évidence, un effet Allee démographique est un des facteurs principaux dans l'effondrement soudain de la population de morue de Newfoundland. Malheureusement, les pilotes de la perte de biodiversité n'actent que rarement singulièrement (Brook2008) illustrée à l'aide de notre exemple de la morue. Rose2004 a montré comment les changements dans les populations de morues ont été mieux décrit en utilisant une combinaison d'exploitation et les changements climatiques. Malheureusement, les populations de morue ne sont pas les seules populations menacées des activités humaines - il y a plus d'espèces menacées par les activités humaines aujourd'hui que jamais (Vitousek1997). Ainsi, il y a aussi une urgence plus grande que jamais d'essayer de comprendre où et quand ils pourraient se manifester les effets Allee composantes et démographiques.

### Au-delà de la morue

Jusqu'à ce point dans l'introduction, j'ai essayé d'illustrer l'effet Allee démographique en utilisant uniquement la morue de l'Atlantique comme un exemple. Néanmoins, il doit être clair dont l'effet Allee composante, et donc l'effet Allee démographique, peut affecter un plus large nombre d'espèces. Kramer2009 a récemment revu les études publiées sur l'effet Allee. En résumé, ils montrent que les effets Allee composantes ont été isolés dans tous les grands groupes taxonomiques, sauf les reptiles, et via un large nombre de mécanismes potentiels. En plus, ils examinent l'évidence pour les effets Allee démographiques qui sortent des métanalyses et suggèrent qu'ils sont rares. Sans tenir compte du biais potentiel que l'incapacité à isoler un effet Allee démographique est moins désirable, et donc moins publiable (ce qu'on appelle «biais de publication»), Kramer2009 suggèrent que les invertébrés terrestres et les mammifères possèdent l'incidence plus forte des effets Allee démographiques. Il y a, cependant, le problème persistant de savoir si les études des effets Allee démographiques se sont taxonomiquement biaisées (Courchamp2008).

En limitant mon explication de l'effet Allee démographique à l'exemple de la morue de l'Atlantique, j'ai insisté sur un point de vue unique pour voir un effet Allee: une réduction de la « fitness » individuelle ou la croissance de la population dans les populations des tailles réduites. Il existe une autre perspective: un effet Allee peut aussi décrire l'augmentation de la « fitness » individuelle ou le taux de croissance de la population avec l'augmentation de taille de la population (Stephens1999). De ce point de vue, l'effet Allee pourrait être considéré comme la coopération intra-spécifique. Dans ce sens, l'effet Allee peut affecter une grande diversité des espèces. Taylor2005 a examiné les rôles des effets Allee dans les invasions biologiques. Ils ont souligné les études montrant comment Allee effets peuvent empêcher l'établissement d'une espèce si la taille des propagules (nombre d'unités de la reproduction) sont trop petites. Les effets Allee peuvent aussi freiner la propagation

d'une espèce établie quand il y a trop peu d'individus pour coloniser de nouvelles régions. Bien sûr, l'idée qu'une augmentation de « fitness » individuelle ou du taux de croissance de la population avec sa taille n'est applicable que pour les espèces exotiques est trompeuse. Les espèces sociales ont besoin de la présence de congénères de participer à des comportements coopératifs ou sociaux, y compris l'élevage, de la défense des prédateurs, ou la thermorégulation, pour n'en nommer que quelques-uns (Stephens1999).

Bien que l'introduction de thèse est un bon réglage pour un traitement approfondi des espèces et des mécanismes donnant lieu à des effets Allee composants et démographiques, c'est l'objectif du chapitre deuxième thèse. Le lecteur intéressé à découvrir d'autres exemples des effets Allee sont encouragés à lire. D'autre part, le deuxième chapitre de thèse est focalisé sur un mécanisme unique - un effet Allee du à la difficulté de trouver une partenaire sexuelle dans une population de taille réduite. Bien que je pusse fournir un revu des mécanismes qui causent les effets Allee dans cette introduction, il serait d'une grande entreprise et constituerait simplement une mise à jour à une monographie récente (Courchamp2008). Les lecteurs qui désirent lire un examen profond des mécanismes qui causent les effets Allee démographiques sont guidés vers (Courchamp2008). Néanmoins, j'espère que tous les lecteurs continueront à lire cette thèse parce qu'il y aurait de nombreux mécanismes et exemples intéressants.

## Déclaration du problème

“The importance of identifying component Allee effects is usually that their existence indicates the potential for existence of a demographic Allee effect, which is far less easily demonstrated.”

Stephen, Sutherland & Freckleton (Stephens1999a)

Au moins huit études ont été faites au cours des deux dernières décennies afin de quantifier l'évidence empirique des effets Allee démographiques au cours de multiples espèces (daestudies tableau). Dans l'ensemble, les résultats suggèrent que les effets Allee démographiques sont rares, même dans les populations exploitées et fortement perturbées. À l'exception de Sibly2005, toutes ces études ont porté sur un taxon ou un groupe d'organismes spécifiques. Sibly2006 ont analysé populations de différents taxons, mais de nombreuses populations pour chaque espèce qui pourrait avoir biaisé les résultats. En plus, à l'exception de Walters2001, toutes ces études ont utilisé une approche métá-analyse pour détecter les effets Allee démographiques dans les séries temporelles individuelles. Walters2001 ont demandé aux scientifiques leur avis expert pour identifier les effets Allee démographiques; une analyse subjective et non-reproductible. Les résultats des analyses des séries temporelles, cependant, seront très sensibles aux caractéristiques des séries temporelles.

Malgré le consensus que les effets Allee démographiques sont rares, les évidences pour les effets Allee composants et le nombre de populations en déclin sont en augmentation. Ces deux conditions sont favorables de la manifestation d'un effet Allee démographique et méritent une réévaluation de l'évidence des effets Allee démographiques. Selon le spectre taxonomique et les problèmes potentiels dans les méthodes utilisées dans les études énumérées dans le tableau 1, l'appréciation des évidences empiriques des effets Allee démographiques bénéficieraient d'une multi-espèces meta-analyse des populations naturelles, avec une analyse des problèmes qui empêchent la détection des effets Allee dans les séries temporelles. En plus, la recherche d'évidence empirique des effets Allee démographiques pourraient bénéficier du développement d'une méthode statistique permettant de surmonter les problèmes associés avec le modèle ajusté pour les séries temporelles individuelles.

Tableau 1. Une liste des études méta-analyse qui vise à quantifier l'évidence empirique («Support») pour les effets Allee démographiques chez plusieurs espèces. Support est classé comme «Oui» si une proportion non négligeable des cas analysés ont montré des effets Allee démographique.

| Groupe taxonomique | Référence     | Support | Détails  |
|--------------------|---------------|---------|--|
| Poisson            | Myers1995     | Non     | Support en 3 / 128 populations exploitées            |
| Oiseaux            | Saether1996   | Non     | Pas de support dans 11 petites populations           |
| Poisson            | Liermann1997  | ?       | Et faible soutien Bayésienne en 4 taxons de poissons |
| Phoques            | Gerber2001    | Non     | Pas de support dans 25 populations réduites          |
| Poisson            | Walters2001   | Oui     | Support en 112/330 populations exploitées            |
| Salmon             | Barrowman2003 | Non     | Aucune aide les femmes à moins <1 / km de rivière    |
| Plants             | Reed2005      | Oui     | Support « de remise en forme» de 11 populations      |
| Divers             | Sibly2005     | Non     | Support quadratique en série 20/3269                 |

### But et objectifs de thèse

L'objectif principal de cette thèse était de déterminer la fréquence de l'effet Allee démographique et si les méthodes que nous utilisons pour les détecter pourraient influencer notre réponse à cette question. Les objectifs principaux étaient les suivants: (i) D'examiner le concept et l'évidence empirique de l'effet Allee et l'utiliser comme une plate-forme de spéculer sur la fréquence des effets Allee démographiques dans les populations naturelles. (ii) D'examiner un grand nombre de populations diverses taxonomiques pour évidence empirique des effets Allee démographiques et d'identifier les biais dans les données et méthodes utilisées pour les détecter. (iii) Mettre en évidence les biais des méthodes utilisées pour détecter les effets Allee démographiques chez les populations naturelles et de proposer une méthode alternative. Et (iv) utiliser la méthode alternative pour rechercher évidence empirique d'effets Allee démographiques dans un groupe d'espèces sociales.

Chaque objectif a été abordé dans un chapitre distinct, comme indiqué ci-dessous, et la mesure dans laquelle j'ai atteint l'objectif global de la thèse est évaluée à la discussion.

### Structure de thèse et les articles

En excluant cette introduction, les chapitres de thèse ont été écrits comme des articles à soumettre à des revues scientifiques internationales. Par conséquent, ils sont tous rédigés en anglais sous la forme d'un article scientifique (par exemple, Résumé, Introduction, Méthodes, etc) et sont accompagnés de leurs bibliographies. Les chapitres sont les suivants:

I: Gascoigne, J., Berec, L., Gregory, S., and Courchamp, F. (2009) Dangerously few liaisons: a review of mate-finding Allee effects, *Population Ecology*, 51:355-372

II: Gregory, S.D., Bradshaw, C.J.A., Brook, B.W., Courchamp, F. (2010) Limited evidence for the demographic Allee effect from numerous species across taxa, *Ecology*

III: Gregory, S.D., Sutherland, W.J., Haysom, K.A., Courchamp, F. (in prep) Population variability and the demographic Allee effect, *Methods in Ecology and Evolution*

IV: Gregory, S.D., Haysom, K.A., Briggs, P.A., Courchamp, F. (submitted) Examining evidence for demographic Allee effects in nine UK bat species, *Journal of Applied Ecology*

La thèse se termine par une discussion générale, dont une partie était un article invité «Focus» publié en tant que:

V: Gregory, S.D., Courchamp, F. (2010) Safety in numbers: extinction arising from predator-driven Allee effects, *Journal of Animal Ecology*

## **Pourquoi j'ai fait cette thèse?**

Enfin, il me reste à répondre à la question: pourquoi j'ai fait une thèse sur ce sujet? ou plus simplement pourquoi j'ai fait cette thèse?

Pour moi, la réponse à cette question est très simple. J'étudie l'écologie parce que je veux que mon travail ait utilisé dans la préservation de la biodiversité. Je crois que tous l'écologie doit être l'écologie appliquée ; toutes les études écologiques doivent avoir un aspect appliqué ou de faire progresser notre compréhension de l'écologie pour mieux appliquer nos connaissances à la préservation de la biodiversité, grâce à la conservation et la gestion. Je crois que je peux apporter une contribution substantielle à l'étude des effets Allee démographiques qui peuvent être appliquées à la gestion des populations de plantes et animales menacées. Ma raison pour vouloir faire ce travail de thèse est donc d'améliorer notre capacité à détecter les effets Allee démographiques pour faciliter la gestion des populations d'espèces menacées et d'espèces invasives.

Mais, pourquoi, si je voulais aider à préserver la biodiversité, je n'ai pas choisi d'étudier l'un des grands facteurs de perte de biodiversité, comme la destruction des habitats, le changement climatique, ou la surexploitation? Pourquoi j'ai fait une étude des effets Allee démographiques? En 1989, Jared Diamond a défini le « Evil Quartet » ; les quatre facteurs principaux de perte de biodiversité (Diamond1989) qui sont la surexploitation, la destruction des habitats, les espèces invasives et les cascades d'extinction. Aujourd'hui, il y a de bonnes raisons d'inclure le changement climatique dans cette définition (Brook2008). Bien que les effets Allee démographiques ne cause pas la perte de biodiversité *per se*, ils peuvent catalyser l'extinction des populations réduite en taille par un des facteurs de le « Evil Quartet ». En plus, en catalysant les extinctions, ils peuvent provoquer des cascades d'extinction. Par conséquent, il serait très important de comprendre comment détecter et prédire quand et où les effets Allee démographiques seraient se manifester.

## Chapter 2

# Dangerously few liaisons: a review of mate–finding Allee effects

## Abstract

In this paper, we review mate-finding Allee effects from ecological and evolutionary points of view. We define ‘mate-finding’ as mate searching in mobile animals, and also as the meeting of gametes for sessile animals and plants (pollination). We consider related issues such as mate quality and choice, sperm limitation and physiological stimulation of reproduction by conspecifics, as well as discussing the role of demographic stochasticity in generating mate-finding Allee effects. We consider the role of component Allee effects due to mate-finding in generating demographic Allee effects (at the population level). Compelling evidence for demographic Allee effects due to mate-finding (as well as via other mechanisms) is still limited, due to difficulties in censusing rare populations or a failure to identify underlying mechanisms, but also because of fitness trade-offs, population spatial structure and metapopulation dynamics, and because the strength of component Allee effects may vary in time and space. Mate-finding Allee effects act on individual fitness and are thus susceptible to change via natural selection. We believe it is useful to distinguish two routes by which evolution can act to mitigate mate-finding Allee effects. The first is evolution of characteristics such as calls, pheromones, hermaphroditism, etc. which make mate-finding more efficient at low density, thus eliminating the Allee effect. Such adaptations are very abundant in the natural world, and may have arisen to avoid Allee effects, although other hypotheses are also possible. The second route is to avoid low density via adaptations such as permanent or periodic aggregation. In this case, the Allee effect is still present, but its effects are avoided. These two strategies may have different consequences in a world where many populations are being artificially reduced to low density: in the first case, population growth rate can be maintained, while in the second case, the mechanism to avoid Allee effects has been destroyed. It is therefore in these latter populations that we predict the greatest evidence for mate-finding Allee effects and associated demographic consequences. This idea is supported by the existing empirical evidence for demographic Allee effects. Given a strong effect that mate-finding appears to have on individual fitness, we support the continuing quest to find connections between component mate-finding Allee effects (individual reproductive fitness) and the demographic consequences. There are many reasons why such studies are difficult, but it is important, particularly given the increasing number of populations and species of conservation concern, that the ecological community understands more about how wide-spread demographic Allee effects really are, and why.

**Keywords** Component Allee effect, Demographic Allee effect, Positive density dependence, Mate search

## 2.1 Introduction

Ever since Stephens et al. (1999) coined the terms, it has been traditional to start a review paper on Allee effects with the definition of ‘demographic’ vs. ‘component’ Allee effects. It is likely that by now the interested reader will be familiar with the concepts, but to be safe, and with apologies for the repetition, we have nonetheless decided to start this review in the standard way. A ‘component Allee effect’ is a positive relationship between a given fitness component (e.g., number of matings, number of seeds produced, survival of pups to one year, etc.) and population size or density. A ‘demographic Allee effect’ is a positive relationship between mean overall fitness and population size or density, leading to a positive relationship between the per-

capita population growth rate and population size or density (Stephens et al. 1999). Component Allee effects are of interest from the point of view of understanding the ecology of a particular species, but from a ecological and particularly conservation perspective, it is demographic Allee effects which are of most concern, since they have the potential to lead to catastrophic population collapse and to prevent or slow recovery from low density and population establishment or re-establishment.

One of the most intuitive and best-understood mechanisms for generating a component Allee effect is mate-finding. Indeed, so intuitive is this mechanism that, as Stephens et al. (1999) highlight, many authors use it as their definition of an Allee effect. It is easy to understand that when populations are at a reduced density, individuals may face difficulties finding a mate. It follows that this should have an impact on some component of their reproductive fitness. There have been several modelling studies which consider the process of mate searching and demonstrate how it is related to population density (Berec et al. 2001, Dennis 1989, McCarthy 1997, Philip 1957; see also Courchamp et al. 2008 for a concise review). Although based on different assumptions concerning the subtleties of the actual mating process, all these models imply that fertilisation is more likely if more males are present, either in terms of absolute numbers or relative to the number or density of females.

Mate-finding Allee effects can be more subtle than a straightforward issue of mate search at reduced density. Individuals may need to mate several times to maximise their reproductive output. This means that, in low density populations, females may receive some matings, but not enough to fertilise all the eggs they have available. Males may likewise not be able to fulfil their full reproductive potential, even if they mate. Furthermore, in many populations, one or both sexes exercise mate choice. At low population density, mate choice may be more limited, and individuals therefore may have to settle for lower quality mates than in higher density populations. Unlike the straightforward search issue, these issues - lack of multiple matings and poor mate quality - may also arise in dense populations, if they are relatively small.

Mate-finding can also be a passive process, for example in broadcast spawners or in plant pollination. In this case, rather than a requirement for males and females to meet, there is a requirement for male and female gametes to meet - but functionally this is also 'mate-finding', albeit in a broader sense. There are further subtleties - for instance in situations where the sex ratio is very skewed - which we also consider below.

Such component Allee effects are of interest in themselves, but it is also important to try and follow the link, if any, from component effects to population dynamics. If some proportion of individuals in a population are not mated, or not mated to their full potential, there may well be demographic consequences - fewer offspring per individual is likely to lead to a decline in the per capita population growth rate. However, if individuals lose out on matings which they would otherwise gain at the expense of other individuals (e.g., a reduction in the harem size of alpha males), the demographic consequences may be negligible or even positive (e.g., a genetic consequence such as an increase in the effective population size). Furthermore, it is possible that under-performance in one fitness component is offset by over-performance in another. For example, individuals at low density may obtain fewer matings but more resources. If the strength of mate-finding Allee effects varies temporally and/or spatially, individuals unable to find mates may reallocate resources from reproduction to growth, thereby improving mating success later on. We discuss various examples of such trade-offs below. Overall, for various reasons, component mate-finding Allee effects may not translate to demographic Allee effects and population processes in a straightforward way.

Mate-finding Allee effects are also of significant interest from the genetic and evolutionary

perspective. There are many striking evolutionary adaptations which may have arisen in whole or in part to avoid mate–finding Allee effects - or at least more broadly to enhance individual ability to find an appropriate mate over the range of densities experienced by the population. These may include bird song, pheromones, reproductive aggregations and many others. We suggest that these adaptations can be usefully divided into two groups: (1) adaptations that mitigate the effect of low density (such as bird song and pheromones), and (2) adaptations that avoid low density altogether (such as reproductive aggregations). After reviewing the mechanisms for mate–finding Allee effects and their demographic consequences, we consider the circumstances under which these different adaptations arose, and their consequences under the impact of anthropogenic activity.

## **2.2 Mate–finding Allee effects**

### **2.2.1 Searching for and attracting mates**

This type of straightforward ‘mate–finding’ - individual animals moving around to find one another for purposes of mating - is probably the most well known of all types of Allee effect. The basic theory is simple and intuitive: at a reduced density, individuals will not always be able to find a suitable, receptive mate during their own receptive period, and their reproductive output will decrease accordingly.

There are a number of models that can be used to quantify the increase in mate search time or the decrease in female mating rate with decreasing population density (reviewed in Courchamp et al. 2008, Dennis 1989, Liermann and Hilborn 2001). They predict (unsurprisingly) that a mate–finding Allee effect is most likely in species which have limited dispersal ability (Philip 1957), in populations which are dispersed in space rather than aggregated (Dobson and Lyles 1989) and where individuals are only reproductive intermittently and asynchronously (Calabrese and Fagan 2004). Other than these ‘pointers’ it is difficult to predict *a priori* whether this mechanism will exist in a given population. Although mate–finding Allee effects might be expected to arise mainly among animals with a solitary life style, social species may also be affected. In particular, mate location or acceptance may become a problem if breeding pairs have to be formed by individuals from different (native) social groups (e.g., African wild dogs; McCreery and Robbins 2001).

Mate–finding Allee effects due to individual searching have been proposed in terrestrial species from sheep ticks to condors and marine species from zooplankton to whales. We do not have space here to list every study on the topic and every species potentially affected, and instead direct the reader to existing reviews (Dennis 1989, Fowler and Baker 1991, Sæther et al. 1996, Wells et al. 1998, Courchamp et al. 1999, Courchamp et al. 2000, Courchamp et al. 2008, Stephens and Sutherland 1999, Stephens and Sutherland 2000, Liermann and Hilborn 2001, Peterson and Levitan 2001, Gascoigne and Lipcius 2004a, Levitan and McGovern 2005, Berec et al. 2007).

The strongest evidence for mate–finding Allee effects can probably be found in invertebrates (although this may be confounded by ethical or logistical constraints of experimenting on vertebrates). For example, mate–finding Allee effects are proposed in some species of copepods (Kiørboe 2006), and as the mechanism through which some pastures stay mysteriously free of sheep ticks (Milne 1950, cited in Liermann and Hilborn 2001). Mate–finding Allee effects do not necessarily require two separate sexes in the usual ‘human’ sense; the wheat pathogen *Tilletia indica* reproduces via encounters between sporidia of different mating strains, which are less fre-

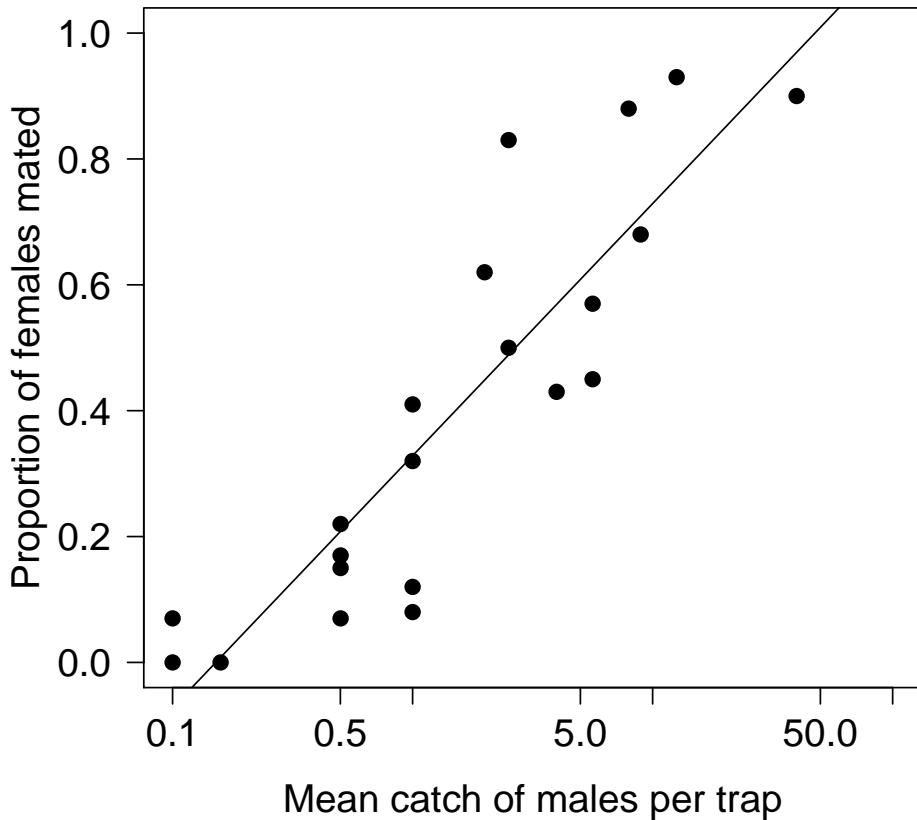


Figure 2.1: A higher population density of gypsy moths (*Lymantria dispar*) (as measured by the number of males caught in pheromone traps over a given time period) resulted in a higher proportion of tethered female moths being mated; at low population densities, few females were mated, suggesting a mate-finding Allee effect (Tcheslavskaya et al. 2002)

quent at low density (Garrett and Bowden 2002). They may occur in the malaria parasite *Plasmodium* spp. within the body of mosquitoes where sexual reproduction takes place; mosquitoes sucking blood from infected humans must suck up enough male and female *Plasmodium* gametocytes for successful reproduction within the mosquito (Pichon et al. 2000).

Studies of Allee effects, mate-finding and otherwise, have frequently focused on invasive species (see review by Taylor and Hastings 2005). A compelling example of a component Allee effect in mate-finding, leading to a demographic Allee effect, can be found in the invasive gypsy moth (*Lymantria dispar*) in North America. In a field experiment, where pheromone traps (which attract male moths) were placed next to tethered female moths, gypsy moth were found to have a positive relationship between the probability of a female being mated and the density of males, as measured by the number of moths in the traps (Tcheslavskaya et al. 2002; Figure 2.1).

Some of the most striking elements of animal behaviour are adaptations for finding mates, including, for example, calls and song, displays, odour and pheromone marking and reproductive aggregations. A mate-finding Allee effect may arise if these mate-finding behaviours are themselves disrupted at low density. For example, heavy fishing on spawning aggregations of reef fish results in the loss of knowledge of spawning sites and migration routes from the popu-

lation, as well as disruption of spawning behaviour via the removal of dominant males (Sadovy 2001). Similarly, the loss of older, more knowledgeable matriarchs is believed to result in reduced per capita reproductive success among the remaining members of African elephant groups (McComb et al. 2001). In neither of these cases, however, have Allee effects been specifically demonstrated. The disruption of mating aggregations through exploitation and its implications are also discussed from a more general perspective in Rowe and Hutchings (2003).

It is clear from models (e.g., Berec and Boukal 2004, Philip 1957) that dispersal or movement rates are key to creating (or avoiding) mate–finding Allee effects. Although small populations of Roesel’s bush cricket (*Metrioptera roeseli*) have a small probability of persistence compared to larger populations (Berggren 2001), an increase in movement rates within low density populations can effectively counteract mate–finding Allee effects (Kindvall et al. 1998). If, however, individuals are more likely to disperse away from small or low density populations in search of mates (or more generally in search of a higher fitness habitat), this can exacerbate the Allee effect by reducing the per capita population growth rate of these populations still further. In the Glanville fritillary butterfly (*Melitaea cinxia*; an endangered species of northern European dry meadows), a higher proportion of males emigrate out of small populations in search of mates, and a lower proportion of females are thus mated (Kuussaari et al. 1998; Figure 2.2).

## 2.2.2 Dispersal of gametes

Sessile organisms live permanently attached to land or seabed - plants are an obvious example but many animals are also sessile during reproductive maturity; notably many marine invertebrates. Others are not obligately sessile but nonetheless move around very little; this includes most bivalves and echinoderms and many polychaete worms, as well as others. This mode of life requires individuals to reproduce without coming into direct contact with conspecifics. They therefore have to rely on gametes encountering a suitable ‘mate’ while travelling through the surrounding medium (whether water or air).

In essence this ‘mate–finding’ (or gamete–finding) Allee effect arises out of the physics of diffusion, which dictates that the further the gamete cloud from an individual travels the more dilute it becomes. It thus follows that individuals in sparse populations are likely to encounter fewer gametes from other individuals, making fertilisation less efficient and potentially causing a problem for sexual reproduction at low density. Most work on this type of Allee effect has been done on plants, but there are also some seminal studies of Allee effects of this type in broadcast spawning invertebrates, mainly echinoderms (see reviews in Levitan and McGovern 2005 and Courchamp et al. 2008, among others).

In both plants and invertebrates, fertilisation efficiency has frequently been found to be positively related to population density. A series of studies demonstrating this relationship are summarised in Figs. 2.3 and 2.4. Note that in Figure 2.3 the x-axis is an (inverse) function of population density (nearest–neighbour distance), while in Figure 2.4 it is a function of population size. This reflects the fact that most work on pollen limitation in plants has been done on plants pollinated by some animal vector (usually insects). These actively seek out flowers, complicating the issue of dilution by diffusion. Instead, pollen limitation in these plants is driven by the fact that most pollinators move relatively short distances and are less likely to find, visit and spend time in a small or isolated patch relative to a large or interconnected patch (Ashman et al. 2004, Sih and Baltus 1987, Wilcock and Neiland 2002). Also, a generalist pollinator (the majority) will visit plants of other species - and a higher proportion of these when the species of interest is at low density. Thus individuals in low density populations receive both less pollen and a lower

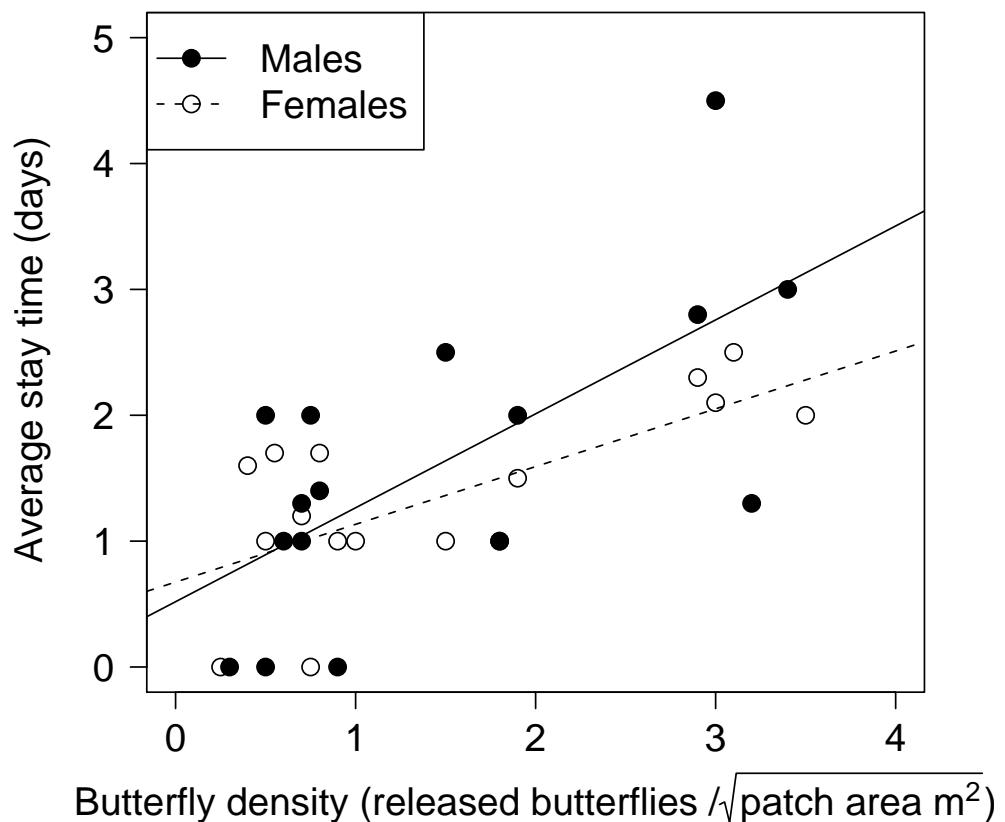


Figure 2.2: Movement of newly emerged Glanville fritillaries (*Melitaea cinxia*) in relation to population density. Both male and female butterflies released in smaller groups had a higher tendency to emigrate out of the patch in search of mating opportunities (Kuussaari et al. 1998)

proportion of conspecific pollen than those in dense populations (Ashman et al. 2004, Wagenius 2006).

Wind pollination is more directly analogous to broadcast spawning and pollen limitation is hypothesised to be very common in wind-pollinated species (Wilcock and Neiland 2002). For example, pollen limitation has been recorded in invasive annual cordgrass (*Spartina alterniflora*) where small, isolated patches of clones at the leading edge of an invasion set little seed (Davis et al. 2004). In European beech (*Fagus sylvatica*) trees in smaller habitat patches set less seed (Nilsson and Wastljung 1987), and seed set in the blue oak (*Quercus douglasii*) may also be limited by the number of neighbours in a  $\approx 60\text{m}$  radius (Knapp et al. 2001). Indeed, pollen limitation may drive the mass synchronous seed set characteristic of wind-pollinated masting species (Koenig and Ashley 2003). We must not assume, however, that high seed set in larger populations is always a consequence of pollination. In the pale swallow-wort (*Vincetoxicum rossicum*; an invasive vine) larger populations had higher seed set as a consequence of the suppression of other plant species, and hence reduced interspecific competition in large patches (Cappuccino 2004). This is of course still an Allee effect, but with a different mechanism unrelated to mate-finding in any sense.

One additional complication encountered by some out-crossing plant species is the issue of self-incompatibility. Self incompatible plant species cannot cross with individuals that possess the same self-incompatibility or S-alleles meaning that populations of self-incompatible species should have a reduced number of potential mates, further compounding pollen limitation. On the balance of probability, fewer mating types are likely to be represented in a small population than in a large one, and therefore the likelihood of a mate-finding Allee effect is enhanced in populations with self-incompatibility. For example, plants of native perennial herb *Burchardia umbellata* set less seed following experimental selfing compared to out-crossing (Ramsey and Vaughton 2000) as was the case for experimental populations of the known invasive wild radish (*Raphanus sativus*) (Elam et al. 2007). In an extreme case, an Illinois population of the self-incompatible Lakeside daisy (*Hymenoxous acaulis*) is considered functionally extinct because the last individuals are all of the same mating type (Demauro 1993).

### **2.2.3 Sperm limitation**

Sperm limitation may often arise in sessile or broadcast spawning organisms as described above. However, in mobile organisms, it is generally a question of mate-finding. However, it is not enough for a female just to find a mate: in order to maximise her reproductive output, she must find enough mates, or a large enough mate, to provide enough compatible sperm to fertilise all her eggs. In populations reduced in size or density, this may not always be possible.

Evidence for sperm limitation in natural populations of mobile species is somewhat limited. Studies have mainly focused on exploited populations, and must be treated with caution as examples of Allee effects because sperm limitation may arise due to the exploitation itself, as well as due to reduced population size e.g., as when the fishery targets large males. Females in heavily exploited populations of blue crab (*Callinectes sapidus*) Caribbean spiny lobster (*Panulirus argus*) and New Zealand rock lobster (*Jasus edwardsii*) for example, are frequently sperm-limited because fisheries have reduced the abundance of large males, reducing mate choice and reproductive output of individual females (Carver et al. 2005, Hines et al. 2003, MacDiarmid and Butler 1999). The distinction between sperm limitation due to low density and sperm limitation due to lack of mate choice (lack of large males) would become important if the fishery were to be stopped, because in the former case the rate of recovery of the population would be low (an Allee effect), while in the latter case it would be rapid once enough of the small males had grown

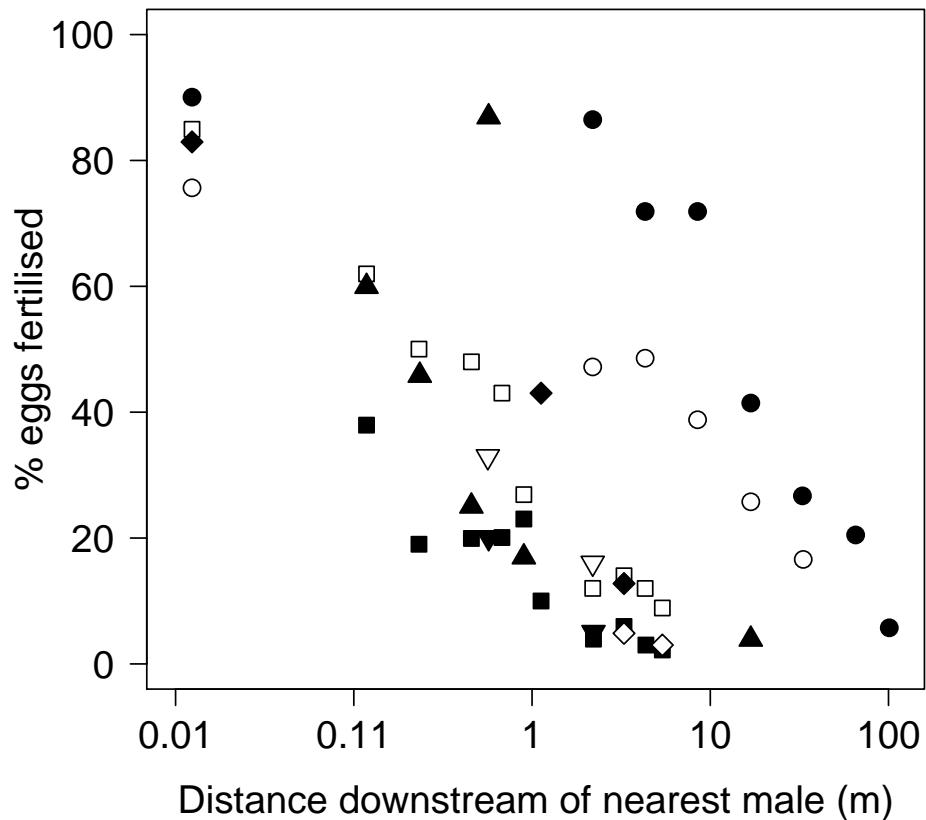


Figure 2.3: Fertilisation efficiency in broadcast spawning invertebrates (four echinoderms, one gastropod), showing a general trend of exponential decline in the proportion of eggs fertilised with increasing nearest neighbour distance. Data from Babcock et al. (1994) (crown of thorns starfish, *Acanthaster planci*; ● Davis Reef, ○ Sesoko Island); Levitan (1991) (red sea urchin, *Strongylocentrotus franciscanus*; ▼ group of 4, ▽ group of 16); Pennington (1985) (green sea urchin, *S. droebachiensis*; ■ current > 0.2 m/s, □ current < 0.2 m/s); Levitan (1991) (Caribbean long-spined sea urchin, *D. antillarum*; ◆ free eggs, ◇ eggs in bag); Babcock and Keesing (1999) (greenlip abalone, *Haliotis laevigata*; ▲)

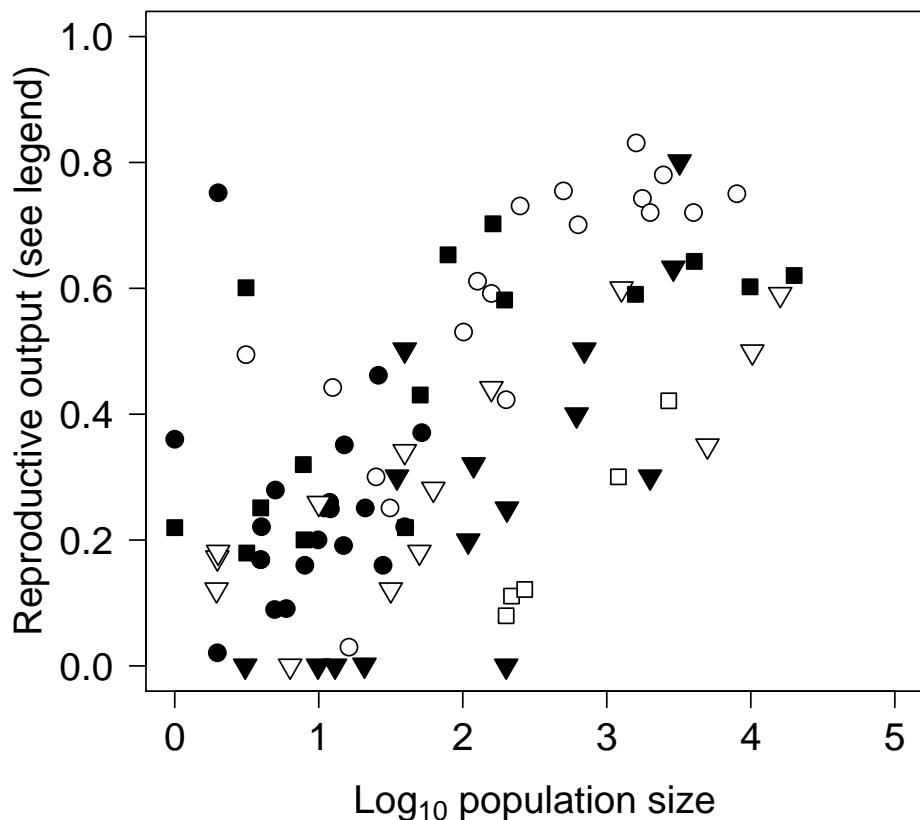


Figure 2.4: Reproductive output of flowering plants as a function of population size. American ginseng (*Panax quinquefolius*; ●): green fruits per flower versus number of individuals flowering (Hackney and McGraw 2001); *Senecio integrifolius* (○): proportion of seeds set versus number of individuals flowering (Widen 1993); *Banksia goodii* (▼): proportion of plants fertile versus population size in m<sup>3</sup> (Lamont et al. 1993); *Lythrum salicaria* (▽ 1993, ■ 1994): seeds per flower/100 versus number of individuals flowering (Agren 1996); *Haleakala silversword* (*Argyroxiphium sandwicense macrocephalum*; □): proportion of seeds set versus number of individuals flowering synchronously (Forsyth 2003)

to become large males. In practice, however, it is probably very difficult to distinguish the two effects in the field.

#### **2.2.4 Physiological stimulation**

In some species, individuals who do not encounter enough conspecifics do not become reproductive, not directly because they cannot find a mate, but rather because they need the presence of conspecifics to come into physiological condition to reproduce. This kind of physiological facilitation has been observed in captive populations, for example lemurs and flamingoes (Hearn et al. 1996, Stevens and Pickett 1994, Studer-Thiersch 2000). Presumably, the evolutionary purpose for this is to avoid wasting resources on gamete production if populations are too sparse for reproduction (i.e., if a mate-finding Allee effect is present). The specific mechanism may vary; individuals may require stimuli through exposure to conspecifics, potential mates, courtship or mating behaviour or perhaps some other related factor - in most cases the precise mechanism is unknown.

Such effects may be significant in some groups of insects. One of W.C. Allee's best-known experiments, in laboratory populations of the flour beetle (*Tribolium confusum*), showed that a dome - shaped relationship between per capita reproductive rate and density arise because the beetles need to encounter a certain density of conspecifics or mates to come into reproductive condition (Allee 1941, Allee et al. 1949). Mated queen European honey bees (*Apis mellifera*) produce structurally different pheromones to unmated queen bees, which drones respond to with increased attention and matings (Richard et al. 2007). Female golden egg bugs (*Phyllophorpha laciniata*) housed among conspecifics can lay twice as many eggs as isolated females (Garcia-Gonzalez and Gomendio 2003, Miettinen et al. 2006).

Reproductive facilitation may also be important in queen and milk conch (*Strombus gigas* and *S. costatus*), large gastropods native to the sub-tropical western Atlantic and Caribbean. Queen conch have been heavily exploited throughout their range and, in Bermuda and Florida, populations have crashed and are showing limited signs of recovery (Berg and Olsen 1989). A survey of extensive deep-water populations of queen conch showed that there was no reproductive activity below a critical density of  $\approx 50$  animals per ha (Stoner and Ray-Culp 2000). Furthermore, a translocation experiment in shallow-water populations also suggested an Allee effect (Gascoigne and Lipcius 2004b). This may be a straightforward problem of mate-finding, but reproductive facilitation may occur, because conch females engaged in egg-laying are subsequently eight times more likely to copulate than those not laying eggs (Appeldoorn 1988). Abalone (*Haliotis* spp.) is another large gastropod that may require reproductive stimulation by conspecifics. Abalones are broadcast spawners, but increase fertilisation rates by aggregating to spawn. As density declines, a decreasing proportion of reproductive adults participate in reproductive aggregations, reducing per capita reproductive output (Shepherd and Brown 1993). Multiple matings also has benefits in guppies (*Poecilia reticulata*) which produce bigger broods of fitter young (Evans and Magurran 2000), and in two-spotted crickets (*Gryllus bimaculatus*) where eggs from females mated several times have greater hatching success (Tregenza and Wedell 1998).

Animals which can reproduce asexually may nevertheless have higher reproductive output in the presence of other individuals (Thomas and Benjamin 1973). In self-fertile snails, *Biomphalaria glabrata*, and parthenogenetic female lizards, *Cnemidophorus uniparens*, individuals housed in isolation produce fewer offspring than individuals housed in groups, apparently because of exposure to courtship behaviour, although they do not actually mate (Crews et al. 1986, Vernon 1995). It is not clear what effect this might have in nature (if any) but it is interesting and counter-intuitive that even species which are self-fertile have the potential to suffer from repro-

ductive Allee effects, particularly since self-fertilisation itself may be an evolutionary adaptation to avoid Allee effects - this is discussed further below.

### **2.2.5 Female choice and reproductive investment**

Sexual selection - selection pressure on various characteristics via mate choice - plays an important role in the ecology as well as the evolution of many species. Mate choice is usually (not always) exercised by females and can take various forms, depending on the benefits which females accrue from mating with more attractive males - these benefits can be direct (male parental care) or indirect (more genetically fit or attractive male offspring) (Møller and Thornhill 1998). In small or low-density populations where females cannot choose between males, or where choice is limited to males which are not particularly attractive, or where available males are kin, females may choose not to mate, or may invest less in reproduction and offspring, leading to lower reproductive success (Kokko and Mappes 2005, Lehmann and Perrin 2003, Møller and Legendre 2001; but see Kokko and Rankin 2006 for alternative outcomes). In mathematical models, this scenario can lead to a demographic Allee effect (Møller and Legendre 2001), but its importance in nature is less clear, although it may be one of the causes for difficulties with captive breeding programmes (Møller and Legendre 2001).

### **2.2.6 Mate-finding and demographic stochasticity**

The link between demographic stochasticity and Allee effects, and more specifically whether demographic stochasticity should be considered an Allee effect mechanism, has exercised ecologists a fair amount over the last few years (Bessa-Gomes et al. 2004, Engen et al. 2003, Lande 1993, Lande 1998, Stephens et al. 1999). Certainly, it acts mainly in small populations and increases the risk of extinction, so to that extent it looks and smells like an Allee effect. In our view, however, demographic stochasticity cannot be considered an Allee effect mechanism by itself, but it can act to create a mechanism if it has an impact on mate-finding at low density.

This becomes clear if we consider the two types of demographic stochasticity currently recognised by population ecologists: (1) random fluctuations in population size resulting from individual birth and death events, and (2) random fluctuations in the adult sex ratio in populations with two sexes. Random fluctuations in birth and death rates do not fit our Allee effect definition because individual fitness, or a component of individual fitness, is not affected in a density-dependent way. Instead, chance events drive individuals out of the population or allow them to reproduce with a probability that is density-independent. A sequence of detrimental chance events may drive the entire population to extinction, and this is obviously more likely when there are fewer individuals: as a result, the probability that the population size collapses increases as the population declines. However, because Allee effects concern individual fitness, demographic stochasticity in births and deaths cannot in our view be classified as an Allee effect mechanism, even though it increases extinction risk in small populations (Bessa-Gomes et al. 2004, Stephens et al. 1999).

On the other hand, sex ratio fluctuations arguably do reduce mean individual fitness as the population declines, via the mechanism of mate-finding. They arise both as a consequence of chance in determining offspring sex, and because of demographic stochasticity in male and female deaths which, even if the male and female death rates are equal, causes male-to-female ratio to vary unpredictably. As the population size increases, the adult sex ratio is less and less likely to deviate from the mean sex ratio 1:1 so that nearly every individual within the population will be able to find a mate. Because demographic stochasticity due to random fluctuations in

the adult sex ratio reduces a component of individual fitness, via mate–finding as the population declines, it can be reasonably considered an Allee effect mechanism (Bessa-Gomes et al. 2004, Stephens et al. 1999). This kind of Allee effect is more likely to occur in monogamous than polygynous populations (Bessa-Gomes et al. 2004, Engen et al. 2003), and has been modelled in marmots (Stephens et al. 2002) and measured in small plant populations (Soldaat et al. 1997), although in neither case were individual fitness or per capita population growth rate measured directly. Another case, widely advertised at the time, is the kakapo (*Strigops habroptilus*) a lek–breeding giant, flightless parrot native to New Zealand. In 2001, the world population of this flightless bird consisted of 54 individuals, of which only 21 were female (with only few of these being fertile), distributed across several islands. An intensive breeding program has resulted in the birth of several chicks, but only six female fledglings have been produced since 1982 (Elliott et al. 2001, Sutherland 2002). The smaller the breeding population, the more likely are random fluctuations in the adult sex ratio to lead to a dramatically male–biased population, with little possibility of recovery.

## 2.3 From mate–finding to demographic Allee effects

As mentioned in the introduction, the connection from component Allee effects via mate–finding to demographic Allee effects is not always clear. Nonetheless, there are convincing examples of demographic Allee effects which arise from mate–finding. These currently include the Glanville fritillary, the gypsy moth, the smooth cordgrass and a copepod *Hesperodiaptomus shoshone* (Table 2.1). In addition, Table 2.1 lists those species we know of in which evidence for the link between a mate–finding Allee effect and a demographic Allee effect is somewhat weaker, often mediated by population models, and those studies in which the link is promising yet remains speculative.

A productive approach in linking component with demographic Allee effects has been to combine field data with population modelling. This cannot, of course, give a definitive causal connection between population size and population growth rate, but it can nonetheless be highly instructive. For example, in an invasive population of the wind–pollinated grass *Spartina alterniflora*, population models suggested that pollen limitation in sparsely populated areas would reduce the per capita population growth rate, although it still remained positive at all sites (a ‘weak’ demographic Allee effect; Davis et al. 2004, Taylor et al. 2004). The same approach was used on reintroduced populations of the field gentian (*Gentianella campestris*) a herb of rare low–nutrient grasslands (Lennartsson 2002). Some individuals of *G. campestris* are self–fertile while others are not, and the trait is heritable. Non–selfing populations showed a threshold patch size below which seed set fell dramatically, and demographic models suggested that these populations had high extinction probabilities. In self–compatible populations, no such critical thresholds were predicted. A mate–finding (pollen–limitation) Allee effect may thus be a driver for the evolution of self–fertile strains within some species (see the next section). This approach is equally applicable to animals and can be used with great success to understand the dynamics of biological invasions. Using independent estimates of life–history parameters, Veit and Lewis (1996) constructed a model that closely mirrored the observed dynamics of the invasion of the house finch (*Carpodacus mexicanus*) in North America, including a 3– to 10–year lag from its initial introduction to its first recorded instances of breeding that they speculated was caused by a mate–finding Allee effect.

## Mate-finding Allee effects

**Table 2.1: Studies where an evidence for a demographic Allee effect was brought up and a link to a mate-finding Allee effect either demonstrated or suggested**

| Species  | Mechanism  | Evidence   | Human impacts?                                   | Refs   |
|--|--|--|--|--|
| <i>Strong evidence for the link between a mate-finding Allee effect and a demographic Allee effect</i>                 |  |  |  |  |
| <i>Spartina alterniflora</i>   | Pollination failure  | Reduced (but still positive) per capita population growth rate at low density in front of invasion   | Yes - invasive species                           | Davis et al. (2004), Taylor et al. (2004)                                  |
| Gypsy moth, <i>Lymantria dispar</i>  | Mate-finding   | Threshold colony size below which colony goes extinct  | Yes - introduced species                         | Liebold and Bascompte (2003), Tcheslavskia et al. (2002)                   |
| Glanville fritillary, <i>Melitaea cinxia</i>   | Mate-finding   | Hump-shaped relationship between per capita population growth rate and population size   | Yes - habitat loss and fragmentation             | Kuussaari et al. (1998)  |
| Copepod, <i>Hesperodiaptomus shoshone</i>  | Mate-finding   | Failure of populations to establish in experimental lakes  | Yes - fish stocking reduced original populations | Sarnelle and Knapp (2004)  |
| <i>Weak evidence for the link between a mate-finding Allee effect and a demographic Allee effect</i>                   |  |  |  |  |
| <i>Genitianella campestris</i>   | Pollination failure  | Threshold in extinction probability in non-selfing populations   | Yes - extinction and reintroduction              | Lennartsson (2002)   |
| House finch, <i>Carpodacus mexicanus</i>   | Mate-finding   | Modelling confirmation of Allee effect due to mate-finding in early stages of establishment  | Yes - introduced species                         | Veit and Lewis (1996)  |
| <i>Likely but speculative evidence for the link between a mate-finding Allee effect and a demographic Allee effect</i> |  |  |  |  |
| Various parasitoids  | Mate-finding leading to skewed sex ratios                      | Persistence of populations was positively related to the propagule size or number of releases  | Yes - biocontrol species                         | Hopper and Roush (1993)  |
| Queen conch, <i>Strombus gigas</i>   | Reproductive failure possible; predation may be more important | $\approx 100\%$ mortality of juveniles away from aggregation; reduced reproduction at low density; collapse and failure to recover in many areas | Yes - heavy fishing pressure                     | Berg and Olsen (1989), Ray and Stoner (1994), Stoner and Ray (1993)        |
| Atlantic cod, <i>Gadus morhua</i>  | Mate-finding and/or cultivation effect                         | Per capita population growth rate $\approx$ zero in population reduced by overfishing  | Yes - overfishing                                | Rowe et al. (2004), Swain and Sinclair (2000), Walters and Kitchell (2001) |
| Elk, <i>Cervus elaphus nelsoni</i>   | Mate-finding possible; acclimatisation may be more important   | Higher breeding in years following introduction than in the year of introduction   | Yes - reintroduction programme                   | Larkin et al. (2002)   |
| <i>Banksia goodii</i>  | Pollination failure  | Reproductive failure of smallest populations   | Yes - habitat loss and fragmentation             | Lamont et al. (1993)   |
| <i>Clarkia concinna</i>  | Pollination failure  | Reproductive failure of smallest populations if isolated   | No   | Groom (1998)   |

There are, however, many studies that demonstrate mate-finding Allee effects but do not attempt to demonstrate ensuing demographic Allee effects, and vice versa. The majority of studies that consider mate-finding at low density consider processes at an individual rather than a population level (i.e., component rather than demographic Allee effects). Studies which have attempted to uncover empirical evidence of demographic Allee effects (e.g., Liermann and Hilborn 1997, Myers et al. 1995, Sæther et al. 1996, Sibly et al. 2005) have not found much empirical support. This failure to detect demographic Allee effects may be simply because overall fitness and per capita population growth rate are both very difficult to measure in the field, as well as because of methodological biases which make it more difficult to detect positive than negative density dependence (reviewed in Courchamp et al. 2008). However, component mate-finding Allee effects may be disconnected from demographics for more substantive reasons. In particular, two main issues arise which may mitigate the effect of a component Allee effect at the population level: fitness trade-offs and spatial structure in populations or metapopulations.

Fitness trade-offs occur when different components of fitness have different density-dependent relationships. For example, reproductive output may be positively related to density via mate-finding, but other fitness components may be negatively density-dependent. In the island fox (*Urocyon littoralis*), for example, low density results in a lower proportion of mated females, but eventually leads to more pups per female since (presumably) more resources are available to each female (Angulo et al. 2007). In this case, however, the effect of multiple component Allee effects tipped the cost-to-benefit balance of low density towards the side of cost, and a demographic Allee effect was observed.

These trade-offs are well illustrated with some examples from plant pollination and broadcast spawners. Plants that have high rates of seed set (i.e., close to 100% fertilisation efficiency) can suffer reduced growth and reproduction the following year. This cost associated with high seed set can mean that populations with low fertilisation efficiency have a similar overall population growth rate as populations with high fertilisation efficiency (Ehrlen 1992, Ehrlen and Eriksson 1995). Pollen limitation could also in theory trade off with reduced intraspecific competition at low density, but we have not come across a study which has addressed this hypothesis in plants. In sea urchins, however, this hypothesis has been tested. Echinoderms can pull off a variety of neat physiological tricks, including the ability to shrink their body mass when times get hard (Levitin 1991). Individuals in sparse populations are thus generally larger, because competition for resources is lower. In the Caribbean long-spined sea urchin (*Diadema antillarum*), increased gamete production by larger individuals at low density seems to offset the reduction in fertilisation efficiency, so that individual reproductive output remains broadly similar across a wide range of densities (Levitin 1991). If population density, and thus Allee effects, fluctuate significantly in time and space, individuals unable to find mates may reallocate resources from current reproduction to future growth which may improve mating success in subsequent seasons, as observed, for example, in the pipefish (*Syngnathus typhle*) (Berglund 1991).

The other confounding issue in converting mate-finding component Allee effects into demographic consequences is population spatial structure. Populations or sub-populations which are connected to their neighbours via dispersal can be brought back from below the Allee threshold by immigration from nearby patches (the ‘rescue’ effect). The two significant factors which determine whether the chance of extinction due to a demographic Allee effect will be mitigated via immigration are (1) the isolation of the (sub-) population and (2) the cost of dispersal across the intervening matrix. This is not the place to enter a discussion of Allee effects and metapopulation dynamics (see reviews in Amarasekare 1998 and Courchamp et al. 2008), but it is interesting to note the important role that population isolation often plays when demographic Allee effects are

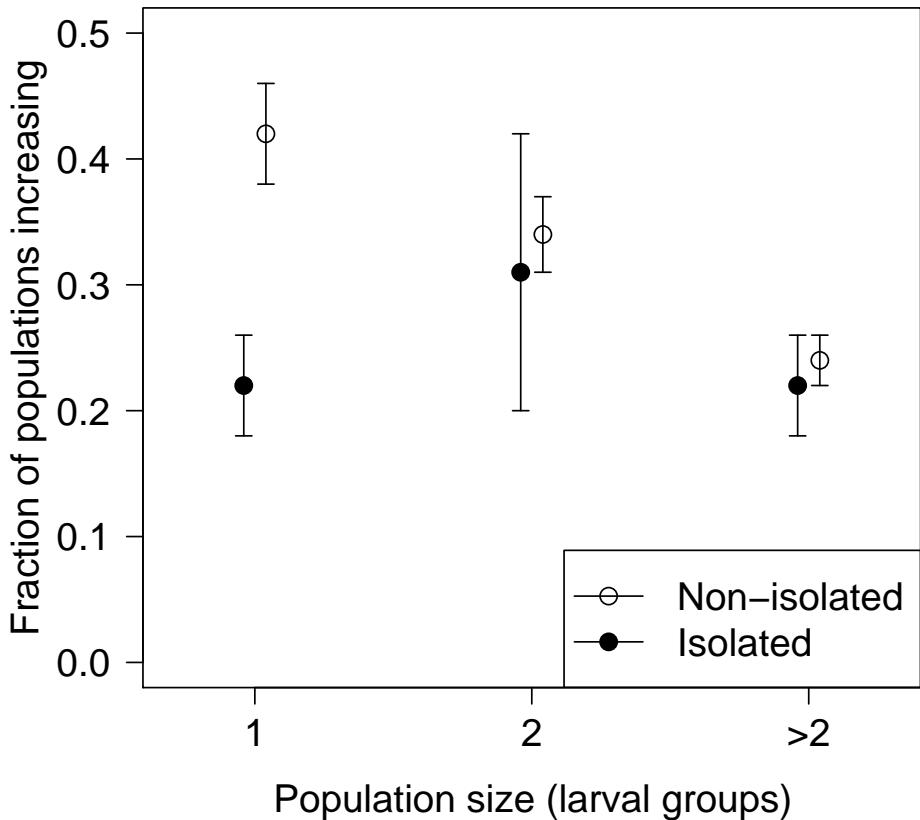


Figure 2.5: The mate-finding Allee effect in the Glanville fritillary shown in Figure 2.2 leads to a demographic Allee effect in the isolated populations, whereby population growth rate is depressed at low population size. In non-isolated populations, there is no such Allee effect

detected in populations with component mate-finding Allee effects.

As an example, we return to the Glanville fritillary, which has a component Allee effect in mate-finding, illustrated in Figure 2.5. This component Allee effect was shown in this case to lead to a demographic Allee effect in isolated populations, with a dome-shaped relationship between per capita population growth rate (measured as the proportion of populations increasing versus decreasing, as with the gypsy moth) and population size. In non-isolated populations, there was no demographic Allee effect (Kuussaari et al. 1998; Figure 2.5). The role of isolation in converting component mate-finding Allee effects into demographic Allee effects has also been illustrated in studies of plants (Groom 1998) and echinoderms (Levitán 2002b).

Measuring demographic Allee effects directly usually requires very extensive datasets. On the one hand, we may attempt to detect a demographic Allee effect in a single population monitored over consecutive years. While this approach has been attempted on a number of occasions (e.g., Barrowman et al. 2003, Liermann and Hilborn 1997, Myers et al. 1995, Reed 2005, Sæther et al. 1996, Sibly et al. 2005, Walters and Kitchell 2001), none have revealed extensive evidence for demographic Allee effects and all have, at least in part, suggested that this might be due to data constraints. On the other hand, we may attempt to measure a demographic Allee effect with replicate populations - quite a rarity particularly for species of interest to conservation biologists,

but there are exceptions. In their island fox study, Angulo et al. (2007) used populations on different islands in an archipelago as replicates. In the gypsy moth, an extensive network of 150,000 pheromone traps across the northeastern USA has provided a very large data set which can be analysed to look at trends in population dynamics in relation to population density (Johnson et al. 2006, Tobin et al. 2007).

Tobin et al. (2007) used a subset of this trap data to calculate for each integer value of population size the proportion  $P$  of populations which increased from one year to the next. At the Allee threshold  $P = 0.5$  because a population at the threshold size is equally likely to increase or decrease the following year. They found an Allee threshold, with smaller populations more likely to decrease because of a failure to find mates (Tcheslavskia et al. 2002), while larger populations were more likely to increase (Figure 2.6). (There is also a higher density threshold at which  $P = 0.5$ , this corresponds to the carrying capacity.)

Intriguingly, the Allee threshold in the gypsy moth is not consistent in space or time, with a lower Allee threshold in Wisconsin than Virginia and a lower threshold in 2002–3 than 2003–4. The geographical variation in the threshold was strongly correlated with geographical variation in the invasion rate (Tobin et al. 2007, Whitmire and Tobin 2006) in line with general model predictions (Almeida et al. 2006). It may be that the effectiveness of mate–finding (pheromone transmission) varies depending on the environment (although Tcheslavskia et al. (2002) speculate that predation also plays an important role) in a similar way to pollination with an animal vector (Wilcock and Neiland 2002), although Tcheslavskia et al. (2002) speculate that predation may play an important role. Also, it appears that the optimal environment for gypsy moths at high densities is not necessarily the best at low densities - Virginia and North Carolina had a higher Allee threshold than Wisconsin (i.e. provided a less good environment for low density populations) but also had an estimated carrying capacity more than twice as high (i.e. they provided a better environment for high density populations; Tobin et al. 2007).

## **2.4 Evolution to mitigate or avoid mate–finding Allee effects: consequences for depleted populations**

In this review, we also consider mate–finding Allee effects from an evolutionary point of view. Since an Allee effect is, by definition, a process that affects individual fitness, it is subject to natural selection. We therefore ask whether a risk of suffering from mate–finding Allee effects might have been a significant evolutionary driver for different mate–finding adaptations and even mating systems.

Adaptations for finding a mate - and finding the best mate - are very widespread, ranging from sex or aggregation pheromones to bird songs, to ability to move faster or more efficiently to pollination mutualisms, to mass spawning to quality advertising through honest signals. We believe it is useful to distinguish between mechanisms which allow mate–finding at low density (e.g., long–distance attractants such as calling and pheromones) and adaptations which reduce the likelihood of encountering low density *per se* (e.g., mass spawning or reproductive aggregations). This is because, from a theoretical perspective, the consequences of these two types of adaptations in terms of Allee effects are different. If the mate–finding mechanism has evolved to function well even at low density, it seems likely that the population will not be particularly vulnerable to Allee effects at low density. If, however, the mate–finding mechanism has evolved to ensure that low density is avoided, it seems to us reasonable to hypothesise that this population will be vulnerable to mate–finding Allee effects should it ever meet with low density. Thus, al-

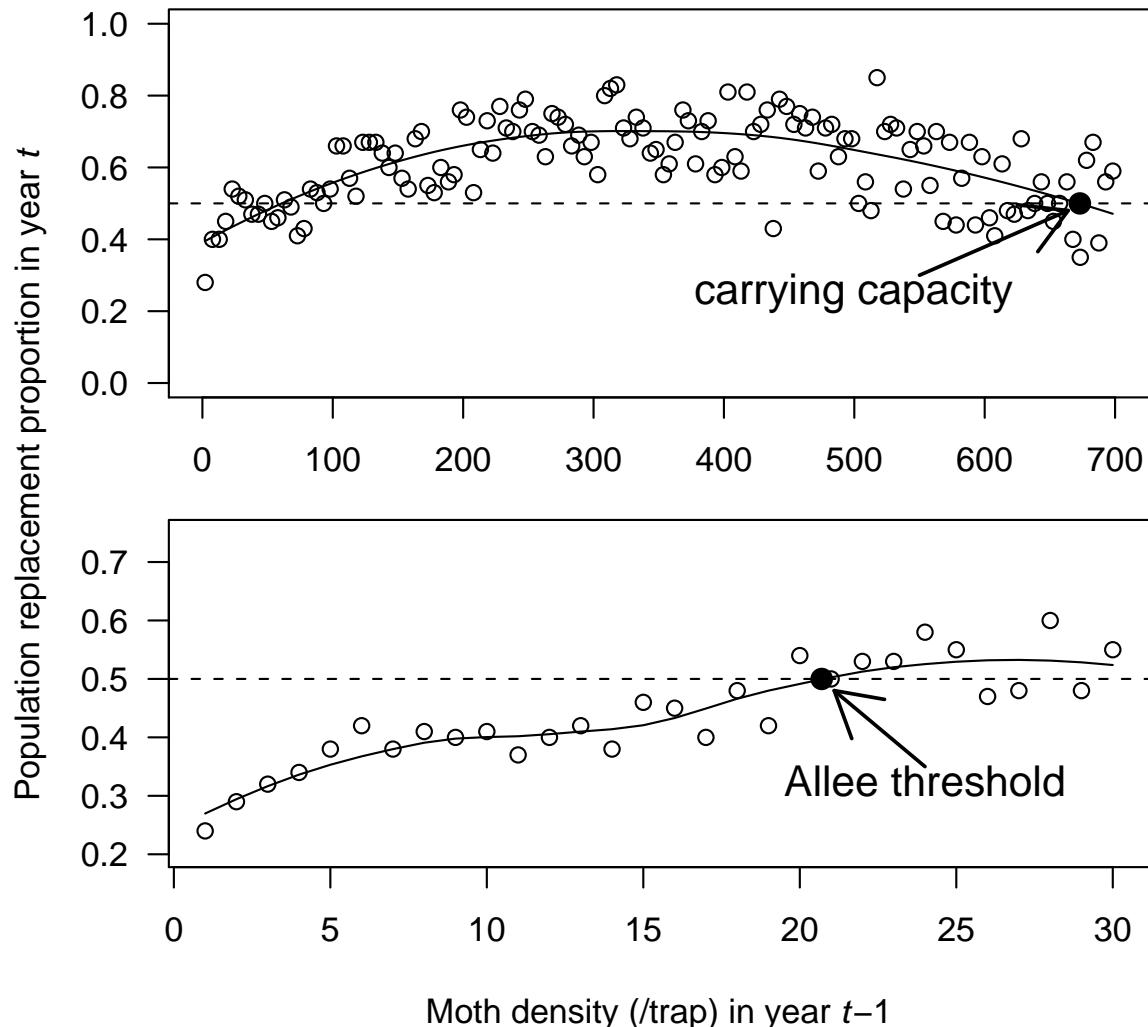


Figure 2.6: The proportional size  $P$  of the population in year  $t$  (y-axis) relative to the population size in year  $t-1$  (x-axis). The Allee threshold at  $P = 0.5$  works out at  $\approx 20.7$  moths per trap, the carrying capacity at  $\approx 673$  moths per trap. The bottom panel is a close-up of the low-density populations of the top one. Redrawn from Tobin et al. (2007)

though gregariousness can still be an adaptation to mitigate or avoid a mate-finding Allee effect, the Allee effect is still there and is only circumvented. Both types of adaptation may thus have a similar purpose, but in the context of populations reduced by anthropogenic impacts their effects can be diametrically opposed. Species with the former types of adaptation are unlikely to suffer from mate-finding Allee effects, since they are already adapted to cope with low density. Conversely, species with the latter type may suffer very severely if their populations are artificially reduced to low density, since their mating system is predicated on avoiding low density. Paradoxically, therefore, species which have adapted mechanisms to circumvent mate-finding Allee effects may now be precisely those which find themselves most vulnerable. The fourth column in Table 2.1, which indicates whether there has been an anthropogenic impact on the populations in question, suggests that this ‘evolutionary’ classification of mate-finding adaptations might have merit.

Modelling studies suggest that mate-finding adaptations can indeed mitigate mate-finding Allee effects. For example, Jonsson et al. (2003) compared the efficiency of a pheromone and a non-pheromone mate-finding strategy at different conspecific densities. Whereas there were only small differences between these strategies at high density, the pheromone strategy was more efficient when conspecific density declined. With another simulation model, Berec et al. (2001) showed that mate-finding Allee effects can be avoided either by a large number of individuals with relatively low mate-finding ability or a few individuals with high mate-finding ability - an increase in the mate detection distance significantly decreased strength of the mate-finding Allee effect.

In reality, it is not usually possible to say whether a particular evolutionary adaption arose specifically because of a mate-finding Allee effects. For example, bird songs or amphibian advertisement calls apparently help individuals increase their probability of mating if they are dispersed and potentially difficult to locate, such as in the Cuban tree frog (*Osteopilus septentrionalis*; Vargas-Salinas 2006). However, such signals may serve as a tool in intense intra-sexual competition in male-biased breeding aggregations - indeed, call duration was shown to be an indicator of genetic quality in males of the grey tree frog (*Hyla versicolor*; Welch et al. 1998). In such instances, it is possible that the signal originated in sparse populations so as to facilitate mate-finding (you are chosen because you are audible), before it became exaggerated and used for sexual selection (you are noticed because you are louder than your competitors). However, it is also possible that it originated in large populations for exactly the same reason: to increase the chance that you are noticed by a female earlier than your mute competitors. Thus, any adaptation likely to arise as a response to mate-finding Allee effects in rare populations should be scrutinised from the perspective of its origin. Below, we consider some of the adaptations that allow mate-finding at low density and therefore might arise as a response to mate-finding Allee effects in rare populations.

Traits that have only a negligible adaptive value in large and dense populations might turn out to be strong determinants of fitness when populations become small and sparse, i.e., during population bottlenecks. The case of biological invasions is a particularly significant example of this. During the early founding of an invading population, these populations may be exposed to situations that are very different from normal conditions and thus for which they may not be pre-adapted. Specifically, founding populations differ from established populations in that not only are they at very low densities but they are also extremely isolated spatially from other populations. This can promote a diversification of mate-finding traits between invading and source populations, a situation that would not be experienced in continuously established populations.

### **2.4.1 Mate encounters in animals**

Behaviourally plastic strategies which mitigate mate-finding Allee effects have been observed in Roesel's bush cricket (*Metrioptera roeseli*) (faster movement at low population densities; Kindvall et al. 1998) and the European field cricket (*Gryllus campestris*) (higher proportions of males calling at low population densities; Hissmann 1990). Some adaptations decrease the frequency at which mate-finding needs to occur. Such adaptations may be highly advantageous at low density, but are possibly of little benefit or even disadvantageous at high density. They include the ability of females to store viable sperm (e.g., the box turtle, *Terrapene carolina*; Ewing 1943, and many invertebrates), induced ovulation (e.g., the red deer, *Cervus elaphus*; Jabbour et al. 1994), and ability to maintain long-term or even life-long pair bonds (e.g., the wandering albatross, *Diomedea exulans*; Dubois et al. 1998: in migrating species, such as the albatross, this works together with breeding site fidelity - another adaptation - allowing them to find each other in the breeding season). The ability of females to store sperm is important in many marine species, particularly in crustaceans where mating usually has to coincide with molting and therefore where only short mate-finding windows are available. In the blue crab, females only mate once, during their terminal molt, and store sperm which is used for the rest of their reproductive life (up to several years) (Carver et al. 2005).

Adaptations to mitigate or avoid mate-finding Allee effects might also involve shifts in mating systems. Mating systems as diverse as parthenogenesis, hermaphroditism, arrhenotoky, or even density-dependent sex determination all help individuals in mating in low-density populations. Parthenogenesis requires no mate-finding at all, and can be permanent, such as in some whiptail lizards, (*Cnemidophorus* sp.; Cole 1984), or only seasonal such as in various nematodes, rotifers, (parasitic) wasps, mites or aphids. Simultaneous (self-incompatible) hermaphrodites such as hamlets (coral reef fish, *Hoploplectrus* spp.) effectively double the density of mating partners relative to species with separate sexes, since any two individuals can in principle mate. Some hermaphrodites, such as tapeworms and perhaps some mollusks, may even evolve selfing when mate availability is limited (Klomp et al. 1964). Sometimes, the shift in reproductive strategy may impact female reproductive behaviour. Hopper and Roush (1993) showed that a change from virgin females producing no progeny to virgin females producing all males (arrhenotoky; sexual reproduction with haplo-diploid sex determination) decreased the critical number of females by over 30%. In some cases, introduced species which were biparental in their native ranges appear to have become parthenogenetic in their introduced ranges where finding mates becomes difficult (Hopper and Roush 1993 and references therein). Finally, copepodites (juvenile stage) of the parasitic copepod *Pachypygus gibber* (Becheikh et al. 1998) or sexually undifferentiated larvae of the echiuran worm *Bonellia viridis* (Berec et al. 2005 and references therein) become males or females (in part) depending on availability of sexual partners.

### **2.4.2 Pollen limitation in plants**

From the above, it is clear that low density or rarity may induce shifts in animal mating systems towards cloning or selfing. A similar shift may also occur in plants. However, the genetic costs associated with high selfing rates (i.e., inbreeding depression) may mean that populations of rare plants may suffer two opposing Allee effects, one related to inbreeding where self-pollination dominates and the other to mate-finding where self-pollination is prohibited. Where inbreeding depression strongly reduces individual fitness, evolution may 'prefer' inbreeding avoidance and lead to a self-incompatibility system, dioecy or heterostyly. On the other hand, where inbreeding depression is weak, rare populations of outcrossing plants may avoid mate-finding Allee

effects by evolving self-pollination (Herlihy and Eckert 2002, Lloyd 1992). In the California annual *Clarkia xantiana*, for example, small populations isolated from congeners exhibited reduced herkogamy and protandry (traits promoting self-fertilisation avoidance) relative to large populations or small populations mingled with congeners (Moeller and Geber 2005). Outcrossing is ancestral in *C. xantiana* and self-pollination has likely evolved in small or sparse populations living in inferior, arid habitats and hence suffering lower pollinator visitation rates (Fausto et al. 2001, Moore and Lewis 1965).

Modelling studies support these predictions. Cheptou (2004) and Morgan et al. (2005) showed that natural selection might lead plants to evolve either complete selfing in which case an Allee effect due to pollen-limitation disappears, or complete non-selfing with a strong Allee effect due to pollen-limitation (Figure 2.7). The evolutionary endpoint depends on a variety of population characteristics, such as the degree of inbreeding depression, strength of pollen-limitation Allee effect, fertility, and the initial state of partial selfing. At least in theory, selection for selfing may even lead to population extinction, a phenomenon termed ‘evolutionary suicide’ (Cheptou 2004, Morgan et al. 2005). Such models usually consider inbreeding depression to be constant (i.e., not specified by an underlying population genetic model nor dependent on population size or density). This assumption may not be robust and implies that more detailed models should be developed and analysed. This new generation of models might also shed some light on the idea that the (often) intermediate selfing rates seen in nature could be viewed as a trade-off between maximising fertilisation (mate-finding) on the one hand and avoiding inbreeding depression on the other - trying to avoid two kinds of Allee effects simultaneously.

Rare plants may also mitigate pollen-limitation Allee effects by evolving higher pollinator attraction (Haig and Westoby 1988), allocating more resources to clonal growth (Eckert 2002), or ‘sacrificing’ dioecy for simultaneous hermaphroditism (Wilson and Harder 2003; see also Ashman et al. (2004) for a comprehensive review). Many sparse plant species have succeeded in avoiding both pollen limitation and inbreeding, by evolving highly specific mutualisms between one plant species and one species of pollinator (often insects but also bats: Jackson 2004, Maia and Schlindwein 2006, Muchhala 2006, Sakai 2002).

### 2.4.3 Broadcast spawning in marine invertebrates

Adaptations that mitigate Allee effects via reduced fertilisation success at low density in broadcast spawning marine invertebrates are reviewed by (Levitin 1998). These include spawning synchrony (using cues such as day length, lunar period, or phytoplankton concentration), increased mobility and aggregation, sperm filtering and storage, hermaphroditism, and selfing.

A nice comparison of three congeneric sea urchins shows how sperm limitation may stimulate the evolution of gamete morphology and performance (Levitin 2002a). The urchin (*Strongylocentrotus droebachiensis*) living at lowest density has evolved gametes that perform best under sperm limitation (larger eggs and slow, long-lived sperm). On the other hand, the urchin (*S. purpuratus*) that lives at highest density has evolved gametes that perform best under sperm competition (smaller eggs and fast, short-lived sperm). *S. franciscanus* lives at an intermediate density and its gametes are somewhere in between. These observations suggest that gametes of *S. purpuratus* would perform suboptimally when density of this species is abruptly reduced, since any mutation of the egg or sperm in the direction of *S. droebachiensis* would be advantageous and quickly spread through the population, and vice versa. Interestingly, *S. droebachiensis*, evolving a fertilisation system with higher success rates at low sperm concentrations than the other two urchins, bears a cost in the form of higher rates of hybridisation with the other species at high (total) sperm density (Levitin 2002b).

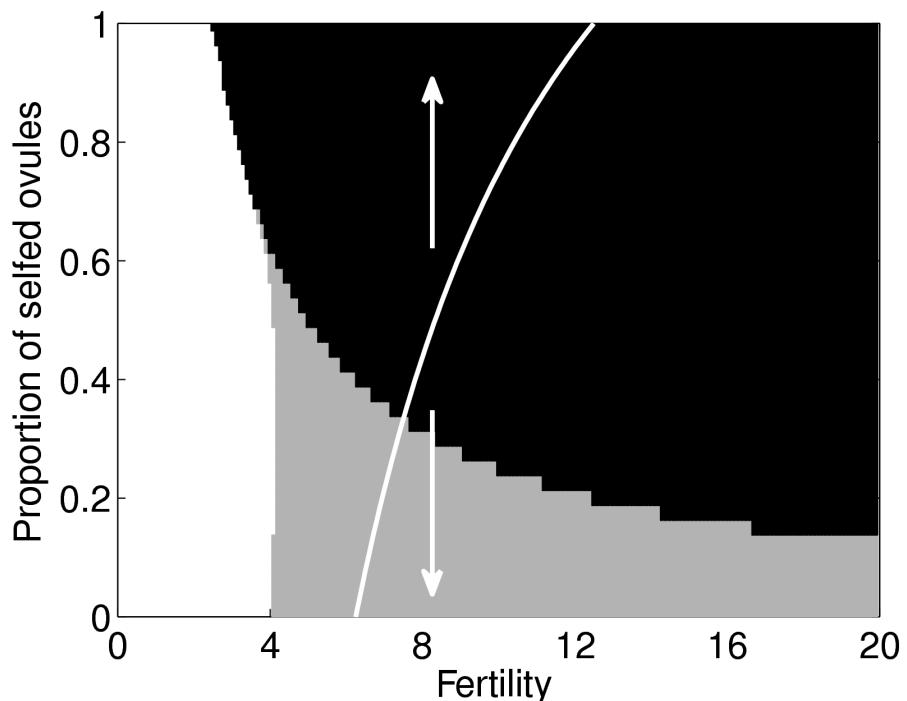


Figure 2.7: An outcome of a model examining the evolution of selfing as a function of fertility and initial proportion of selfed ovules. The plant population suffers from effect with an Allee threshold in the grey area and a weak or no demographic Allee effect in the black area; the population goes extinct from any initial size in the white area. The white curve delimits the area in which plants evolve complete selfing (above the curve) from the area where they evolve complete non-selfing (below the curve); the arrows demonstrate the route of evolution. Adapted from Cheptou (2004)

#### 2.4.4 A word of caution

One can think of many adaptations that might have been selected in small or sparse populations as an evolutionary response to mate-finding Allee effects. On the other hand, as exemplified by evolution of sexual reproduction, large or dense populations might have acquired traits that generate Allee effects that start imposing costs as the population declines. Many of the above ideas and considerations are only suggestive, not conclusive. However appealing these may be, only a careful examination of the advantages of an evolutionary strategy among a sea of other strategies may help us to assess the extent to which the observed adaptations has evolved as a response to mate-finding Allee effects. As we already cautioned above; some adaptations that may appear to be a result of natural selection in small or sparse populations may equally be seen as outcomes of sexual selection acting in large or dense populations.

In our opinion, convincing evidence of evolution to mitigate or avoid Allee effects needs to show that increasing fitness at low density has a cost associated with it at high density. This is not to say that such a trait must necessarily have a cost at high density, but rather that if we found such an example it would be the most convincing evidence that evolution had occurred to avoid some cost of low density (as in the example of *S. droebachiensis* above). Mathematical models of evolution, such as those considering competitive dynamics between initially small populations of mutants and large populations of resident phenotypes, could also help discriminate from among many of the above possible evolutionary outcomes. It is notable that, although there are many population dynamical models involving Allee effects, relatively few models have been developed that consider how individuals respond evolutionarily to mate-finding (or other) Allee effects.

The amazingly rich world of mating systems and mate-finding adaptations, some of which may have evolved as a response to mate-finding Allee effects, leads us to ask whether there is any chance of observing demographic Allee effects at all, or whether these adaptations, the ‘ghosts of Allee effects past’, are all we can expect to see in natural populations. Given this possibility, we suggest that it would be most productive to look for demographic Allee effects in species which are ‘anthropogenically’ rather than ‘naturally’ rare (i.e., populations reduced greatly in size due to habitat loss, exploitation, etc., or non-native populations at the start of an invasion). This is because such populations (although they are now small or sparse) may have an evolutionary history of being large or dense. This means that they have not experienced the conditions over evolutionary time which would result in selective pressure to mitigate the negative impacts of low density (i.e., of Allee effects). It is thus these populations that we would expect to be most vulnerable to demographic Allee effects when they are reduced by human activity. Again, a brief glance at Table 2.1 suggests that this hypothesis has merit, since all but one presented example of demographic Allee effects demonstrated or suggested to be driven by mate-finding are in populations affected by human activity.

### 2.5 Conclusions

In this paper, we have reviewed just one of the many possible mechanisms giving rise to component Allee effects - mate-finding - and done so with numerous examples. We have also discussed populations which show compelling evidence of demographic Allee effects arising from mate-finding; however, there are significantly fewer examples of these in the scientific literature at the moment (we have found four). Given the huge number of populations of sexually reproducing species that could, according to the arguments we present above, suffer from mate-finding component Allee effects, not to mention all the other populations that may be susceptible to other

Allee effect mechanisms, we might ask why are there so few empirical examples of ensuing demographic Allee effects? If component Allee effects were widespread and potent enough to drive evolutionary selection of adaptations to avoid them, as argued above, we should be able to detect more demographic Allee effects, particularly in populations which are threatened, endangered or otherwise reduced in number or density, of which there are (alas) many examples (see <http://www.iucnredlist.org/>).

We believe that the lack of hard experimental evidence for the effects of mate–finding Allee effects on demography results from the difficulties of studying field populations at small sizes or low densities. Indeed, there are real difficulties associated with the empirical investigation of Allee effects in natural populations. These include, among other things, the need for a long time–series or a wide spectrum of densities, technical problems associated with statistical analysis, non–independence and replication, issues around the definition of a population, and of population spatial structure and metapopulation dynamics, and logistical problems in working in the field–issues with which many readers will no doubt be all too familiar (see review in Courchamp et al. 2008). Studies which do provide convincing demonstrations of demographic Allee effects have often studied rather exceptional systems (e.g., many replicate populations of different densities in a wide geographical area; Johnson et al. 2006). As a matter of fact, only a small number of studies demonstrating mate–finding Allee effects undertook a way of demonstrating presence or absence of a demographic Allee effect.

Negative density dependence is now considered by most to be a real population regulatory phenomenon (Berryman 2002), to the extent that proponents argue that it should be considered a ‘principle’ of population ecology (Berryman 2003). This is at least in part due to the strength of empirical evidence for negative density dependence dynamics in natural populations (e.g., Brook and Bradshaw 2006). It has also been argued that positive density dependence, or Allee dynamics, should also be upgraded to the status of a ‘principle’ of population ecology; however, with the presently limited empirical evidence we struggle to support such claims convincingly.

The visible importance of adaptations for mate–finding implies that mate–finding Allee effects may have been an important source of selection pressure on populations in the past. Given our role in reducing many populations to small size or low density, it seems likely that they may continue to be so. In our view, and in the view of others (Brook 2008), we need to work hard to surmount the obstacles associated with studying Allee effects at the population level, or find imaginative means of circumventing them, if we are ever to have convincing evidence that demographic Allee effects are of general importance in population dynamics, whether as a consequence of mate–finding or of some other mechanism, and that they are (or are not) as widespread as we suspect.

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## References

- Agren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* **77**:1779–1790.
- Allee, W. C. 1941. Animal aggregations, a study in general sociology. University of Chicago Press, Chicago.
- Allee, W. C., O. Emerson, T. Park, and K. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia.
- Almeida, R. C., S. A. Delphim, and M. I. D. Costa. 2006. A numerical model to solve single-species invasion problems with Allee effects. *Ecological Modelling* **192**:601–617.
- Amarasekare, P. 1998. Allee effects in metapopulation dynamics. *The American Naturalist* **152**:298–302.
- Angulo, E., G. W. Roemer, L. Berec, J. Gascoigne, and F. Courchamp. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**:1082–1091.
- Appeldoorn, R. S. 1988. Fishing pressure and reproductive potential in strombid conchs: is there a critical stock density for reproduction? *Memorias de la Sociedad de Ciencias Naturales "La Salle"* **48**:275–288.
- Ashman, T. L., T. M. Knight, J. A. Steets, P. Amarasekare, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, S. J. Mazer, R. J. Mitchell, M. T. Morgan, and W. G. Wilson. 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology* **85**:2408–2421.
- Babcock, R., and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1668–1678.
- Babcock, R. C., C. N. Mundy, and D. Whitehead. 1994. Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. *Biological Bulletin* **186**:17–28.
- Barrowman, N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecological Applications* **13**:784–793.
- Becheikh, S., M. Michaud, F. Thomas, A. Raibaut, and F. Renaud. 1998. Roles of resource and partner availability in sex determination in a parasitic copepod. *Proceedings of the Royal Society B: Biological Sciences* **265**:1153–1156.
- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. *Trends in Ecology and Evolution* **22**:185–191.
- Berec, L., and D. S. Boukal. 2004. Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. *Oikos* **104**:122–132.

- Berec, L., D. S. Boukal, and M. Berec. 2001. Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. *The American Naturalist* **157**:217–230.
- Berec, L., P. J. Schembri, and D. S. Boukal. 2005. Sex determination in *Bonellia viridis* (Echiura: Bonelliidae): population dynamics and evolution. *Oikos* **108**:473–484.
- Berg, C. J., and D. Olsen, 1989. Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. *in* J. F. Caddy, editor. *Marine invertebrate fisheries: their assessment and management*. Wiley, New York.
- Berggren, A. 2001. Colonization success in Roesel's bush-cricket *Metrioptera roeseli*: The effects of propagule size. *Ecology* **82**:274–280.
- Berglund, A. 1991. Egg competition in a sex-role reversed pipefish - subdominant females trade reproduction for growth. *Evolution* **45**:770–774.
- Berryman, A. A. 2002. Population regulation, emergent properties, and a requiem for density dependence. *Oikos* **99**:600–606.
- Berryman, A. A. 2003. On principles, laws and theory in population ecology. *Oikos* **103**:695–701.
- Bessa-Gomes, C., S. Legendre, and J. Clobert. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters* **7**:802–812.
- Brook, B. 2008. The allure of the few. *PLoS Biology* **6**:e127 10.1371/journal.pbio.0060127.
- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**:1445 – 1451.
- Calabrese, J. M., and W. F. Fagan. 2004. Lost in time, lonely, and single: Reproductive asynchrony and the Allee effect. *The American Naturalist* **164**:25–37.
- Cappuccino, N. 2004. Allee effect in an invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepiadaceae). *Oikos* **106**:3–8.
- Carver, A. M., T. G. Wolcott, D. L. Wolcott, and A. H. Hines. 2005. Unnatural selection: Effects of a male-focused size-selective fishery on reproductive potential of a blue crab population. *Journal of Experimental Marine Biology and Ecology* **319**:29–41.
- Cheptou, P. O. 2004. Allee effect and self-fertilization in hermaphrodites: Reproductive assurance in demographically stable populations. *Evolution* **58**:2613–2621.
- Cole, C. J. 1984. Unisexual lizards. *Scientific American* **250**:94–100.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. *Allee effects in ecology and conservation*. Oxford University Press.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* **14**:405–410.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 2000. Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. *Animal Conservation* **3**:277–285.

- Crews, D., M. Grassman, and J. Lindzey. 1986. Behavioral facilitation of reproduction in sexual and unisexual Whiptail lizards. *Proceedings of the National Academy of Sciences, USA* **83**:9547–9550.
- Davis, H. G., C. M. Taylor, J. G. Lambrinos, and D. R. Strong. 2004. Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proceedings of the National Academy of Sciences, USA* **101**:13804–13807.
- Demauro, M. M. 1993. Relationship of breeding system to rarity in the Lakeside Daisy (*Hymenoxys-acaulis* var *glabra*). *Conservation Biology* **7**:542–550.
- Dennis, B. 1989. Allee effects: population growth, critical density and the chance of extinction. *Natural Resource Modeling* **3**:481–538.
- Dobson, A. P., and A. M. Lyles. 1989. The population-dynamics and conservation of primate populations. *Conservation Biology* **3**:362–380.
- Dubois, F., F. Cezilly, and M. Pagel. 1998. Mate fidelity and coloniality in waterbirds: a comparative analysis. *Oecologia* **116**:433–440.
- Eckert, C. G. 2002. The loss of sex in clonal plants. *Evolutionary Ecology* **15**:501–520.
- Ehrlen, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. *Ecology* **73**:1820–1831.
- Ehrlen, J., and O. Eriksson. 1995. Pollen limitation and population-growth in a herbaceous perennial legume. *Ecology* **76**:652–656.
- Elam, D. R., C. E. Ridley, K. Goodell, and N. C. Ellstrandt. 2007. Population size and relatedness affect fitness of a self-incompatible invasive plant. *Proceedings of the National Academy of Sciences, USA* **104**:549–552.
- Elliott, G. P., D. V. Merton, and P. W. Jansen. 2001. Intensive management of a critically endangered species: the kakapo. *Biological Conservation* **99**:121–133.
- Engen, S., R. Lande, and B. E. Saether. 2003. Demographic stochasticity and Allee effects in populations' with two sexes. *Ecology* **84**:2378–2386.
- Evans, J. P., and A. E. Magurran. 2000. Multiple benefits of multiple mating in guppies. *Proceedings of the National Academy of Sciences, USA* **97**:10074–10076.
- Ewing, H. 1943. Continued fertility in female Box turtles following mating. *Copeia* **1943**:112–114.
- Fausto, J. A., V. M. Eckhart, and M. A. Geber. 2001. Reproductive assurance and the evolutionary ecology of self-pollination in *Clarkia xantiana* (Onagraceae). *American Journal of Botany* **88**:1794–1800.
- Forsyth, S. A. 2003. Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. *Oecologia* **136**:551–557.
- Fowler, C., and J. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. *Reports to the International Whaling Commission* **41**:545–554.

- Garcia-Gonzalez, F., and M. Gomendio. 2003. Oviposition site selection and oviposition stimulation by conspecifics in the golden egg bug (*Phyllomorphula laciniata*): implications for female fitness. *Behavioral Ecology and Sociobiology* **53**:385–392.
- Garrett, K. A., and R. L. Bowden. 2002. An Allee effect reduces the invasive potential of *Tilletia indica*. *Phytopathology* **92**:1152–1159.
- Gascoigne, J., and R. N. Lipcius. 2004a. Allee effects in marine systems. *Marine Ecology Progress Series* **269**:49–59.
- Gascoigne, J., and R. N. Lipcius. 2004b. Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. *Marine Ecology Progress Series* **284**:185–194.
- Groom, M. J. 1998. Allee effects limit population viability of an annual plant. *The American Naturalist* **151**:487–496.
- Hackney, E. E., and J. B. McGraw. 2001. Experimental demonstration of an Allee effect in American ginseng. *Conservation Biology* **15**:129–136.
- Haig, D., and M. Westoby. 1988. On limits to seed production. *The American Naturalist* **131**:757–759.
- Hearn, G. W., R. W. Berghaier, and D. D. George. 1996. Evidence for social enhancement of reproduction in two *Eulemur* species. *Zoo Biology* **15**:1–12.
- Herlihy, C. R., and C. G. Eckert. 2002. Genetic cost of reproductive assurance in a self-fertilizing plant. *Nature* **416**:320–323.
- Hines, A. H., P. R. Jivoff, P. J. Bushmann, J. van Montfrans, S. A. Reed, D. L. Wolcott, and T. G. Wolcott. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. *Bulletin of Marine Science* **72**:287–310.
- Hissmann, K. 1990. Strategies of mate finding in the European field cricket (*Gryllus-campestris*) at different population-densities - a field-study. *Ecological Entomology* **15**:281–291.
- Hopper, K. R., and R. T. Roush. 1993. Mate finding, dispersal, number released, and the success of biological-control introductions. *Ecological Entomology* **18**:321–331.
- Jabbar, H. N., F. A. Veldhuizen, R. C. Mulley, and G. W. Asher. 1994. Effect of exogenous gonadotropins on estrus, the Lh surge and the timing and rate of ovulation in red deer (*Cervus-elaphus*). *Journal of Reproduction and Fertility* **100**:533–539.
- Jackson, A. P. 2004. Cophylogeny of the *Ficus* microcosm. *Biological Reviews* **79**:751–768.
- Johnson, D. M., A. M. Liebold, P. C. Tobin, and O. N. Bjornstad. 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature* **444**:361–363.
- Jonsson, M., O. Kindvall, M. Jonsell, and G. Nordlander. 2003. Modelling mating success of saproxylic beetles in relation to search behaviour, population density and substrate abundance. *Animal Behaviour* **65**:1069–1076.

- Kindvall, O., K. Vessby, A. Berggren, and G. Hartman. 1998. Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study. *Oikos* **81**:449–457.
- Kiørboe, T. 2006. Sex, sex-ratios, and the dynamics of pelagic copepod populations. *Oecologia* **148**:40–50.
- Klomp, H., M. A. J. van Monfort, and P. M. L. Tammes. 1964. Sexual reproduction and under-population. *Archives Neerlandaises de Zoologie* **16**:105–110.
- Knapp, E. E., M. A. Goedde, and K. J. Rice. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* **128**:48–55.
- Koenig, W. D., and M. V. Ashley. 2003. Is pollen limited? The answer is blowin' in the wind. *Trends in Ecology and Evolution* **18**:157–159.
- Kokko, H., and J. Mappes. 2005. Sexual selection when fertilization is not guaranteed. *Evolution* **59**:1876–1885.
- Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical Transactions of the Royal Society of London, Series B* **361**:319–334.
- Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* **82**:384–392.
- Lamont, B. B., P. G. L. Klinkhamer, and E. T. F. Witkowski. 1993. Population fragmentation may reduce fertility to zero in *Banksia-goodii* - a demonstration of the Allee effect. *Oecologia* **94**:446–450.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist* **142**:911–927.
- Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* **83**:353–358.
- Larkin, J. L., D. S. Maehr, J. J. Cox, M. W. Wichrowski, and R. D. Crank. 2002. Factors affecting reproduction and population growth in a restored elk *Cervus elaphas nelsoni* population. *Wildlife Biology* **8**:49–54.
- Lehmann, L., and N. Perrin. 2003. Inbreeding avoidance through kin recognition: choosy female boost male dispersal. *The American Naturalist* **162**:638–652.
- Lennartsson, T. 2002. Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. *Ecology* **83**:3060–3072.
- Levitian, D., and T. McGovern, 2005. The Allee effect in the sea. Pages 47–57 in E. Norse and L. Crowder, editors. *Marine conservation biology: the science of maintaining the sea's biodiversity*. Island Press.
- Levitian, D. R. 1991. Influence of body size and population-density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* **181**:261–268.

- Levitán, D. R., 1998. Sperm limitation, sperm competition and sexual selection in external fertilizers. Pages 173–215 in T. R. Birkhead and A. P. Møller, editors. *Sperm competition and sexual selection*. Academic Press.
- Levitán, D. R. 2002a. Density-dependent selection on gamete traits in three congeneric sea urchins. *Ecology* **83**:464–479.
- Levitán, D. R. 2002b. The relationship between conspecific fertilization success and reproductive isolation among three congeneric sea urchins. *Evolution* **56**:1599–1609.
- Liebhold, A., and J. Bascompte. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. *Ecology Letters* **6**:133–140.
- Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierachic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1976–1984.
- Liermann, M., and R. Hilborn. 2001. Depensation: evidence, models and implications. *Fish and Fisheries* **2**:33–58.
- Lloyd, D. G. 1992. Self-fertilization and cross-fertilization in plants. 2. the selection of self-fertilization. *International Journal of Plant Sciences* **153**:370–380.
- MacDiarmid, A. B., and M. J. Butler. 1999. Sperm economy and limitation in spiny lobsters. *Behavioral Ecology and Sociobiology* **46**:14–24.
- Maia, A. C. D., and C. Schlindwein. 2006. *Caladium bicolor* (Araceae) and *Cyclocephala celata* (Coleoptera, Dynastinae): A well-established pollination system in the northern Atlantic rainforest of Pernambuco, Brazil. *Plant Biology* **8**:529–534.
- McCarthy, M. A. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling* **103**:99–102.
- McComb, K., C. Moss, S. M. Durant, L. Baker, and S. Sayialel. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* **292**:491–494.
- McCreery, E. K., and R. L. Robbins. 2001. Proximate explanations for failed pack formation in *Lycaon pictus*. *Behaviour* **138**:1467–1479.
- Miettinen, M., A. Kaitala, R. L. Smith, and R. M. Ordonez. 2006. Do egg carrying and protracted copulation affect mobility in the golden egg bug? *Journal of Insect Behavior* **19**:171–178.
- Moeller, D. A., and M. A. Geber. 2005. Ecological context of the evolution of self-pollination in *Clarkia xantiana*: Population size, plant communities, and reproductive assurance. *Evolution* **59**:786–799.
- Møller, A. P., and S. Legendre. 2001. Allee effect, sexual selection and demographic stochasticity. *Oikos* **92**:27–34.
- Møller, A. P., and R. Thornhill. 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour* **55**:1507–1515.
- Moore, D. M., and H. Lewis. 1965. The evolution of self-pollination in *Clarkia xantiana*. *Evolution* **19**:104–114.

- Morgan, M. T., W. G. Wilson, and T. M. Knight. 2005. Plant population dynamics, pollinator foraging, and the selection of self-fertilization. *The American Naturalist* **166**:169–183.
- Muchhala, N. 2006. Nectar bat stows huge tongue in its rib cage. *Nature* **444**:701–702.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenburg. 1995. Population-dynamics of exploited fish stocks at low population-levels. *Science* **269**:1106–1108.
- Nilsson, S. G., and U. Wastljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus-sylvatica*) patches. *Ecology* **68**:260–265.
- Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biological Bulletin* **169**:417–430.
- Peterson, C., and D. Levitan, 2001. The Allee effect: a barrier to recovery by exploited species. Chapter the allee effect: A barrier to recovery by exploited species, pages 281–300 in J. D. Reynolds, G. M. Mace, K. H. Redford, and J. G. Robinson, editors. *Conservation of exploited species*. Cambridge University Press, Cambridge.
- Philip, J. R. 1957. Sociality and sparse populations. *Ecology* **38**:107–111.
- Pichon, G., H. P. Awono Ambene, and V. Robert. 2000. High heterogeneity in the number of *Plasmodium falciparum* gametocytes in the bloodmeal of mosquitoes fed on the same host. *Parasitology* **121**:115–120.
- Ramsey, M., and G. Vaughton. 2000. Pollen quality limits seed set in *Burchardia umbellata* (Colchicaceae). *American Journal of Botany* **87**:845–852.
- Ray, M., and A. W. Stoner. 1994. Experimental-analysis of growth and survivorship in a marine gastropod aggregation - balancing growth with safety in numbers. *Marine Ecology Progress Series* **105**:47–59.
- Reed, D. H. 2005. Relationship between population size and fitness. *Conservation Biology* **19**:563–568.
- Richard, F., D. R. Tarpy, and C. M. Grozinger. 2007. Effects of insemination quantity on honey bee queen physiology. *PLoS ONE* **2**:e980 doi.org/10.1371/journal.pone.0000980.
- Rowe, S., and J. A. Hutchings. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* **18**:567–572.
- Rowe, S., J. A. Hutchings, D. Bekkevold, and A. Rakitin. 2004. Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). *ICES Journal of Marine Science* **61**:1144–1150.
- Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. *Journal of Fish Biology* **59**:90–108.
- Sæther, B. E., T. H. Ringsby, and E. Roskaft. 1996. Life history variation, population processes and priorities in species conservation: Towards a reunion of research paradigms. *Oikos* **77**:217–226.

- Sakai, S. 2002. A review of brood-site pollination mutualism: plants providing breeding sites for their pollinators. *Journal of Plant Research* **115**:161–168.
- Sarnelle, O., and R. A. Knapp. 2004. Zooplankton recovery after fish removal: Limitations of the egg bank. *Limnology and Oceanography* **49**:1382–1392.
- Shepherd, S. A., and L. D. Brown. 1993. What is an Abalone stock - implications for the role of refugia in conservation. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2001–2009.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* **309**:607–610.
- Sih, A., and M. S. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in Catnip. *Ecology* **68**:1679–1690.
- Soldaat, L. L., B. Vetter, and S. Klotz. 1997. Sex ratio in populations of *Silene otites* in relation to vegetation cover, population size and fungal infection. *Journal of Vegetation Science* **8**:697–702.
- Stephens, P., and W. Sutherland, 2000. Vertebrate mating systems, Allee effects and conservation. Pages 186–213 in M. Apollonio, M. Festa-Bianchet, and D. Mainardi, editors. *Vertebrate mating systems*. World Scientific Publishing, Singapore.
- Stephens, P. A., F. Frey Roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology* **71**:343–361.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* **14**:401–405.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185–190.
- Stevens, E. F., and C. Pickett. 1994. Managing the social environments of flamingos for reproductive success. *Zoo Biology* **13**:501–507.
- Stoner, A. W., and M. Ray. 1993. Aggregation dynamics in juvenile Queen conch (*Strombus gigas*) - population-structure, mortality, growth, and migration. *Marine Biology* **116**:571–582.
- Stoner, A. W., and M. Ray-Culp. 2000. Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Marine Ecology Progress Series* **202**:297–302.
- Studer-Thiersch, A. 2000. What 19 years of qbservation on captive Greater flamingos suggests about adaptations to breeding under irregular conditions. *Waterbirds* **23**:150–159.
- Sutherland, W. J. 2002. Conservation biology - Science, sex and the kakapo. *Nature* **419**:265–266.
- Swain, D. P., and A. F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:1321–1325.

*Gregory*

- Taylor, C. M., H. G. Davis, J. C. Civille, F. S. Grevstad, and A. Hastings. 2004. Consequences of an Allee effect in the invasion of a pacific estuary by *Spartina alterniflora*. *Ecology* **85**:3254–3266.
- Taylor, C. M., and A. Hastings. 2005. Allee effects in biological invasions. *Ecology Letters* **8**:895–908.
- Tcheslavskiaia, K., C. C. Brewster, and A. A. Sharov. 2002. Mating success of gypsy moth (Lepidoptera: Lymantriidae) females in Southern Wisconsin. *Great Lakes Entomologist* **35**:1–7.
- Thomas, J., and M. Benjamin. 1973. The effects of population density on growth and reproduction of *Biomphalaria glabrata* (Say) (Gasteropoda: Pulmonata). *Journal of Animal Ecology* **43**:31–50.
- Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjornstad, and A. M. Liebhold. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecology Letters* **10**:36–43.
- Tregenza, T., and N. Wedell. 1998. Benefits of multiple mates in the cricket *Gryllus bimaculatus*. *Evolution* **52**:1726–1730.
- Vargas-Salinas, F. 2006. Breeding behavior and colonization success of the Cuban treefrog *Osteopilus septentrionalis*. *Herpetologica* **62**:398–408.
- Veit, R. R., and M. A. Lewis. 1996. Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *The American Naturalist* **148**:255–274.
- Vernon, J. G. 1995. Low reproductive output of isolated, self-fertilizing snails - inbreeding depression or absence of social facilitation. *Proceedings of the Royal Society B: Biological Sciences* **259**:131–136.
- Wagenius, S. 2006. Scale dependence of reproductive failure in fragmented *Echinacea* populations. *Ecology* **87**:931–941.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:39–50.
- Welch, A. M., R. D. Semlitsch, and H. C. Gerhardt. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science* **280**:1928–1930.
- Wells, H., E. G. Strauss, M. A. Rutter, and P. H. Wells. 1998. Mate location, population growth and species extinction. *Biological Conservation* **86**:317–324.
- Whitmire, S. L., and P. C. Tobin. 2006. Persistence of invading gypsy moth populations in the United States. *Oecologia* **147**:230–237.
- Widen, B. 1993. Demographic and genetic-effects on reproduction as related to population-size in a rare, perennial herb, *Senecio-integrifolius* (Asteraceae). *Biological Journal of the Linnean Society* **50**:179–195.

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Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science* **7**:270–277.

Wilson, W. G., and L. D. Harder. 2003. Reproductive uncertainty and the relative competitiveness of simultaneous hermaphroditism versus dioecy. *The American Naturalist* **162**:220–241.

# **Chapter 3**

## **Limited evidence for the demographic Allee effect from numerous species across taxa**

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## Abstract

Extensive theoretical work on demographic Allee effects has led to the latent assumption that they are ubiquitous in natural populations, yet current empirical support for this phenomenon is sparse. We extended previous single-taxon analyses to evaluate the empirical support for demographic Allee effects in the *per capita* population growth rate of 1198 natural populations spanning all major taxa. For each population, we quantified the empirical support for five population growth models: no growth (random walk); exponential growth, with and without an Allee effect; and logistic growth, with and without an Allee effect. We used two metrics to quantify empirical support, information-theoretic and Bayesian strength of evidence, and observed top-rank frequency. The Ricker logistic model was both the most supported and most frequently top-ranked model, followed by random walk. Allee models had a combined relative support of 12.0% but were top-ranked in only 1.1% of the time series. Accounting for local climate variation and measurement error caused the loss of top-ranked Allee models, although the latter also increased their relative support. The 13 time series exhibiting Allee models were shorter and less variable than other time series, although only 3 were non-trending. Time series containing observations at low abundance were not more likely, and did not show higher support for Allee effect models. We conclude that there is relatively high potential for demographic Allee effects in these 1198 time series but comparatively few observed cases, perhaps due to the influences of climate and measurement error.

**Keywords** AIC, BIC, demographic Allee effect, empirical support, evidence, exponential, population dynamics, random walk, Ricker

### 3.1 Introduction

An Allee effect describes a positive relationship between fitness and population size (or density; Courchamp et al. 2008). It is further classified into either a component Allee effect, which modifies one or multiple surrogate measures of fitness (Berec et al. 2007), or a demographic Allee effect, which is a manifestation of a component Allee effect whereby the growth rate increases with population size (hereafter termed ‘positive density feedback’; Stephens et al. 1999). The Allee effect, named after zoologist W.C. Allee (Odum 1953), was first described as an improvement in fitness with increasing population size and discussed in terms of cooperation (Allee et al. 1949). Thirty years later, however, M.A. Soulé highlighted declines in animal and plant populations (Gibbons 1992), which prompted population biologists to view the Allee effect in terms of a reduction in fitness with decreasing population size and issue warnings of its threat to population persistence (Lande 1988, Dennis 1989, Fowler and Baker 1991).

Following the focal shift from cooperation to conservation, theoretical and empirical studies of Allee effects proliferated (Kramer et al. 2009). Empirical support for Allee effects has now been provided for a wide range of species and mechanisms. For example, Davis et al. (2004) experimentally demonstrated that sparse invasive cordgrass (*Spartina alterniflora*) at the leading edge of an estuarine invasion were pollen limited compared to plants in established aggregations. Angulo et al. (2007) showed how the survival of adult Californian Channel Island foxes (*Urocyon littoralis*) increased when elevated predation risk was shared among more individuals. Almost without exception, however, empirical studies of Allee effects have focused on component Allee effects; studies of demographic Allee effects remain largely in the theoretical domain

and predict their widespread existence in natural (Liermann and Hilborn 1997) and invasive (Taylor and Hastings 2005) populations. Given the abundant empirical support for component Allee effects (Kramer et al. 2009) and their predicted dynamical consequences (Berryman 2003), the latent assumption held by many population biologists is that demographic Allee effects must be widespread (Courchamp et al. 2008).

Notwithstanding some noteworthy examples, there are few studies demonstrating empirical evidence of demographic Allee effects. Johnson et al. (2006) used a rigorous empirical approach to reveal the existence of a demographic Allee effect at the leading edge of the Eurasian Gypsy moth (*Lymantria dispar*) invasion in northeastern United States. Davis et al. (2004) showed that the pollen-limited cordgrass also suffered a demographic Allee effect. Interestingly, both examples may be driven by a mate-finding component Allee effect (Tcheslavskaya et al. 2002, Davis et al. 2004; see Gascoigne et al. 2009 for a review). Angulo et al. (2007) revealed a demographic Allee effect in island fox populations, together with component Allee effects in their adult survival and reproduction. In this case, the demographic Allee effect was weak because it did not cause the population growth rate to become negative (the condition that defines a strong demographic Allee effect; Wang and Kot 2001). Rather, it appeared that the release from competition in small fox populations favored larger litters and higher juvenile survival, which compensated reduced adult survival and reproduction (Angulo et al. 2007).

As illustrated by Angulo et al. (2007), a demographic Allee effect is an unstable population state emerging from the interplay between density-dependent fitness-regulating mechanisms. Central to its theory is the assumption that a strong demographic Allee effect acts around an unstable threshold population size known as the ‘Allee threshold’. Above the Allee threshold, the net effect of the underlying mechanisms is increased fitness and the population grows, but below this threshold the net effect is decreased fitness, causing the population to decline (Courchamp et al. 1999). Such instability in populations within the range of population sizes affected by demographic Allee effects will, paradoxically, render them difficult to detect (Stephens et al. 1999). Further, if demographic Allee effects modify dynamics of small populations as predicted (Courchamp et al. 1999), then detecting demographic Allee effects might be complicated by increased temporal variance in abundance at small population sizes. For example, Lande et al. (2003) showed how demographic stochasticity in small populations could produce population dynamics mirroring those driven by Allee effects. Finally, environmental stochasticity plays an important regulatory role in the population dynamics of animals, from butterflies (Nowicki et al. 2009) to ungulates (Forchhammer et al. 1998), and can affect population growth rate directly (Rothery et al. 1997) or indirectly through its influence on vegetation quality and abundance (e.g., Månssson and Lundberg 2006). While its influence can act independently of population size (Lande et al. 2003), extreme climatic variability, or catastrophes that have high impact but low frequency, can have a disproportional effect on small and declining populations (Lande 1993). Beyond its particular effects on small and declining populations, climatic variability in population growth rate, unless explicitly investigated, might be misinterpreted as process variability, which in turn, can lead to overestimation of the role of density feedback in population regulation (Rothery et al. 1997).

Besides the aforementioned issues, there is a large literature devoted to factors inhibiting the statistical detection of density feedback (negative or positive) in time series (recall that demographic Allee effects are observable in population dynamics as positive density feedback). The existence of deterministic trends (Turchin 2003) accompanied by unbounded variance (Lande et al. 2003), which are both more likely in shorter time series (Solow and Steele 1990), will confound any density feedback signal. Furthermore, Shenk et al. (1998), and later Freckleton

et al. (2006), demonstrated how density feedback could be masked or spuriously emerge if the populations monitored were not closed. Importantly, Freckleton et al. (2006) also showed how measurement error in population observations could lead to a spurious negative correlation between population growth rate and population size even for density-independent time series. In addition to factors affecting both positive and negative density feedback, sparse observations at low population sizes might further inhibit detection of positive density feedback (Fowler and Baker 1991, Myers et al. 1995, Sæther et al. 1996, Shelton and Healey 1999).

Here, we examine the latent assumption of abundant demographic Allee effects given by the widespread empirical support for component Allee effects. We test the hypothesis that demographic Allee effects are abundant using multi-model, information-theoretic and Bayesian inferential approaches to provide measures of empirical support for five population growth models (including Allee effect models) in population time series of 1198 species across a wide range of taxa (Brook and Bradshaw 2006). This approach reduces the problem of model misspecification inherent in hypothesis testing (Zeng et al. 1998). We use two measures of empirical support: (1) relative strength of evidence (Brook and Bradshaw 2006), which measures the likelihood of observing each model fit in the population growth rate given the data, and (2) top-ranked frequency (Zeng et al. 1998), which measures the frequency with which each model is the most parsimonious descriptor of population growth rate. In addition, we evaluate the effects of local climate variation, measurement error and time series attributes (length, variation, trend and skew) on our results. We predict that these factors will quantitatively, but not qualitatively change the spread of empirical support between population growth dynamics, but will generally diminish detection of positive density feedback due to their potentially disproportional effects on small population observations. We consider a strong positive density feedback signal as suggestive of a demographic Allee effect; however, we defer asserting the existence of a demographic Allee effect until further study reveals the existence of an underlying component Allee effect mechanism in each case.

## 3.2 Methods

### 3.2.1 Population time series

We used a database of 1198 population time series, which differed from other databases previously examined for positive density feedback in two major aspects. First, it comprised nearly twice as many species as other examined databases (1198 species vs. 674 species in Sibly et al. 2005). Second, it incorporated representatives from several major taxonomic groups and biomes (compared to Myers et al. 1995, Sæther et al. 1996, Liermann and Hilborn 1997, Barrowman et al. 2003, and Reed 2005 who all examined single-taxon databases). The time series were drawn primarily from the Global Population Dynamics Database (GPDD; NERC Centre for Population Biology 1999) but also from the peer-reviewed literature, grey literature and online sources (Brook et al. 2006). Specifically, time series were only included if they possessed: (1) a minimum of eight year-to-year census transitions, and (2) a minimum of four different census values to ensure sufficient variation for analysis. Where the GPDD held more than one time series for a single species, only the highest quality time series was selected to avoid biasing our findings towards a few well-studied species (Brook and Bradshaw 2006). We also collated geographical and temporal metadata for all 1198 time series, which were used in the climate analysis (see below). All analyses were done using R (R Development Core Team 2008).

Some time series contained missing values. To maximize the number of suitable time series

for analysis (i.e., with eight year-to-year transitions), we treated missing values as follows. Single missing values were substituted with the mean of their two neighboring points. This assumed that a single missing value was a failure to census and its value was best predicted as a linear function of local observations. The first missing value in a string of missing values was substituted for the lowest value in the time series. This assumed that a string of values was a failure to record individuals at low abundance or population extirpation, and there was a negligible effect of the lowest value substitution. In practice, 175 and 216 time series were treated for single and strings of missing values, respectively. We investigated the possible effect of applying these treatments by repeating our main analysis without them. Missing values falling outside of these categories were removed.

### 3.2.2 Modeling population growth dynamics

We modelled per capita population growth rate ( $r = \log_e(N_{t+1}/N_t)$ ) using a set of five nested models, representing a set of working hypotheses, to examine the 1198 population time series for empirical support for positive density feedback. The five models of population growth rate were: a no growth model (random walk), two density-independent growth models (with and without an Allee effect), and two negative density feedback growth models (with and without an Allee effect). The decision was reached to assess support for strong demographic Allee effects so density-independent and negative density feedback models could be nested within the Allee effect models. In addition, the chosen Allee effect term enabled the Allee effect to be characterized by a single parameter thereby minimizing the penalty imposed on Allee fits by the empirical model evaluation measures. The final model set represented population growth dynamics increasing incrementally in complexity from a null model of no growth to a model including both negative and positive density feedback in  $r$ , and was used by Berryman (2003) in his development of a general theory of population growth.

Specifically, the models were: (1) random walk (RW) that assumes  $r = 0$  and all variation in  $r$  is due to random fluctuations in population size ( $N$ ) over  $t$  time units. It is modelled as  $r = 0 + \sigma$ , where  $\sigma$  is a stochastic Gaussian variable with mean 0 and variance  $\sigma^2$  that encapsulates the process error (but not measurement error; see below); (2) exponential growth (EX) that assumes constant  $r$  independent of population size and is modelled as  $r = r_m(N_t/N_t)\sigma$ , where  $r_m$  is the maximum intrinsic growth rate; (3) exponential Allee growth (EA) that assumes constant  $r$  independent of population size until the population declines beneath a critical lower ‘Allee’ threshold ( $A$ ), beyond which  $r$  rapidly decreases and becomes negative. It is modelled as  $r = r_m((N_t - A)/N_t) + \sigma$ ; (4) Ricker logistic (RL) negative density feedback model that assumes a linear decline in  $r$  with increasing population size and is modelled as  $r = r_m(1 - (N_t/K)) + \sigma$ , where  $K$  is the carrying capacity; (5) Ricker Allee (RA) positive density feedback model that assumes  $r$  decreases linearly both as the population increases to  $K$  but also as the population declines towards  $A$ . It is modelled as  $r = r_m(1 - (N_t/K))((N_t - A)/N_t) + \sigma$ . We chose to use the same models with (EA and RA; hereafter ‘Allee models’) and without (EX and RL; hereafter ‘non-Allee models’) an Allee term to minimise differences in model performance due to differences in model specification.

Least squares model fits were estimated using a sequential quadratic programming algorithm (donlp2; Spellucci 1998) subject to box constraints  $0 \leq r_m$ ,  $0 \leq K$  and  $0 \leq A$  and an additional linear constraint  $A \leq K$  for the Ricker Allee model. We used the free parameter  $\sigma$  to calculate Akaike’s information criterion (adjusted for small sample sizes; AIC<sub>C</sub>) and Bayesian information criterion (BIC) to measure the strength of evidence for each candidate model (Brook and Bradshaw 2006). We compared models using the difference in AIC<sub>C</sub> between the top-ranked and

current model ( $\Delta\text{AIC}_C$ ) and calculated the empirical support for each model as its  $\text{AIC}_C$  weight ( $w\text{AIC}_C$ ). We employed the evidence ratio (ER), calculated as the ratio of model  $a$   $w\text{AIC}_C$  to model  $b$   $w\text{AIC}_C$ , to compare the more complex model  $a$  to the simpler model  $b$  (Burnham and Anderson 2002). The top-ranked model in a model set was selected using  $w\text{AIC}_C$ .  $R^2$  was calculated as a measure of a model's structural goodness-of-fit.

Our model set excluded weak Allee effect models that depress  $r$  above  $A$  without requiring  $0 < A$  (Wang and Kot 2001). We did not include weak Allee models primarily because they require an additional parameter to admit the exponential and Ricker logistic models as special cases and we wanted to characterize the Allee effect using a single parameter in a set of nested models. Nevertheless, weak Allee effect models would represent an additional step of complexity in our hypothesis set, and their exclusion will bias our findings. To investigate the degree of bias, we repeated our main model-fitting exercise including a weak Ricker Allee effect model and present summary background and results of this modified model set in Appendix A.

### 3.2.3 Including climatic variation

We investigated whether interannual climatic variation affected the support for the population growth dynamics by directly incorporating climate variables into models as covariates (Rothery et al. 1997). Climate variables were drawn from the Climate Research Unit's 2.1 time series database (CRU\_TS\_2.1; available at [www.cru.uea.ac.uk](http://www.cru.uea.ac.uk)), which includes nine climate variables measured (or extrapolated) at a  $0.5^\circ$  scale for every month from 1901 to 2002 (Mitchell and Jones 2005). This database provided us with fine-scale climate variables for most time series. We calculated the mean annual temperature ( $^\circ\text{C}$ ), mean annual precipitation (mm), annual frost day frequency (days) and annual wet day frequency (days) for each year.

For each time series falling between 1901 and 2002, we used census dates and geographical coordinates to extract the corresponding climate variables and incorporated these into the model fits as variables representing mean climate ( $mc$ ; an orthogonal regression of mean annual temperature and mean annual precipitation) and extreme climate ( $xc$ ; an orthogonal regression of annual frost day frequency and annual wet day frequency). We used orthogonal combinations of climate variables derived using principle components analysis to encapsulate the principal variation in and interactions between the underlying variables (Hallett et al. 2004) while minimising the number of parameters added to each model. We defined mean and extreme climate combinations because they might influence population dynamics differently, via, for example, differences in mortality (e.g., Frederiksen et al. 2008), and might affect populations differently depending on their size (Lande 1993). For this analysis, our model set included all models both with and without all possible combinations of climate parameters (a total of  $5 \times 4 = 20$  models).

### 3.2.4 Examining measurement error and data biases

We assumed that populations were censused without measurement error and  $\sigma$  represented only process error or random fluctuations in population size. In fact, it is likely that  $\sigma$  encapsulates both process and measurement error (Brook and Bradshaw 2006). Although without empirically estimating measurement error it is difficult to calculate its relative contribution to  $\sigma$ , we attempted to understand the effect of assuming no measurement error by repeating our analyses on simulated time series with randomized measurement error. For a time series  $U$  with observations  $i = 1, 2, \dots, j$ , we resampled  $i$  with replacement  $j$  times to create a bootstrap time series  $U^*$  and calculated its mean  $\bar{U}^*$ . We repeated this 1000 times to create a bootstrap distribution of 1000  $\bar{U}^*$  from which we calculated the bootstrap standard error of  $U$  ( $\text{SE}_U$ ). This assumed

that any signal in the original time series could have been produced spuriously by measurement error. We parameterized a Gaussian distribution for each time series observation  $U_i$  with mean =  $i$  and variance =  $\text{SE}_U$  from which we randomly drew a population estimate. We repeated this for all  $U_i$  to construct a new time series of length  $j$  with randomized measurement error. We did this for all 1198 species and subjected the resulting time series to the analyses described in section 3.2.2. We repeated this entire procedure 200 times and estimated the support for each population growth model given randomized measurement error.

Previous studies have stressed how the probability of detecting density feedback depends, to some extent, on whether the time series is trending (Turchin 2003). To determine if our results were sensitive to the inclusion of trending time series, we examined each time series for a linear trend between  $N_t$  and  $t$  (compared to a no-trend null model using  $\text{AIC}_C$ ; Kölzsch et al. 2007) and investigated how support for non-Allee and Allee models was affected. Likewise, detection probability depends on the length of monitoring period (Solow and Steele 1990) and variation in the time series (Brook and Bradshaw 2006). We examined the relationships between support for non-Allee and Allee models, length of monitoring period and variation in time series for all 1198 time series. Finally, detection of positive density feedback may require that a time series includes population censuses lower than some threshold proportion of the maximum population census. For example, Fowler and Baker (1991) only used time series for which the minimum  $N$  was  $\leq 10\%$  of the maximum  $N$ , while Sæther et al. (1996) set the threshold at 15%. We calculated the minimum  $N$  of each of our 1198 time series as a proportion of the maximum  $N$  and examined how the support for non-Allee and Allee models was related to minimum  $N$ .

### 3.3 Results

#### 3.3.1 Support for population growth models

Our model-fitting procedure achieved model fits satisfying parameter constraints for 99.4% of the 1198 time series using the Ricker logistic model, 98.2% using the exponential Allee model, 97.9% using the Ricker Allee model, and 100% using each of the remaining models, confirming that the procedure was robust and adequate to compare model fits among time series (see examples in Figure 3.1).

Overall  $w\text{AIC}_C$  support was highest for the Ricker logistic (45.3%) and random walk (32.2%) models (Table 3.1). Support for the Allee models was low (exponential Allee: 2.2%; Ricker Allee: 9.8%), being highest for birds and mammals (Table 3.1) and exceptionally high for 61 time series (open circles [ $\circ$ ] in Figure 3.2a) including 3.3% and 2.7% of the mammal (MAM) and bird (BIR) time series, respectively. The Ricker logistic and exponential growth models had higher  $w\text{AIC}_C$  support than their Allee counterparts despite their similar overall goodness-of-fit, as did the random walk model despite, as the null model, explaining zero deviance (Figure 3.2b).

The spread of  $w\text{AIC}_C$  support was similar for each taxonomic group (Table 3.1) and was reflected in the numbers of top-ranked models (Figure 3.2a). Interestingly, Allee models were only the top-ranked models in 13 (1.1%) of the 1198 time series, and none of these was due to the exponential Allee model. BIC support was generally lower than AIC support for the Ricker logistic model and higher for the Ricker Allee model, particularly among those taxonomic groups with fewest representative time series (Table 3.1).

Including a weak Allee effect model did not qualitatively change these findings (Table 3.3). In summary, the weak Ricker Allee effect model had similar support to the strong Ricker Allee effect model, and took most  $w\text{AIC}_C$  support from the Ricker logistic model. On the other hand,

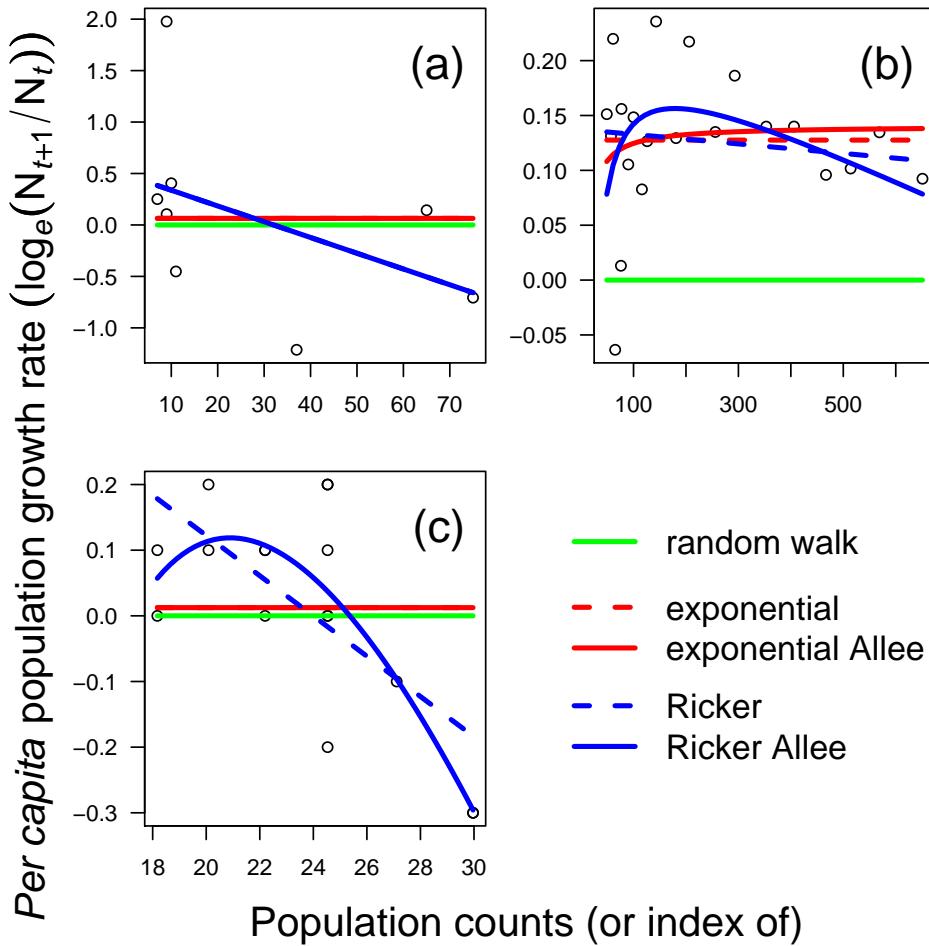


Figure 3.1: Three example datasets showing fits of the five population growth dynamic models measured in this study. Panel (a) shows data for the small blue butterfly (*Cupido minimus*) for which the random walk (RW) is the best model. The exponential (EX) and exponential Allee (EA) growth models achieve the same fit, as too do the Ricker (RL) and Ricker Allee (RA) logistic growth models. Panel (b) shows data for the muskox (*Ovibos moschatus*) for which EX is the top-ranked model, but both Allee models acquire good support. Panel (c) shows data for the lilac beauty moth (*Apeira syringaria*) for which the RA is the top-ranked model, and EX and EA achieve the same fit.

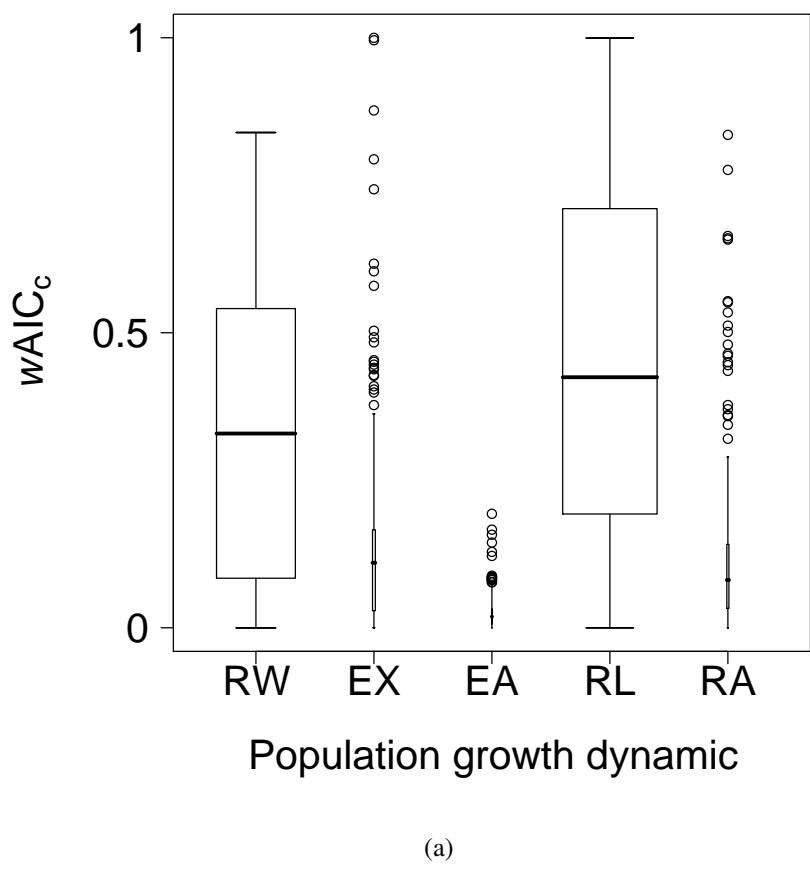


Figure 3.2: (a) Support for each population growth model where bar width represents the frequency the model was top-ranked. The Ricker logistic model (RL) received highest empirical support in these data followed by random walk (RW) and exponential growth (EX) models. Ricker Allee (RA) and exponential Allee (EA) models received the least support.

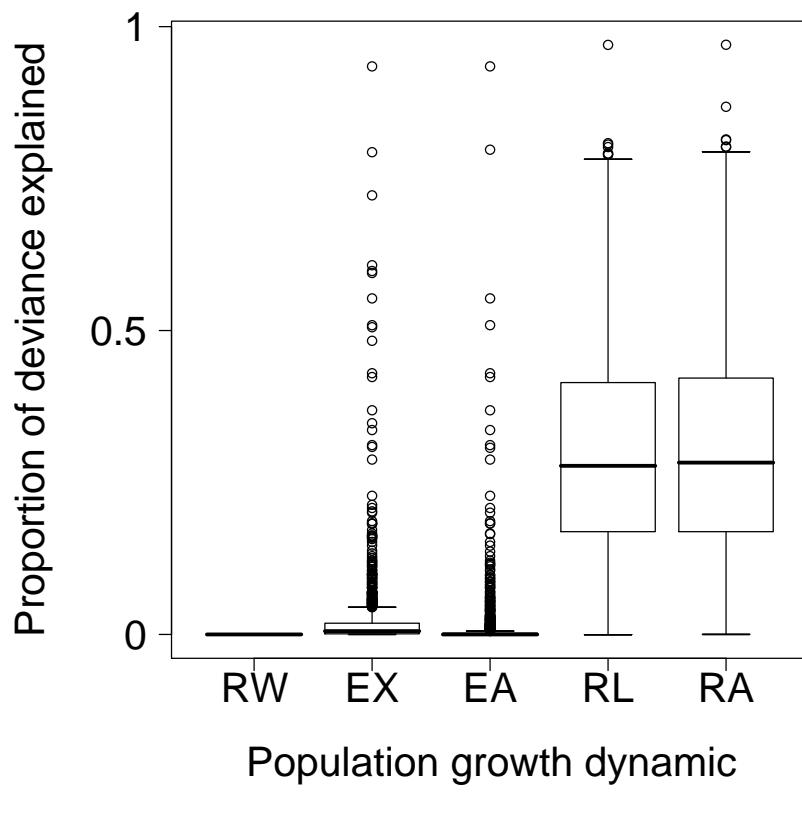


Figure 3.2: (b) Boxplot showing the deviance explained for each population growth model, where the random walk (RW) model is taken to be the null model (zero deviance explained). Exponential growth (EX) generally explained more deviance than the exponential Allee (EA) growth model, whereas the Ricker (RL) and Ricker Allee (RA) logistic growth models explained similar deviance. Boxes delimit the 25–75% interquartile range (IQR) and open circles ( $\circ$ ) represent extreme values  $\geq 1.5 \times \text{IQR}$ .

**Table 3.1:** Overall and major taxonomic group support (Akaike weights;  $wAIC_c$ ) for population growth models and overall  $wAIC_c$  and Bayesian Information Criterion (BIC) support for non-Allee (nAE) and Allee (AE) models as a percentage of all support.

|         | <i>n</i> | Model $wAIC_c$ |       |       |       |       | AIC (%) |      | BIC (%) |      |
|---------|----------|----------------|-------|-------|-------|-------|---------|------|---------|------|
|         |          | RW             | EX    | EA    | RL    | RA    | nAE     | AE   | nAE     | AE   |
| overall | 1198     | 0.322          | 0.106 | 0.022 | 0.453 | 0.098 | 55.9    | 12.0 | 52.8    | 20.9 |
| INS     | 603      | 0.304          | 0.089 | 0.018 | 0.488 | 0.101 | 57.8    | 11.9 | 54.9    | 14.3 |
| BIR     | 225      | 0.287          | 0.113 | 0.025 | 0.457 | 0.118 | 57.0    | 14.3 | 52.7    | 12.2 |
| MAM     | 152      | 0.337          | 0.119 | 0.027 | 0.413 | 0.104 | 53.3    | 13.1 | 48.7    | 12.3 |
| FIS     | 115      | 0.449          | 0.114 | 0.020 | 0.368 | 0.049 | 48.2    | 6.9  | 50.3    | 14.0 |
| RAM     | 37       | 0.363          | 0.146 | 0.026 | 0.386 | 0.078 | 53.2    | 10.5 | 50.1    | 12.6 |
| AQI     | 36       | 0.470          | 0.146 | 0.028 | 0.304 | 0.053 | 45.0    | 8.0  | 43.9    | 13.4 |
| PLA     | 30       | 0.431          | 0.120 | 0.017 | 0.396 | 0.036 | 51.6    | 5.4  | 53.4    | 13.9 |

Taxonomic groups: INS, insects; BIR, birds; MAM, mammals; FIS, fish; RAM, reptiles and amphibians; AQI, aquatic invertebrates; PLA, plants. Model abbreviations: RW, random walk; EX, exponential growth; EA, exponential Allee; RL, Ricker logistic; RA, Ricker Allee logistic. *n*, number of time series.

the weak Allee model increased the number of top-ranked Allee models from 13 to 22, despite reducing the number of top-ranked strong Allee models to nine.

Finally, our missing-value treatment resulted in qualitatively identical results, and slightly higher support for the Ricker logistic model over the exponential and random walk models (Table 3.5).

### 3.3.2 Influence of climate variation

Local climate variables were obtained for the full temporal duration of 1015 time series, including 11 which exhibited a top-ranked Allee model in the population growth analysis. In most cases, the addition of local climate variables improved model fits but, when the information theoretic bias-correction was applied for the additional parameters, the general effect was to reduce the model's  $wAIC_c$ . Reduction in  $wAIC_c$  was largest for the Ricker logistic model, and within model types was largest for models including both mean and extreme composite climate variables (Figure 3.3).

The frequency with which the addition of climate variables improved the non-climate model fit was higher among those 11 time series with a top-ranked Allee model (45.5% of cases) compared to the remaining 1004 time series (28.2% of cases). Of the former time series, 27.3% supported a random walk or non-Allee model with climate variable(s) and only 1.2% of the latter time series supported an Allee model with climate variable(s). Six time series with top-ranked Allee models showed improved support with inclusion of both mean and extreme climate variables compared to one time series for each climate variable separately.

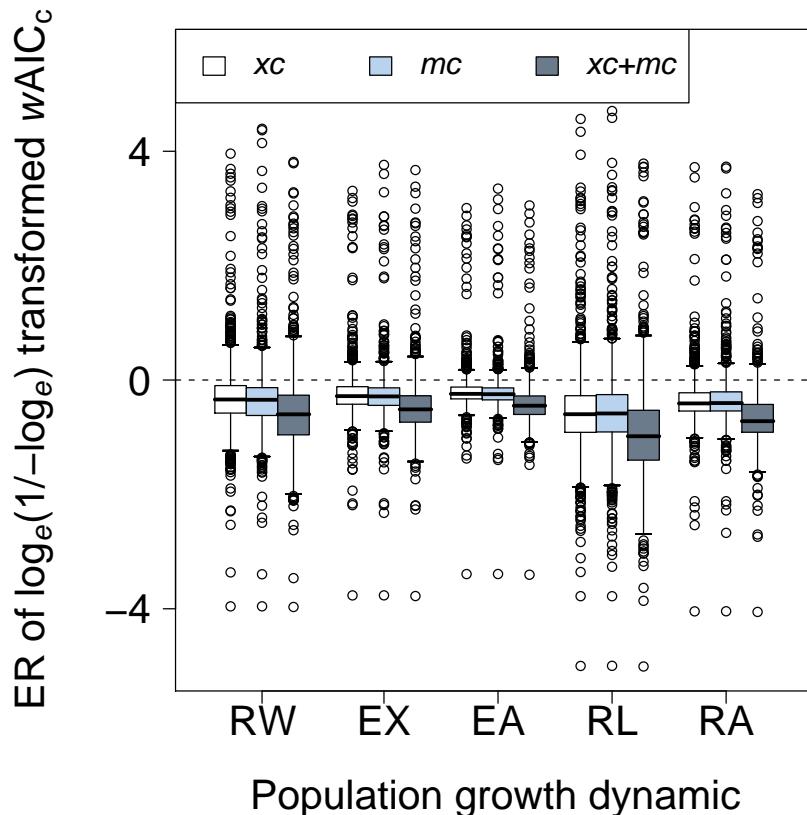


Figure 3.3: Relative support for each population growth model combined with extreme (xc), mean (mc) or both climate variables compared to support for the population growth model without climate variables (using evidence ratio [ER] of  $\log_e(1/\log_e)$  transformed  $wAIC_c$ ). The general effect of including climate variables in model fits was to decrease their  $wAIC_c$ , particularly for the Ricker logistic (RL) and random walk (RW) models. Other models were exponential (EX) and exponential Allee (EA) growth, and Ricker Allee (RA) logistic growth. Boxes delimit the 25-75% interquartile range (IQR) and open circles ( $\circ$ ) represent extreme values  $\geq 1.5 \times IQR$ .

### 3.3.3 Influence of measurement error and data attributes

Repeating our population growth analysis using time series with randomized measurement error revealed a qualitatively similar spread of  $wAIC_C$  support to that obtained under the assumption of negligible measurement error (Table 3.6). However, randomized measurement error shifted  $wAIC_C$  support toward the Allee models from the random walk and non-Allee models (Table 3.6). In addition, the top-ranking model changed more frequently among the 13 time series originally exhibiting a top-ranked Ricker Allee model (median = 51.0% of cases, 25-75% interquartile range based on 200 replicate treatments ( $IQR_r$ ) = 44.5-68.5) compared to time series originally exhibiting either a top-ranked Ricker logistic (median = 9.5% of cases,  $IQR_r$  = 1.5-35.5) or random walk model (median = 2.0% of cases,  $IQR_r$  = 0.0-16.0).

Median  $wAIC_C$  support for non-Allee and Allee models was higher in non-trending time series ( $n = 732$ ; non-Allee median = 0.541, 25-75% interquartile range based on 1000 bootstrap resamples ( $IQR_b$ ) = 0.521-0.549; Allee median = 0.095,  $IQR_b$  = 0.092- 0.099) compared to trending time series ( $n = 466$ ; non-Allee median = 0.277,  $IQR_b$  = 0.272-0.301; Allee median = 0.058,  $IQR_b$  = 0.054-0.063). Only a few of the 13 time series with top-ranked Allee models were, however, non-trending, and provided less support for positive density feedback ( $n = 3$ ; median = 0.534) than the trending time series ( $n = 10$ ; median = 0.553). The opposite pattern was observed among the time series with top-ranked non-Allee models (non-trending  $n = 452$ , median = 0.729; trending  $n = 184$ , median = 0.623). No pattern in the direction of trends was evident among the 10 trending time series with top-ranked Allee models (6 increasing vs. 4 decreasing trends).

Median  $wAIC_C$  support for non-Allee and Allee models increased in longer time series, but decreased in more variable time series (measured by the coefficient of variation), despite a weak increase in time series variation with time series length (evidence ratio [ER] = 4449,  $R^2 = 1.6\%$ ; Figure 3.4). Indeed, a model including both time series length and variation was ranked above competing models considering each factor separately (although their interaction term could not be disregarded: Table 3.2). While time series with a top-ranked non-Allee model supported this pattern, time series with a top-ranked Allee model were shorter and less variable (median length = 17; median CV = 0.314) compared to the remaining time series (median length = 19; median CV = 0.518).

Table 3.2: Comparison of models examining the influence of time series length (length) and variation (coefficient of variation [CV]) on the  $wAIC_C$  support for negative ( $-dd$ ) and positive ( $+dd$ ) density feedback.  $\dagger$ Evidence ratios (ER)  $> 2.718$  indicate increasingly implausible models compared to the top-ranked model (ER = 1).

|       | Model                        | AICc      | $\Delta AIC$ | ER $^\dagger$ | $R^2$ (%) |
|-------|------------------------------|-----------|--------------|---------------|-----------|
| $-dd$ | length + CV                  | -257.581  | 0.000        | 1.000e+00     | 7.1       |
|       | length + CV + I(length * CV) | -255.583  | 1.998        | 2.716e+00     | 7.1       |
|       | length                       | -206.844  | 50.737       | 1.041e+11     | 2.9       |
|       | CV                           | -211.296  | 46.285       | 1.124e+10     | 3.3       |
| $+dd$ | length + CV                  | -1662.606 | 0.000        | 1.000e+00     | 22.4      |
|       | length + CV + I(length * CV) | -1660.607 | 1.999        | 2.717e+00     | 22.4      |
|       | length                       | -1603.837 | 58.769       | 5.775e+12     | 18.3      |
|       | CV                           | -1391.856 | 270.750      | 6.203e+58     | 2.1       |

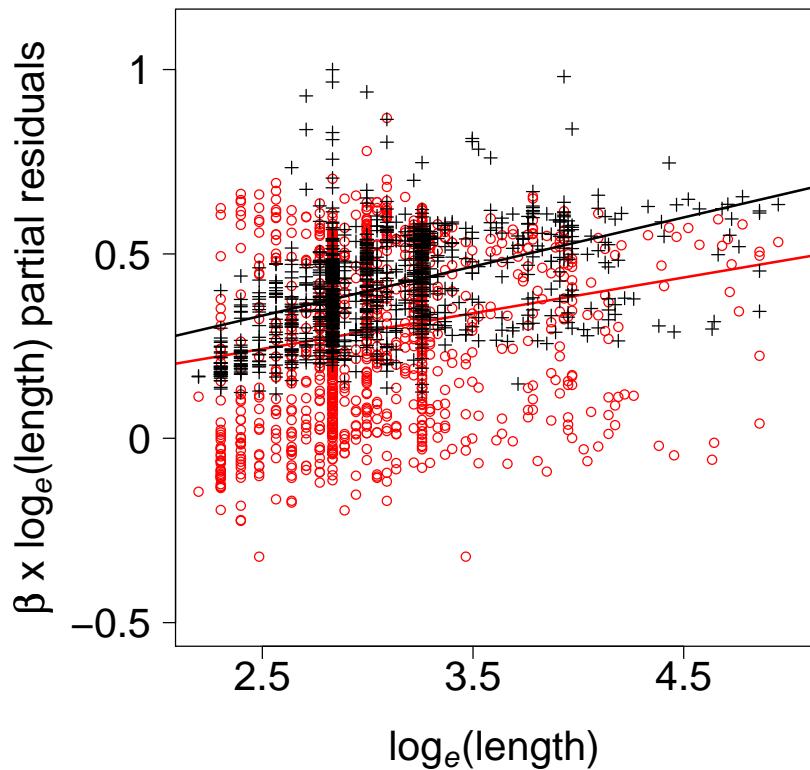


Figure 3.4: Support for non-Allee (o) and Allee (+) models as a function of time series length and variation. Partial residuals of  $w\text{AIC}_C$  and  $\log_e$  time series length multiplied by the correlation coefficient  $\beta$  relating  $w\text{AIC}_C$  and time series variation (measured as the coefficient of variation) are plotted on the y axis.

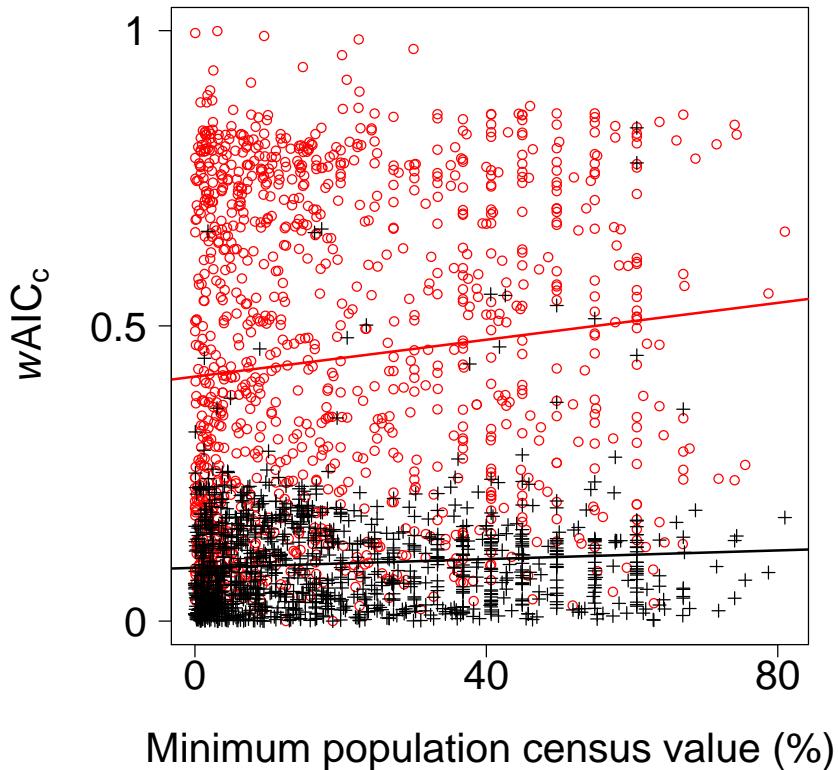


Figure 3.5: Support for non-Allee (○) and Allee (+) models increased with increasing minimum population census value (as a proportion of maximum population census value).

Both non-Allee and Allee  $wAIC_c$  support increased with increasing minimum  $N$  when compared to a null mean model (non-Allee  $\Delta AIC = 12.56$ ; Allee  $\Delta AIC = 5.38$ ; Figure 3.5). Median  $wAIC_c$  support for time series with a minimum  $N$  of  $\leq 10\%$  ( $n = 533$ ) was 0.373 for non-Allee models ( $IQR_b = 0.359-0.383$ ) and 0.067 for Allee models ( $IQR_b = 0.064-0.069$ ). Measures of support were higher for those time series with a minimum  $N$  of  $\leq 15\%$  ( $n = 646$ ; non-Allee median = 0.390,  $IQR_b = 0.382-0.406$ ; Allee median = 0.078,  $IQR_b = 0.072-0.080$ ) and  $\leq 50\%$  ( $n = 107$ ; non-Allee median = 0.506  $IQR_b = 0.470-0.516$ ; Allee median = 0.086,  $IQR_b = 0.081-0.092$ ). Median minimum  $N$  was larger for the 13 time series with a top-ranked Allee model (23.5%) than for the median of the other 1185 time series (12.7%).

### 3.4 Discussion

We quantified the empirical support for positive density feedback (suggestive of a demographic Allee effect) in the *per capita* population growth rate of 1198 species and evaluated the factors hypothesized to influence its detection. Overall, we found 12.0% relative model support for positive density feedback compared to 55.9% relative support for the same models without an Allee effect term. Given our results accord with the prevalence of negative density feedback reported in sim-

ilar meta-analyses undertaken for insects (Woiwod and Hanski 1992) and vertebrates (Turchin and Taylor 1992), our result suggests that positive density feedback might influence the growth rate of over one in 10 natural populations. Indeed, we detected strong positive density feedback in populations of 13 species not previously observed to exhibit demographic Allee effects (Table 3.4).

Those 13 populations exhibiting a top-ranked Allee model were, however, the only populations to do so and constituted only 1.1% of the 1198 population time series examined. This support for positive density feedback falls between the 2.3% of 128 fish stocks observed by Myers et al. (1995), and the 0.2% of 3269 time series, including insects, fish, birds and mammals, observed by Sibly et al. (2005). Furthermore, our database included time series for species previously exhibiting either a demographic Allee effect, including gypsy moth (*Lymantria dispar*) and Atlantic cod (*Gadus morhua*), or a component Allee effect, including African Wild dogs (*Lycaon pictus*) and coyotes (*Canis latrans*), but none of our population time series for these species supported a top-ranked Allee model.

The AIC support for positive density feedback was highest for birds and mammals (Table 3.1) and a relatively high proportion of their time series supported top-ranked Allee models (Figure 3.2). Plants, reptiles and amphibians, and aquatic invertebrates, on the other hand, exhibited least support for positive density feedback. These findings are not completely consistent with those emerging from published studies of demographic Allee effects (Kramer et al. 2009), and the reason for this might be due to difficulties in experimenting on some taxa (Gascoigne et al. 2009). Based on the BIC criterion, which supports lower dimensional models whose parameter estimates are nonzero (Burnham and Anderson 2002), plants and aquatic invertebrates show considerably higher support for positive density feedback. Although BIC might support less realistic model fits than AIC (Burnham and Anderson 2002), the high BIC support in these taxa indicates the existence of nonnegligible Allee threshold parameter estimates, which when considered with experimental evidence of component Allee effects in species of these taxa (see Courchamp et al. 2008), means we cannot dismiss the possibility they might exhibit demographic Allee effects.

Our results are based on five population growth models chosen to reflect a set of hypotheses from a null model and incrementally increasing in complexity to a saturated model of population growth including both negative and positive density feedback (see Berryman 2003 for a similar model set). However, our model set excluded weak Allee effect models and will be biased towards a dichotomous ‘strong Allee effect or no Allee effect’ result. To investigate this bias while retaining our simple non-Allee / Allee model set, we repeated our model-fitting analysis using the same model set modified to include a weak Allee effect version of the Ricker logistic model (Appendix A). In summary, the weak Allee effect model usurped most  $wAIC_c$  support from the Ricker logistic model, as expected, and then from the random walk and Ricker Allee growth models. Its inclusion, however, did not qualitatively change the spread of support over the population growth dynamics. This suggests our measure of support for Allee effects was not highly sensitive to exclusion of weak Allee effects, and is likely to be an underestimate. Similarly, although the number of time series with a top-ranking Allee model increased from 13 (1.1%) to 22 (1.8%) (i.e., a 69% increase) this increase would not change our finding that occurrence of Allee effects is low.

Given the high relative  $wAIC_c$  support for positive density feedback (a measure of its bias-corrected likelihood), one might ask why a higher number of these 1198 population time series did not exhibit a top-ranked Allee model? We investigated several major factors previously proposed to explain this discrepancy. Local climate variation can directly influence population growth rate and thus conclusions on the role of density feedback in population regulation (Roth-

ery et al. 1997). We found inclusion of climate variables generally improved growth model fits but the improvement was usually offset by the AIC<sub>C</sub> bias-correction, so the non-climate growth models were generally most parsimonious. This contrasts with the growing evidence that climate, and more generally environmental stochasticity, can play an important role in population regulation (Turchin 2003). On the other hand, these results might be due to factors inherent in a meta-analytic approach such as, for example, whether the defined climate variables are equally appropriate for all (or any) of the species analyzed. Interestingly, almost half of the Allee model fits were improved by inclusion of climatic variability (compared to almost 30% of non-Allee model fits) and almost a third of time series with top-ranked Allee models switched to supporting a top-ranked non-Allee or random walk model (compared to just 1.2% of non-Allee models that switched to supporting a top-ranked Allee model). These findings suggest that detection of positive density feedback is sensitive to climatic variability, which should be incorporated in attempts to detect Allee effects. On the other hand, there was no discernable difference between mean and extreme climate influences, despite the higher theoretical influence of extreme climate on population dynamics of small populations (Lande 1993), hinting at ill-defined mean and extreme climate variables.

Measurement error can either generate or mask evidence for density feedback in population time series (Shenk et al. 1998, Freckleton et al. 2006); as such, we investigated the possible consequences of our negligible measurement error assumption. Although relaxing the assumption of negligible measurement error had no qualitative effect on our results (cf. Table 3.1 and Table 3.6), it did cause (1) a shift in  $wAIC_C$  support from the random walk and Ricker logistic models to the Ricker Allee model, and (2) 51% of the 13 time series exhibiting top-ranked Allee models to support a top-ranked random walk or non-Allee model. We conclude that empirical support for positive density feedback can arise spuriously from excessive measurement error, and that detection of positive density feedback might be sensitive to extreme (and possibly erroneous) observations (Freckleton et al. 2006). Because positive density feedback acts around unstable thresholds (Courchamp et al. 1999), observations in the range of population sizes at which it acts should be rare. By definition, such rare observations will be extreme compared to the general pattern in the time series (Chan et al. 2005). Therefore, determining whether observed positive density feedback is real will require careful monitoring and independent assessment of the various sources of measurement error.

The presence of extreme observations in time series exhibiting positive density feedback should be evident in measures of time series variation. However, we found lower variation in the 13 time series exhibiting top-ranked Allee models compared to the remaining time series. Although these 13 time series were shorter than the remaining time series, and time series variation increases with time series length (Inchausti and Halley 2001), these results suggest that detection of positive density feedback in these time series was not necessarily due to extreme values. Rather, we found that empirical support for Allee models generally increased with increasing time series length and decreasing time series variation. This indicates that detection of density feedback (positive and negative) is more likely in non-trending time series (Inchausti and Halley 2001); however, only a quarter of the time series exhibiting positive density feedback here were non-trending (with no pattern among trend directions). This conundrum merits closer study because of the potential practical value in being able to foresee a demographic Allee effect from time series characteristics, as is under investigation for regime shifts (e.g., Carpenter and Brock 2006).

Finally, we found limited support for the prevalent hypothesis that sparse observations at low population sizes might underpin the failure to observe more empirical support for positive density

feedback (Myers et al. 1995, Sæther et al. 1996, Shelton and Healey 1999). We found median support for both negative and positive density feedback increased with increasing minimum population census. Indeed, the minimum census value in the 13 time series exhibiting top-ranked Allee models was higher than that for the remaining time series. Furthermore, the opposite observed relationship to that hypothesized suggest this finding is unlikely to be changed by the inclusion of weak Allee effects. Rather, it seems this criterion has limited value as a requirement to detecting an Allee effect.

We emphasize that (1) our comparative approach ranks models in terms of their relative consistency with patterns in the time series, and thus a top-ranked model can still provide an inadequate structural representation of the underlying dynamical signal (Turchin 2003), and (2) our approach is necessarily general and makes several assumptions to analyze population growth dynamics of a range of species with different life histories and populations with different extrinsic pressures (e.g., Getz and Lloyd Smith 2006). Nevertheless, our ability to detect positive density feedback in some populations given an inherent bias to detect negative density feedback, exaggerated by measurement error (Freckleton et al. 2006) and model oversimplification (Festa Bianchet et al. 2003), could be taken as relatively strong evidence that they do indeed exhibit positive density feedback. Whether an observation of positive density feedback can be considered indicative of a demographic Allee effect will still require a combination of careful monitoring and replicated experimentation (Turchin 2003); however, the higher likelihood of positive density feedback compared to the number of observed cases suggests that there might be more cases present than observed (Stephens et al. 2007).

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## References

- Allee, W. C., O. Emerson, T. Park, and K. Schmidt. 1949. Principles of animal ecology. Saunders.
- Angulo, E., G. W. Roemer, L. Berec, J. Gascoigne, and F. Courchamp. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**:1082–1091.
- Barrowman, N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecological Applications* **13**:784–793.
- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. *Trends in Ecology & Evolution* **22**:185–191.
- Berryman, A. A. 2003. On principles, laws and theory in population ecology. *Oikos* **103**:695–701.

- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**:1445 – 1451.
- Brook, B. W., L. W. Traill, and C. J. A. Bradshaw. 2006. Minimum viable population sizes and global extinction risk are unrelated. *Ecology Letters* **9**:375–382.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.
- Carpenter, S., and W. Brock. 2006. Rising variance: a leading indicator of ecological transition. *Ecology letters* **9**:311.
- Chan, K.-S., A. Mysterud, N. Øritsland, T. Severinsen, and N. Stenseth. 2005. Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. *Oecologia* **145**:556–563.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**:405–410.
- Davis, H. G., C. M. Taylor, J. G. Lambrinos, and D. R. Strong. 2004. Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proceedings of the National Academy of Sciences* **101**:13804–13807.
- Dennis, B. 1989. Allee effects: population growth, critical density and the chance of extinction. *Natural Resource Modeling* **3**:481–538.
- Festa Bianchet, M., J. M. Gaillard, and S. D. Cote. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology* **72**:640–649.
- Forchhammer, M., N. Stenseth, E. Post, and R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proceedings of the Royal Society B: Biological Sciences* **265**:341.
- Fowler, C., and J. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. *Reports to the International Whaling Commission* **41**:545–554.
- Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. Census error and the detection of density dependence. *Journal of Animal Ecology* **75**:837–851.
- Frederiksen, M., F. Daunt, and M. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Ecology* **77**:1020–1029.
- Gascoigne, J., L. Berec, S. Gregory, and F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* **51**:355–372.
- Getz, W. M., and J. O. Lloyd Smith. 2006. Comment on "On the regulation of populations of mammals, birds, fish, and insects" I. *Science* **311**:1100a.
- Gibbons, A. 1992. Conservation biology in the fast lane. *Science* **255**:20–22.

- Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**:71–75.
- Inchausti, P., and J. Halley. 2001. Investigating long-term ecological variability using the Global Population Dynamics Database. *Science* **293**:655–657.
- Johnson, D. M., A. M. Liebhold, P. C. Tobin, and O. N. Bjornstad. 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature* **444**:361–363.
- Kölzsch, A., S. A. Sæther, H. Gustafsson, P. Fiske, J. Höglund, and J. A. Kålås. 2007. Population fluctuations and regulation in great snipe: a time-series analysis. *Journal of Animal Ecology* **76**:740–749.
- Kramer, A., B. Dennis, A. Liebhold, and J. Drake. 2009. The evidence for Allee effects. *Population Ecology* **51**:341–354.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* **241**:1455–1460.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**:911.
- Lande, R., S. Engen, and B. E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.
- Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierachic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1976–1984.
- Månsson, L., and P. Lundberg. 2006. An analysis of the analysis of herbivore population dynamics. *Oikos* **113**:217–225.
- Mitchell, T. D., and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology* **25**:693–712.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenburg. 1995. Population-dynamics of exploited fish stocks at low population-levels. *Science* **269**:1106–1108.
- NERC Centre for Population Biology, I. C., 1999. The Global Population Dynamics Database. URL <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>.
- Nowicki, P., S. Bonelli, F. Barbero, and E. Balletto. 2009. Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics. *Oecologia* **161**:227–239.
- Odum, E. P. 1953. Fundamentals of ecology. Saunders, Philadelphia, Pennsylvannia, USA.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.r-project.org>.
- Reed, D. H. 2005. Relationship between population size and fitness. *Conservation Biology* **19**:563–568.

- Rothery, P., I. Newton, L. Dale, and T. Wesolowski. 1997. Testing for density dependence allowing for weather effects. *Oecologia* **112**:518–523.
- Sæther, B. E., T. H. Ringsby, and E. Roskaft. 1996. Life history variation, population processes and priorities in species conservation: Towards a reunion of research paradigms. *Oikos* **77**:217–226.
- Shelton, P. A., and B. P. Healey. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1521–1524.
- Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological Monographs* **68**:445–463.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science* **309**:607–610.
- Solow, A. R., and J. Steele. 1990. On sample size, statistical power, and the detection of density dependence. *Journal of Animal Ecology* **59**:1073–1076.
- Spellucci, P. A. 1998. A SQP method for general nonlinear programs using only equality constrained subproblems. *Mathematical Programming* **82**:413–448.
- Stephens, P. A., S. W. Buskirk, and C. M. del Rio. 2007. Inference in ecology and evolution. *Trends in Ecology & Evolution* **22**:192–197.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185–190.
- Taylor, C. M., and A. Hastings. 2005. Allee effects in biological invasions. *Ecology Letters* **8**:895–908.
- Tcheslavskaya, K., C. C. Brewster, and A. A. Sharov. 2002. Mating success of gypsy moth (Lepidoptera : Lymantriidae) females in Southern Wisconsin. *Great Lakes Entomologist* **35**:1–7.
- Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* **73**:289–305.
- Wang, M. H., and M. Kot. 2001. Speeds of invasion in a model with strong or weak Allee effects. *Mathematical Biosciences* **171**:83–97.
- Woiwod, I. P., and I. Hanski. 1992. Patterns of density dependence in moths and aphids. *Journal of Animal Ecology* **61**:619–629.
- Zeng, Z., R. M. Nowierski, M. L. Taper, B. Dennis, and W. P. Kemp. 1998. Complex population dynamics in the real world: Modeling the influence of time-varying parameters and time lags. *Ecology* **79**:2193–2209.

### 3.5 Appendices

## Appendix A: Assessing the exclusion of weak Allee effect models.

### Background

The choice of models to include in our model set was the most important decision we made in this analysis, and all results depend upon it. It is for this reason we selected our models carefully based on three main criteria:

1. **The models had to be published:** We chose only models we found in the population growth literature (and we consulted experts to locate these models). We compiled what we considered the optimum model set for our question and found it to be the same model set developed by Berryman (2003). Although the model set excludes weak Allee effect models, it represents a logical model set starting at the null model of no growth (random walk), working up systematically to the most complex model including negative and positive density feedback.
2. **The models should be nested:** We chose an elegant model set reflecting the major population growth dynamics incorporated in a stepwise fashion. Such an attempt was desirable to enable us to assess the additional support attributable to each model term added. Nevertheless, the model set excludes weak Allee effects by imposing the constraint  $0 < A$  in all Allee model fits. Our reason for doing this was to two-fold: (1) it was a requirement to obtain a nested model set. Although several weak Allee models exist (and have been published), they do not admit the Ricker logistic or exponential growth models as special cases when there is no Allee effect, at least not without an additional parameter (see Berryman 2003 and chapter 3 in Courchamp et al. 2008). Also, we do not know of an equivalent weak Allee exponential model. (2) our emphasis on strong Allee effects reflects our perceived importance of this dynamic over weak Allee effects, which do not cause negative growth rate (i.e., population decline).
3. **Numbers of parameters:** We opted to use an information-theoretic approach to model ranking that penalizes models for additional parameters. The number of model parameters therefore became an important selection criterion when searching for Allee effect models. In the model set used in the main text, the Allee effect is incorporated using a single parameter  $A$  (constrained  $0 < A$ ; see point 2 above). While the Allee effects can be incorporated using other formulations, these generally entail additional parameters, or do not admit the Ricker logistic or exponential growth as special cases. For example, one could characterize the Allee effect using two parameters, say  $A$  and  $C$  with  $0 < C$ , which would allow the model greater flexibility to find Allee effects (strong or weak) (see chapter 3 in Courchamp et al. 2008). Including additional parameters, however, will be penalized by  $AIC_C$ .

Nevertheless, our model set biases our results and we wanted to investigate the extent of this bias. We therefore repeated our model-fitting analysis with an additional model; a 4-parameter weak Allee effect version of the Ricker Allee model (WA; Courchamp et al. 2008);  $r = r_m(1 - (N_t/K))((N_t - A)/K)$ . The Allee term in the model is  $(N_t - A)/K$ , and equals 1 when  $N_t$  equals  $(K + A)$ ; for all other  $N$  this term will weight the negative density feedback term preventing us

from assessing the support due to the term in isolation. We fitted this model, along with the others, using the same methods outline in the main text.

## Results

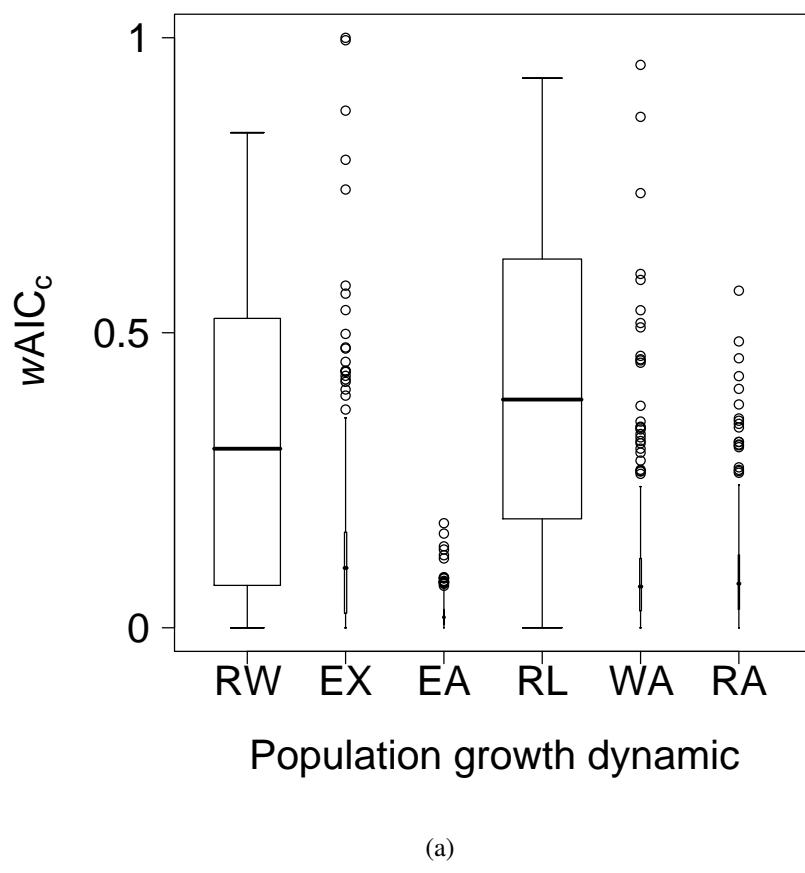
The WA model received similar support to the RA model both overall, and for each taxa considered separately (Table 3.3, Figure 3.6a) but had higher support among the aquatic invertebrate and plant taxa. Furthermore, it was the top-ranked model in 13 cases (Figure 3.6). Although at first sight these results are similar to those for the RA model used in the original model set (1) the WA is an additional model and therefore usurps empirical support from other models in the model set. Specifically, WA appears to take the support from RL, RW and RA, although this causes no overall change to the spread of empirical support across the population growth dynamics examined. (2) As an additional Allee model, the WA top-ranked model count is added to that of RA for a combined top-ranking Allee model count of 22. The RA top-ranked model count was only reduced by 4 (from 13 to 9) when including WA in the model set, and the increase in the top-ranked model count is not sufficiently large to change our findings using the model set excluding weak Allee effects. (3) Finally, the WA model frequently achieved the same fit as the RL and RA models, as indicated from the deviance explained (Figure 3.6b), and the WA model was not the top-ranking mode for any species previously shown to exhibit component or demographic Allee effects (Table 3.4; cross reference main article).

Table 3.3: Overall and major taxonomic group  $wAIC_c$  support for population growth models.

| <i>n</i> |      | Model $wAIC_c$ |       |       |       |       |       |
|----------|------|----------------|-------|-------|-------|-------|-------|
|          |      | RW             | EX    | EA    | RL    | WA    | RA    |
| overall  | 1198 | 0.307          | 0.100 | 0.020 | 0.404 | 0.084 | 0.085 |
| INS      | 603  | 0.288          | 0.085 | 0.017 | 0.436 | 0.086 | 0.088 |
| BIR      | 225  | 0.272          | 0.107 | 0.023 | 0.402 | 0.095 | 0.100 |
| MAM      | 152  | 0.323          | 0.113 | 0.025 | 0.359 | 0.094 | 0.086 |
| FIS      | 115  | 0.438          | 0.111 | 0.019 | 0.343 | 0.043 | 0.046 |
| RAM      | 37   | 0.350          | 0.142 | 0.025 | 0.352 | 0.062 | 0.069 |
| AQI      | 36   | 0.452          | 0.134 | 0.025 | 0.288 | 0.054 | 0.047 |
| PLA      | 30   | 0.417          | 0.116 | 0.016 | 0.366 | 0.051 | 0.033 |

Taxonomic groups: INS, insects; BIR, birds; MAM, mammals; FIS, fish; RAM, reptiles and amphibians; AQI, aquatic invertebrates; PLA, plants.

Model abbreviations: RW, random walk; EX, exponential growth; EA, exponential Allee; RL, Ricker logistic; WA, weak Ricker Allee logistic; RA, strong Ricker Allee logistic.



(a)

Figure 3.6: (a) Support for each population growth model where bar width represents the frequency the model was top-ranked. The Ricker logistic model (RL) received highest empirical support in these data followed by random walk (RW) and exponential growth (EX) models. Ricker Allee (RA) and Weak Allee (WA) models received similar support and both more than the exponential Allee (EA) model.

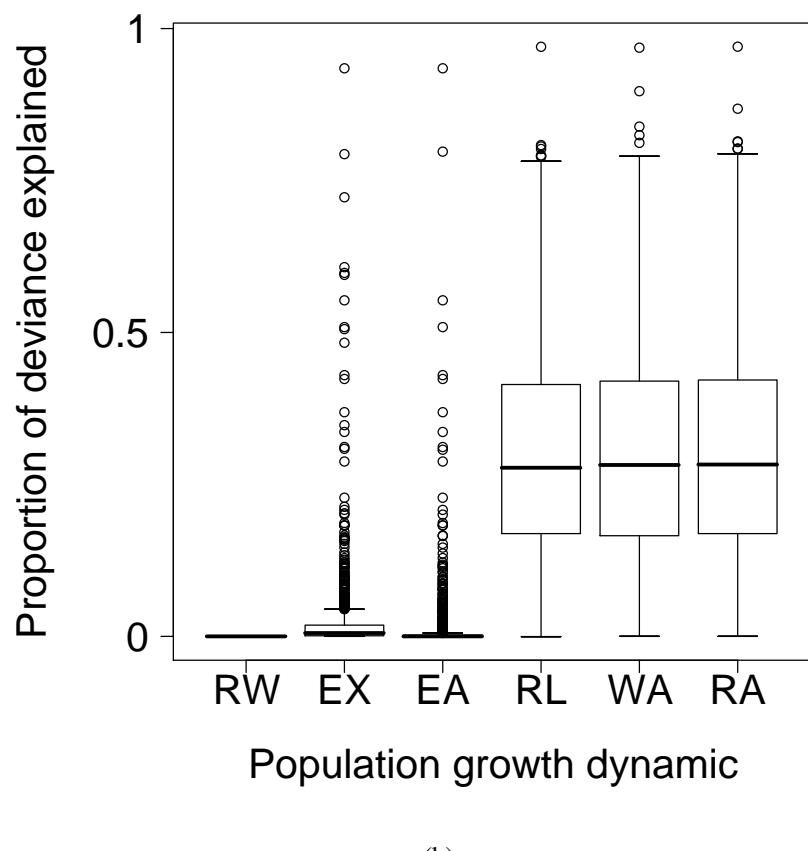


Figure 3.6: (b) Boxplot showing the deviance explained for each population growth model, where the random walk (RW) model is taken to be the null model (zero deviance explained). Exponential growth (EX) generally explained more deviance than the exponential Allee (EA) growth model, whereas the Ricker (RL), Weak Allee (WA) and Ricker Allee (RA) logistic growth models explained similar deviance. Boxes delimit the 25-75% interquartile range (IQR) and open circles ( $\circ$ ) represent extreme values  $\geq 1.5 \times \text{IQR}$ .

Table 3.4: Population time series with greatest  $wAIC_C$  support for either the weak or strong Ricker Allee model. ID, database identification number; TaxG, taxonomic group.

|                          | ID    | TaxG | $\sum wAIC_C$ |       |       |       |       |       |
|--------------------------|-------|------|---------------|-------|-------|-------|-------|-------|
|                          |       |      | RW            | EX    | EA    | RL    | WA    | RA    |
| Four-spotted chaser      | 5     | Ins  | 0.105         | 0.034 | 0.009 | 0.313 | 0.461 | 0.078 |
| American crow            | 1181  | Bir  | 0.000         | 0.000 | 0.000 | 0.250 | 0.265 | 0.485 |
| Spanish sardine          | 1944  | Fis  | 0.000         | 0.000 | 0.000 | 0.289 | 0.140 | 0.571 |
| Chiff chaff              | 2770  | Bir  | 0.002         | 0.001 | 0.000 | 0.335 | 0.323 | 0.340 |
| Barred chestnut          | 6218  | Ins  | 0.046         | 0.013 | 0.003 | 0.248 | 0.336 | 0.355 |
| Least yellow underwing   | 6245  | Ins  | 0.000         | 0.000 | 0.000 | 0.360 | 0.261 | 0.379 |
| Clouded silver           | 6468  | Ins  | 0.008         | 0.002 | 0.000 | 0.079 | 0.600 | 0.311 |
| Lilac beauty             | 6484  | Ins  | 0.011         | 0.003 | 0.001 | 0.075 | 0.453 | 0.457 |
| Northern shrimp          | 6783  | Aqi  | 0.066         | 0.226 | 0.043 | 0.109 | 0.376 | 0.179 |
| Double dart              | 6875  | Ins  | 0.214         | 0.195 | 0.016 | 0.144 | 0.084 | 0.346 |
| Buff ermine              | 6986  | Ins  | 0.028         | 0.013 | 0.002 | 0.416 | 0.449 | 0.092 |
| White-bearded Wildebeest | 7060  | Mam  | 0.000         | 0.001 | 0.000 | 0.195 | 0.737 | 0.067 |
| Laxmann's masked shrew   | 10018 | Mam  | 0.005         | 0.001 | 0.000 | 0.458 | 0.509 | 0.027 |
| European otter           | 10177 | Mam  | 0.298         | 0.227 | 0.013 | 0.085 | 0.027 | 0.351 |
| Roe deer                 | 10331 | Mam  | 0.048         | 0.017 | 0.005 | 0.261 | 0.590 | 0.079 |
| Lord Howe Island woodhen | 20030 | Bir  | 0.022         | 0.022 | 0.004 | 0.281 | 0.266 | 0.405 |
| Snail Kite               | 20063 | Bir  | 0.006         | 0.002 | 0.001 | 0.007 | 0.954 | 0.030 |
| Chillingham cattle       | 20114 | Mam  | 0.011         | 0.010 | 0.003 | 0.046 | 0.866 | 0.064 |
| Horse                    | 20121 | Mam  | 0.157         | 0.046 | 0.007 | 0.199 | 0.538 | 0.053 |
| Feral Goat               | 20158 | Mam  | 0.011         | 0.005 | 0.001 | 0.290 | 0.455 | 0.237 |
| Blue Grama               | 20181 | Pla  | 0.245         | 0.095 | 0.019 | 0.229 | 0.339 | 0.074 |
| Lesser scaup             | 30106 | Bir  | 0.049         | 0.019 |       | 0.148 | 0.516 | 0.268 |

Model abbreviations: RW, random walk; EX, exponential growth; EA, exponential Allee; RL, Ricker logistic; WA, weak Ricker Allee logistic; RA, strong Ricker Allee logistic.

## Appendix B: Missing data

Table 3.5: Overall and major taxonomic group support (Akaike weights;  $wAIC_c$ ) for population growth models and overall  $wAIC_c$  and Bayesian Information Criterion (BIC) support for non-Allee (nAE) and Allee (AE) models as a percentage of all support. Support based on time series without missing value treatment.

|         | <i>n</i> | Model $wAIC_c$ |       |       |       |       | AIC (%) |      | BIC (%) |      |
|---------|----------|----------------|-------|-------|-------|-------|---------|------|---------|------|
|         |          | RW             | EX    | EA    | RL    | RA    | nAE     | AE   | nAE     | AE   |
| overall | 1198     | 0.319          | 0.104 | 0.021 | 0.457 | 0.098 | 56.1    | 11.9 | 53.4    | 13.9 |
| INS     | 602      | 0.303          | 0.090 | 0.018 | 0.489 | 0.099 | 57.9    | 11.8 | 55.0    | 14.4 |
| BIR     | 224      | 0.276          | 0.105 | 0.023 | 0.476 | 0.121 | 58.0    | 14.4 | 54.6    | 13.2 |
| MAM     | 147      | 0.331          | 0.123 | 0.027 | 0.412 | 0.106 | 53.6    | 13.3 | 49.0    | 12.7 |
| FIS     | 114      | 0.443          | 0.116 | 0.019 | 0.376 | 0.046 | 49.2    | 6.5  | 52.3    | 14.5 |
| RAM     | 37       | 0.370          | 0.149 | 0.026 | 0.375 | 0.080 | 52.5    | 10.6 | 50.3    | 13.6 |
| AQI     | 35       | 0.462          | 0.139 | 0.026 | 0.316 | 0.057 | 45.5    | 8.3  | 45.2    | 14.2 |
| PLA     | 30       | 0.454          | 0.115 | 0.015 | 0.381 | 0.035 | 49.6    | 5.1  | 52.9    | 14.9 |

## Appendix C: Measurement error

Table 3.6: Overall and major taxonomic group support (Akaike weights;  $wAIC_c$ ) for population growth models and overall  $wAIC_c$  and Bayesian Information Criterion (BIC) support for non-Allee (nAE) and Allee (AE) models as a percentage of all support. Support based on time series with randomized measurement error.

|         | <i>n</i> | Model $wAIC_c$ |       |       |       |       | AIC (%) |      | BIC (%) |      |
|---------|----------|----------------|-------|-------|-------|-------|---------|------|---------|------|
|         |          | RW             | EX    | EA    | RL    | RA    | nAE     | AE   | nAE     | AE   |
| overall | 1198     | 0.326          | 0.111 | 0.022 | 0.397 | 0.144 | 50.8    | 16.6 | 47.9    | 18.1 |
| INS     | 603      | 0.309          | 0.091 | 0.019 | 0.432 | 0.148 | 52.3    | 16.7 | 49.3    | 19.7 |
| BIR     | 225      | 0.280          | 0.114 | 0.024 | 0.390 | 0.192 | 50.4    | 21.7 | 46.6    | 19.2 |
| MAM     | 152      | 0.342          | 0.125 | 0.026 | 0.364 | 0.142 | 48.9    | 16.8 | 45.1    | 15.6 |
| FIS     | 115      | 0.369          | 0.174 | 0.028 | 0.353 | 0.077 | 52.6    | 10.5 | 49.9    | 12.3 |
| RAM     | 37       | 0.479          | 0.133 | 0.022 | 0.319 | 0.047 | 45.2    | 6.9  | 47.3    | 13.5 |
| AQI     | 36       | 0.443          | 0.144 | 0.028 | 0.267 | 0.118 | 41.1    | 14.6 | 41.1    | 17.4 |
| PLA     | 30       | 0.442          | 0.126 | 0.019 | 0.311 | 0.101 | 43.7    | 12.0 | 47.0    | 18.8 |

## Appendix D: Time series with Allee effects

Table 3.7: Population time series with greatest support for positive density feedback.

|                          | ID    | TaxG | $\sum w\text{AIC}_c$ |       |       |       |       |
|--------------------------|-------|------|----------------------|-------|-------|-------|-------|
|                          |       |      | RW                   | EX    | EA    | RL    | RA    |
| American crow            | 1181  | Bir  | 0.000                | 0.000 | 0.000 | 0.340 | 0.660 |
| Spanish sardine          | 1944  | Fis  | 0.000                | 0.000 | 0.000 | 0.336 | 0.664 |
| Chiff chaff              | 2770  | Bir  | 0.002                | 0.001 | 0.000 | 0.495 | 0.501 |
| Barred chestnut          | 6218  | Ins  | 0.069                | 0.020 | 0.004 | 0.373 | 0.534 |
| Least yellow underwing   | 6245  | Ins  | 0.001                | 0.000 | 0.000 | 0.487 | 0.512 |
| Clouded silver           | 6468  | Ins  | 0.019                | 0.005 | 0.001 | 0.198 | 0.776 |
| Lilac beauty             | 6484  | Ins  | 0.021                | 0.006 | 0.001 | 0.137 | 0.835 |
| Double dart              | 6875  | Ins  | 0.234                | 0.214 | 0.018 | 0.157 | 0.378 |
| European otter           | 10177 | Mam  | 0.306                | 0.233 | 0.013 | 0.087 | 0.361 |
| Lord Howe Island woodhen | 20030 | Bir  | 0.029                | 0.030 | 0.006 | 0.383 | 0.552 |
| Snail Kite               | 20063 | Bir  | 0.127                | 0.046 | 0.011 | 0.158 | 0.658 |
| Chillingham cattle       | 20114 | Mam  | 0.082                | 0.072 | 0.021 | 0.345 | 0.480 |
| Lesser scaup             | 30106 | Bir  | 0.102                | 0.038 |       | 0.306 | 0.554 |

# Chapter 4

## Defying definition: uncovering demographic Allee effects masked by their associated high variation

## **Abstract**

1. Demographic Allee effects manifest in populations at a reduced and unstable size. Yet, most natural populations fluctuate at a large and stable size. To observe a demographic Allee effect, time series should exhibit sufficient variation for the population to reach the reduced size at which demographic Allee effects act.

2. We predicted that the variation required to observe a demographic Allee effect would be high but that such high variation would mask the demographic Allee effect. More formally, we predicted that time series with a demographic Allee effect would show highest empirical support for negative density feedback at low variation, changing to random walk at higher variation, and rarely support a demographic Allee effect.

3. We simulated time series from a stochastic demographic Allee effect model encapsulating negative density feedback, exponential growth and random walk as special cases. We then fitted these models to each time series and measured their relative empirical support after penalising for their complexity. We examined how the empirical support for each model varied with time series variation.

4. Empirical support for the demographic Allee effect model was unrelated to time series variation: time series with low variation showed highest empirical support for negative density feedback, followed by random walk and exponential growth as time series variation increased.

5. To better detect demographic Allee effects, we propose combining qualitative measures of population change for multiple high variation time series - an idea first proposed in Tobin et al. (2007).

6. We apply this statistical procedure to large common and soprano pipistrelle datasets, along with a dataset of simulated demographic Allee effect time series created to mimic them, and reveal expected demographic Allee effects in the soprano pipistrelle and mimic datasets.

7. *Synthesis and applications.* Detecting a demographic Allee effect is confounded by the high variation required for its expression. Due to its easy implementation and extensibility, we advocate the using our statistical procedure to detect demographic Allee effects using multiple time series. Furthermore, we reason that this statistical procedure overcomes problems such as measurement and observer error associated with conventional individual population time series analyses and should be useful in detecting other growth dynamics.

## **4.1 Introduction**

A component Allee effect describes a decrease in a surrogate measure of individual fitness (i.e., survival, reproduction, etc.) at reduced population size or density (Stephens et al. 1999). Recent reviews have highlighted their existence in a wide range of species acting via numerous mechanisms (Courchamp et al. 2008; Kramer et al. 2009). For example, Gascoigne et al. (2009) reviewed the evidence for Allee effects caused by the vanishing chance of finding a sexually receptive mate with decreasing population size - a mate-finding Allee effect. They found examples of mate-finding component Allee effects in species ranging from zooplankton to trees. Very few of these, however, appeared to translate into demographic Allee effects. A demographic Allee effect describes a decrease in population growth rate at reduced population size or density and is the demographic manifestation of one or more underlying component Allee effects (Stephens et al. 1999). Given the abundant evidence for component Allee effects in natural populations, we might expect a corresponding abundance of demographic Allee effect. However, over 15 years

of attempts to quantify their evidence using multi-species meta-analyses have almost invariably arrived at the conclusion that they are rare (Myers et al. 1995; Sæther et al. 1996; Gerber and Hilborn 2001; Gregory et al. 2010).

Various reasons have been proposed to explain the discrepancy between the abundance of observed component Allee effects and the paucity of observed demographic Allee effects. The most parsimonious explanation is that underlying component Allee effects are frequently offset by the benefits accrued from a release from intraspecific competition at reduced population size (Stephens et al. 1999) or are simply not strong enough (Gregory and Courchamp 2010). Assuming the manifestation of a demographic Allee effect, however, various statistical issues might complicate its detection. Gregory et al. (2010) investigated several such issues and found that detecting demographic Allee effect could be complicated by measurement error, time series length, the existence of deterministic trends, or any combination of these factors. Untangling their relative influences will, however, prove exceedingly difficult. Rather, their influences may combine to produce highly variable time series that are unsuitable for univariate analysis. For example, Myers et al. (1995) analysed 128 stock-recruitment fisheries time series for evidence of depensation (a synonym of demographic Allee effect used in the fisheries literature) by comparing compensation and depensation models using a likelihood ratio test. They found only three possible cases of depensation. This paucity of depensation cases was, they suggested, because their statistical procedure only had sufficient power to detect depensation in 26 of their 128 time series. Shelton and Healey (1999) reexamined these 128 stock-recruitment time series and found that they were too variable to detect depensation unless it was very strong.

Myers et al. (1995), and then Shelton and Healey (1999), found that the majority of fisheries stock-recruitment time series were too variable to yield any information about demographic Allee effects. Paradoxically, high variation might be a necessary condition to observe a demographic Allee effect. Most natural populations fluctuate around at a large and stable size where they are regulated by negative density feedback (Brook and Bradshaw 2006). For such populations to reveal a demographic Allee effect, they should transition between this large and stable size and the reduced and unstable size at which demographic Allee effects act. Such dynamics, however, should result in high variation. Disregarding such high variation time series - as did Myers et al. (1995) - might result in throwing out the baby with the bath water. For example, Liermann and Hilborn (1997) reanalysed the stock-recruitment data of Myers et al. (1995) using a partial Bayesian approach, and although not able to conclude that there was abundant evidence for demographic Allee effects, neither could they conclude that there was no evidence. Walters and Kitchell (2001) took a completely different approach; they asked experts whether, in their opinions, they thought species' stock-recruitment plots showed evidence for depensation. Many did.

Several authors have advocated the use of multiple population time series to detect population growth dynamics (specifically negative density feedback). For example, Dennis et al. (1998) extended the parametric bootstrap approach to detect negative density feedback across multiple populations. Their approach estimated density feedback parameters for each population allowing them to assess which showed "statistical density dependence". Langton et al. (2002), on the other hand, estimated a single density feedback parameter using several population time series allowing them reduce its standard error and strengthening inferences about its existence in the populations analysed (akin to using many replicates in an experimental design). In a particularly interesting analysis, Barrowman et al. (2003) examined multiple coho Salmon *Oncorhynchus kisutch* stock-recruitment datasets for evidence of negative density feedback and depensation. They gathered 14 salmon time series, some of which included recruitment observed at low population densities,

and fitted a selection of models to each individual time series and to all time series together in a maximum likelihood mixed-effects model. Moreover, they contrasted their maximum likelihood results to those derived from a full Bayesian analysis. They found that the maximum likelihood and Bayesian analysis results were very similar. More importantly, however, they also found that the individual and multiple time series results were qualitatively different. They argued that the multiple time series approach gave more biologically and statistically meaningful results and, although neither approach found high evidence of depensation, the multiple time series approach at least provided estimates of the depensation parameter not estimable from the individual time series (Barrowman et al. 2003).

In contrast to methods that use multiple time series in parametric analyses of quantitative changes in population size like those used by Langton et al. (2002) and Barrowman et al. (2003), the method used in Johnson et al. (2006), and developed in Tobin et al. (2007), redefined the measure of population change using a non-parametric approach. Johnson et al. (2006) used this method to show strong empirical evidence that Gypsy moths *Lymantria dispar* invading northeastern United States exhibited a demographic Allee effect. Essentially, they detected the demographic Allee effect by calculating the proportion of trap captures that increased from one year to the next for many thousands of traps. Assuming the trap captures were representative of the local population dynamics, they were able to show, using locally weighted least squares regression, that less than 50% of smallest and largest populations increased in the following year, representing a demographic Allee effect and a ‘carrying capacity’, respectively (Johnson et al. 2006). Tobin et al. (2007) examined this method in greater depth and demonstrated that it was able to approximate the Allee threshold parameter used to generate the time series.

Our aim here was twofold. First, we aimed to show that time series with a demographic Allee effect will rarely exhibit a demographic Allee effect because the high variation required for the population to reach the small size where the demographic Allee effect acts will mask its signal. Rather, negative density feedback (also known as classical negative density dependence) will dominate in low variation time series, switching to random walk (also known as no growth) as their variation increases. These predictions are graphically illustrated in Figure 4.1. To test them, we generated a large number of time series from a stochastic demographic Allee effect model, measured their empirical support for four population growth dynamics, and related this to their variation. Second, we aimed to develop a statistical procedure to overcome the high variation masking the demographic Allee effect signal. We built on a method developed by Tobin et al. (2007) by combining it with a multi-model evidence-based approach used by Gregory et al. (2010). This statistical procedure involves redefining the quantitative measure of population growth as a qualitative measure, combining it over multiple time series, and then fitting to it a number of population growth models representing a set of alternative hypotheses. We examined the utility of this statistical procedure by applying it to soprano *Pipistrellus pygmaeus* and common *P. pipistrellus* pipistrelle datasets collected by the Bat Conservation Trust’s National Bat Monitoring Programme: a demographic Allee effect was expected in the soprano but not the common pipistrelle. Furthermore, we applied the statistical procedure to a dataset of time series simulated from the stochastic demographic Allee effect model.

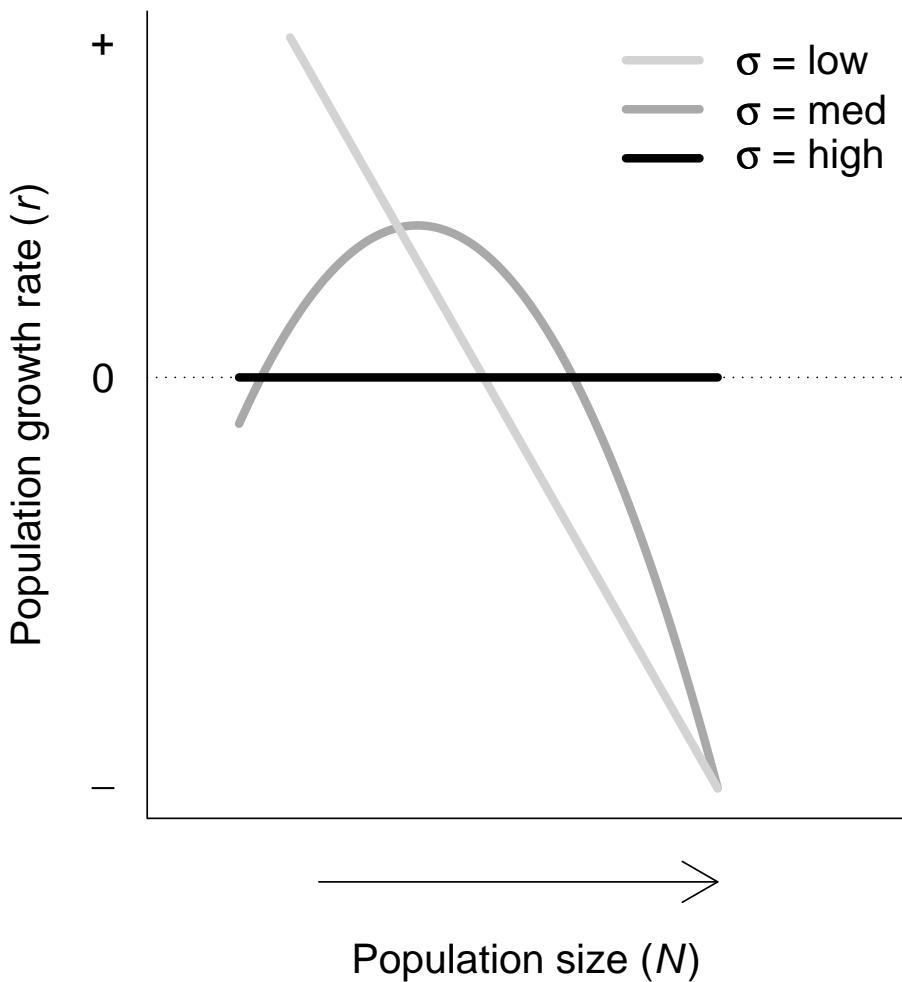


Figure 4.1: Demographic Allee effect (dAE) models will fit negative density feedback (light gray curve) when population variation ( $\sigma$ ) is low because the population will never reach the small sizes where the dAE acts. High  $\sigma$  will result in observations of small population size but the high variation will mask any density feedback signal and the dAE model will fit a random walk (black curve). The highest likelihood of observing a dAE should therefore be at medium  $\sigma$  (dark gray curve). Note that a dAE model will also fit exponential growth if a trend is present, although the exponential growth fit will mirror the random walk fit if no trend is present (as illustrated here).

## 4.2 Methods

### 4.2.1 A stochastic demographic Allee effect model

Population time series were generated with a discrete time autoregressive stochastic model of population growth with negative feedback and a demographic Allee effect (Courchamp et al. 1999):

$$N_{t+1} = N_t \exp[r_m(1 - (N_t/K))((N_t - A)/N_t) + \sigma] \quad (4.1)$$

where  $N_t$  is the time series observation  $N$  taken at time  $t$ ,  $r_m$  is the intrinsic population growth rate,  $K$  is an upper limit to the population size in the occupied habitat (the ‘carrying capacity’), and  $A$  is the ‘Allee threshold’ - an unstable threshold population size, believed to occur at small population size, above which the *per capita* population growth rate ( $r$ ) might be depressed and below which  $r$  becomes negative. Equation 1 prescribes a strong demographic Allee effect characterised by a negative  $r$  at small population size. A weak demographic Allee effect causes reduced - but not negative -  $r$  at small population size (Wang and Kot 2001). We did not fit a weak demographic Allee effect model for two main reasons: (i) extending the above model to permit a weak demographic Allee effect would require an additional parameter (Courchamp et al. 2008) with a corresponding higher penalty, and (ii) Gregory et al. (2010) found sparse evidence for weak demographic Allee effects compared to strong demographic Allee effects (and other population dynamics). These analyses are therefore constrained to strong demographic Allee effects. Demographic stochasticity was incorporated directly into the population growth rate by adding a random parameter  $\sigma \sim \text{normal}(0, \sigma^2)$ . The remaining parameters were set to ensure that the population fluctuated around a relatively small size where demographic stochasticity has the largest influence on population dynamics (Lande 1993). The initial population size,  $N_0$ , was randomly drawn from a vector of integers ranging from 50 to 130, i.e.,  $N_0 \in [50, 51, \dots, 130]$ . Parameters  $A$  and  $K$  were kept constant and were arbitrarily set to 30 and 150, respectively. Parameter  $r_m$  was set to 0.5 - an intermediate value chosen to encourage sufficient, but not excessive, time series variation (Holyoak and Baillie 1996).

### 4.2.2 Measuring demographic Allee effect support in individual time series

The following procedure was used to measure the empirical support for demographic Allee effects in all individual time series. We modeled  $r$  (calculated as  $\log_e[N_{t+1}/N_t]$ ) using four population growth models previously used to illustrate a general theory of population growth (Berryman 2003). The model set included a demographic Allee effect model (AE):

$$r = r_m(1 - (N_t/K))((N_t - A)/N_t) + \epsilon \quad (4.2)$$

and three special case models representing (i) negative density feedback growth (ND) where  $A = 0$ , (ii) exponential growth or decline (EX) where  $A = 0$  and  $K = N_t$ , and (iii) random walk or no growth (RW) where  $A = 0$ ,  $K = N_t$ , and  $r_m = 0$ .  $\epsilon$  was an assumed independent and identically distributed error term.

We fitted these models to  $r$  using ordinary least squares estimated by a sequential quadratic programming algorithm (donlp2; Spellucci 1998) subject to box constraints  $0 \leq r_m$  and  $0 \leq K$  for ND, and additional box constraint  $0 \leq A$  and linear constraint  $A \leq K$  for AE. We used the free parameter  $\epsilon$  to calculate Akaike’s information criterion (adjusted for small sample sizes; AIC<sub>c</sub>) to measure empirical support for each candidate model (Brook and Bradshaw 2006). Empirical

support can be thought of as the parameter-adjusted likelihood of observing the corresponding population growth dynamic. We calculated the empirical support for each model as its AIC<sub>C</sub> weight ( $w\text{AIC}_C$ ) and designated the top-ranked model for each time series as that with the highest  $w\text{AIC}_C$  (a measure of parameter-adjusted detection). The top-ranked model can be thought of as the population growth dynamic best describing the time series growth dynamics.

#### 4.2.3 Combining and measuring demographic Allee effect support in multiple time series

The following procedure was used to measure the empirical support for demographic Allee effects in multiple combined time series. Using the method developed by Tobin et al. (2007), we can combine multiple time series for a single species to create a measure of population change across multiple populations. For each time series we align the population counts in years  $t$  and  $t+1$  and record whether the population increased from the population size observed in year  $t$ . For example, a population monitored for five consecutive years from 2000 would provide four annual transitions 2000/2001, ..., 2004/2005 corresponding to population sizes in 2000, ..., 2004. Essentially, this treatment reduces each time series to a sequence of TRUE or FALSE outcomes reflecting whether or not the population increased from year  $t$  to  $t+1$ . We then calculate the proportion of annual transitions that increased for each observed population size, here called the population replacement rate  $R$ . A value of  $R = 0.5$  means half the populations at an observed population size increased and the other half decreased; values above or below 0.5 represent higher proportions of increasing and decreasing populations, respectively. According to these criteria, a strong demographic Allee effect is characterised by  $R < 0.5$  at small population sizes, while negative density feedback is characterised by  $R < 0.5$  at large population sizes (Tobin et al. 2007).

The main disadvantage to this method is the low level of information afforded by each consecutive pair of time series observations. Rather than providing a quantitative measure of change in population size, this method reduces each consecutive pair of time series observations to a qualitative measure of population change. Consequently, several observations are required at each population size to calculate  $R$ . If there are few time series observations (due to few or many short time series), then a single annual transition will be observed for each population size. The resulting binary variable would be inappropriate for model-fitting using least squares regression. To overcome this scenario we placed time series observations into data bins (i.e., grouped into intervals of values). This can be done using a variety of methods. We preferred the Freedman-Diaconis method that tends to produce numerous narrower bins compared to other methods (Izenman 1991), thereby maximising the number of observations for the model fitting.

We fitted approximations to the same four population models used previously to fit individual time series. They were fitted as: (i) RW as  $R = 0.5 + \epsilon$ , (ii) EX as  $R = \alpha + \epsilon$ , where the best measure of  $\alpha$  is  $\text{mean}(R)$ , (iii) ND as  $R = \alpha + \beta N_t + \epsilon$ , where  $\alpha$  and  $\beta$  are estimated as the intercept and regression coefficient from a linear regression subject to box constraints  $0 < \alpha$  and  $0 > \beta$ , and (iv) AE as  $R = \alpha + \beta_1 N_t + \beta_2 N_t^2 + \epsilon$ , where  $\alpha, \beta_1$  and  $\beta_2$  are estimated as the intercept and regression coefficients from a quadratic regression subject to box constraints  $0 < \alpha$  and  $0 < \beta_2$ . These models were fitted to  $R$  using least squares estimated using a sequential quadratic programming algorithm (donlp2; Spellucci 1998) and used the free parameter  $\epsilon$  to calculate  $w\text{AIC}_C$  to measure empirical support for each candidate model as before.

#### **4.2.4 Measuring time series variation**

Our aim was to see how detection of demographic Allee effects varied with time series variation. However, the issue of how to measure time series variation has itself been at the centre of a long debate (Fraterrigo and Rusak 2008). Two popular measures of variability are the standard deviation of  $\log_e$ -transformed abundance and the coefficient of variation. Both measures, however, can be biased by non-Gaussian data including those data produced by rare events and zero values (Heath 2006). Such data might characterise time series exhibiting threshold behaviours like demographic Allee effects (Stephens et al. 1999). Consequently, we opted to measure time series variation using a measure claimed to be robust to non-Gaussian behaviour - Population Variability (Heath 2006). Population Variability can be briefly described as the average percent difference between all combinations of observed abundances. It has the advantages of being less sensitive to non-Gaussian data, it can incorporate zero values, and it produces variation measures comparable to other popular measures when data are Gaussian (Heath 2006). One potential draw back to Population Variability is it is “less straightforward” to calculate (Fraterrigo and Rusak 2008). To overcome this and encourage its wider use, we provide code to calculate Population Variability in R (R Development Core Team 2008) in the Appendix.

#### **4.2.5 Does high variation mask the demographic Allee effect signal?**

To investigate this question we simulated time series from Equation 4.1. We generated 1000 time series of length  $t = 250$  for each value of  $\sigma$  ranging from 0.50 to 0.75 with interval 0.05, i.e.,  $\sigma \in [0.50, 0.55, \dots, 0.75]$ . This range of  $\sigma$  was chosen to ensure that the simulated time series would cover a wide range of variation. We then selected random sequences of  $n = 20$  observations (excluding the first two observations) from each time series and investigated their relative empirical support for a demographic Allee effect. Twenty was chosen because it was the minimum recommended time series length to detect density feedback dynamics (Fox and Ridsdill-Smith 1995).

For each individual time series sequence, we examined its empirical support for a demographic Allee effect using the individual time series procedure outlined above and measured it variation using Population Variability. We plotted the empirical support for each model as a function of the time series variation and fitted a locally weighted regression (lowess) curve through the median empirical support values for each model. The lowess smoothing parameter was set to 0.5. We investigated how patterns in top-ranked models varied with time series variation by plotting numbers of top-ranked models as a function of the time series variation using boxplots.

#### **4.2.6 Can combining high variation time series help to detect a demographic Allee effect?**

To investigate this question we investigated how the empirical support for each model changed when they were fitted to individual and multiple population time series. We focused on high variation time series because they have a higher chance of reaching small population sizes where demographic Allee effects act but their high variation should mask the demographic Allee effect signal. We compared the individual and multiple time series analyses using two real datasets collected by the Bat Conservation Trust’s National Bat Monitoring Programme (NBMP) and a dataset of simulated time series sequences chosen to imitate the NBMP datasets in variation and length (see below).

Established in 1996, the NBMP was commissioned as a five-year project to develop and test methods to monitor annual population trends of 7 of the UK's 16 breeding bat species. One of the three core survey techniques used is summer maternity roost emergence counts (Walsh et al. 2002). These surveys are carried out between specified dates across the UK by a network of volunteer surveyors coordinated by Bat Conservation Trust staff. To promote complete and consistent data collection, roost count volunteers receive a survey pack including survey instructions and a standardised proforma (see online forms at <http://www.bats.org.uk/pages/nbmp.html>). Among other metadata, surveyors are asked to choose among predefined reasons for terminating roost counts. These metadata permit the NBMP to omit counts which were stopped due to confusing bat behaviour or deteriorating weather conditions, and demonstrate how most roosts are monitored by the same individuals, so minimising the influence of observer error (S. Gregory, unpublished data). Furthermore, the proforma field for recording a zero count, and a freepost service for completed proformae, reduce the probability of missing values in the dataset, even when no bats were observed.

We used NBMP datasets for the soprano pipistrelle and common pipistrelle. Pipistrelles are amenable to roost counts because they form maternity roosts, or single-sex aggregations of breeding female bats, in houses and other man-made structures (Walsh et al. 2002). This tendency for breeding bats to aggregate in single-sex roosts, taken together with their habitual behaviours (Burland and Worthington Wilmer 2001) and their tendency to emergence from roosts at predictable exits and times (Speakman et al. 1995), should provide accurate estimates of roost sizes by minimising measurement errors. Furthermore, data for these species was preferred because: (i) they are closely related and social species (Barratt et al. 1997), (ii) despite their relatedness, they show contrast philopatry to their day roosts; common pipistrelles are considered to be highly vagrant compared to soprano pipistrelles (Davidson-Watts and Jones 2006), (iii) they are both relatively common across the UK and consequently many roosts have been monitored for each species, both as part of the NBMP and by the Robert Stebbings Consultancy National Bat Colony Survey that started in 1977, and (iv) compared to common pipistrelles, the soprano pipistrelle gathers in large groups suggesting that they have a higher susceptibility to a demographic Allee effect (Corbet and Harris 1991). We predicted that the soprano pipistrelle would show a demographic Allee effect and the common pipistrelle would not. The value of including the common pipistrelle in the comparison was primarily to see whether the method of combining multiple time series could itself generate demographic Allee effect dynamics, but also to show that the multiple population methodology might be useful for detecting other population growth dynamics.

We treated the NBMP datasets before analysis. We dropped roost counts that were terminated due to confusion but retained those terminated due to deteriorating weather conditions. We also dropped all missing roost counts and treated the remainder as consecutive. Finally, we used only those NBMP time series of length  $n \geq 7$  because seven is considered the minimum time series length suitable for model-fitting (Brook and Bradshaw 2006). We also square root transformed the time series to reduce the effect of differences in mean roost counts between time series. For each NBMP dataset, we then fitted the four population growth models to each individual time series and to multiple time series using the procedures outlined above, and measured and plotted the empirical support for each model.

To validate the findings for the NBMP datasets, we then created a dataset of time series simulated from Equation 4.1 to mimic the NBMP datasets in length. We randomly selected sequences of  $n$  observations, where  $n$  took values from a mean time series length frequency distribution calculated from the two NBMP datasets. The simulated dataset consisted of approximately the

same number of time series as the mean of the two NBMP datasets. Plots of the datasets can be seen in Figure 4.4. Again, we square root transformed these time series and fitted the four population growth models to each individual time series and to multiple time series using the procedures outlined above, and measured and plotted the empirical support for each model.

## 4.3 Results

### 4.3.1 Does high variation mask the demographic Allee effect signal?

Using simulated individual time series generated from Equation 4.1 we show that empirical support for the demographic Allee effect model was consistently low and did not vary with time series variation (Figure 4.2). The demographic Allee effect model shared a similar level of empirical support to the exponential growth model over much of the time series variation range. This suggests that it was generally fitting deterministic trends. This pattern was reflected in patterns of top-ranked models: contrary to our predictions, the number of top-ranked demographic Allee effect models was highest in time series with high - not medium - variation. However, time series with the highest variation best supported the exponential growth model (Figure 4.2).

Although generated from a demographic Allee effect model, individual simulated time series generally showed highest empirical support for the negative density feedback or the random walk models. Indeed, as predicted, those time series with lower variation had highest empirical support and more top-ranked negative density feedback models (Figure 4.2). Also as predicted, this pattern changed with increasing time series variation when random walk models had higher empirical support and more top-ranked models (Figure 4.2).

### 4.3.2 Can combining high variation time series help to detect a demographic Allee effect?

The soprano and common pipistrelle datasets and the simulated time series dataset all showed very similar patterns of empirical support for the four population models when fitted to individual time series (Figure 4.3a). Empirical support for the exponential growth, negative density feedback and demographic Allee effect models was very low compared to that for random walk model, which was highest across all time series regardless of their variation. It is noteworthy that the demographic Allee effect model achieved the lowest empirical support in all the datasets (Table 4.1).

A similar trend was observed in the numbers of top-ranked models. The random walk model had a substantial majority of top-ranked models over the entire range of time series variation (Figure 4.3b). In the few instances it did occur, the negative density feedback model was top-ranked in time series with similar variation to those exhibiting a top-ranked random walk model. The common pipistrelle dataset never exhibited a top-ranked exponential growth or demographic Allee effect model, and only 10 top-ranked negative density feedback models compared to 72 top-ranked random walk models. The soprano pipistrelle exhibited a single top-ranked exponential growth and two demographic Allee effect models, compared to 7 and 53 top-ranked negative density feedback and random walk models, respectively. As expected, the simulated time series dataset exhibited numbers of top-ranked models intermediate to those of the soprano and common pipistrelles.

The empirical support for the population growth models changed substantially when combining multiple time series. The soprano pipistrelle dataset revealed highest empirical support

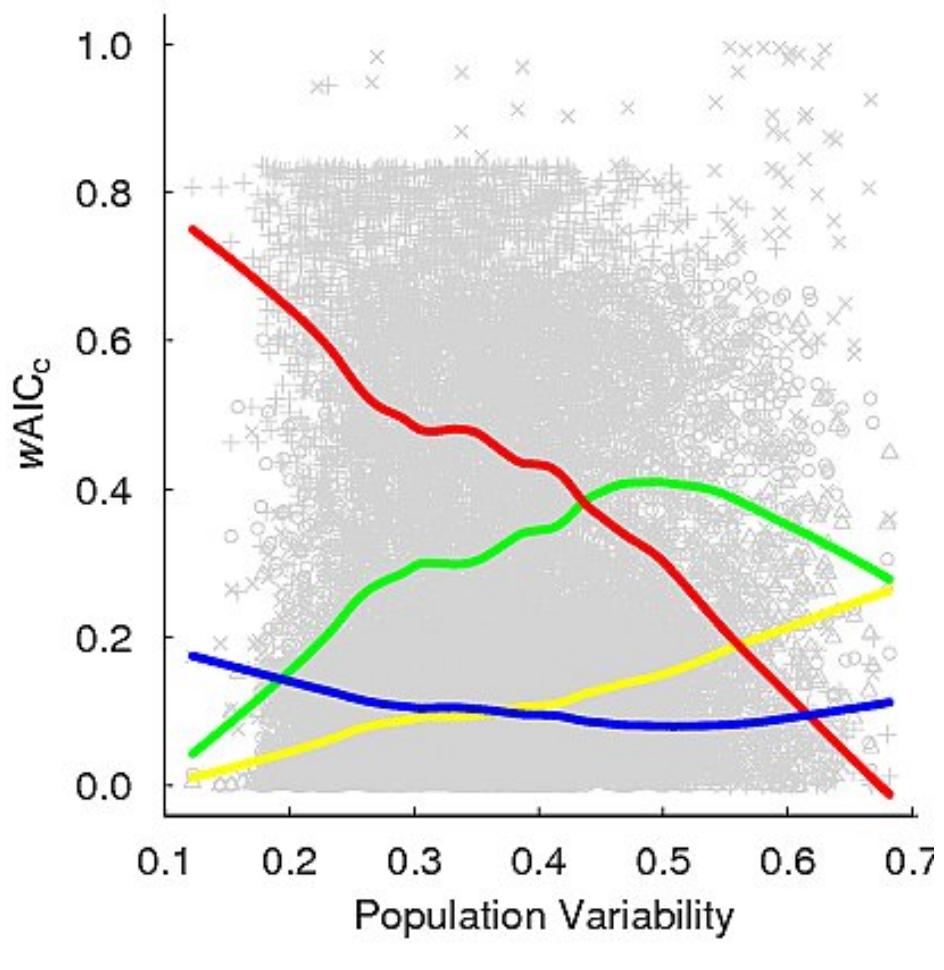
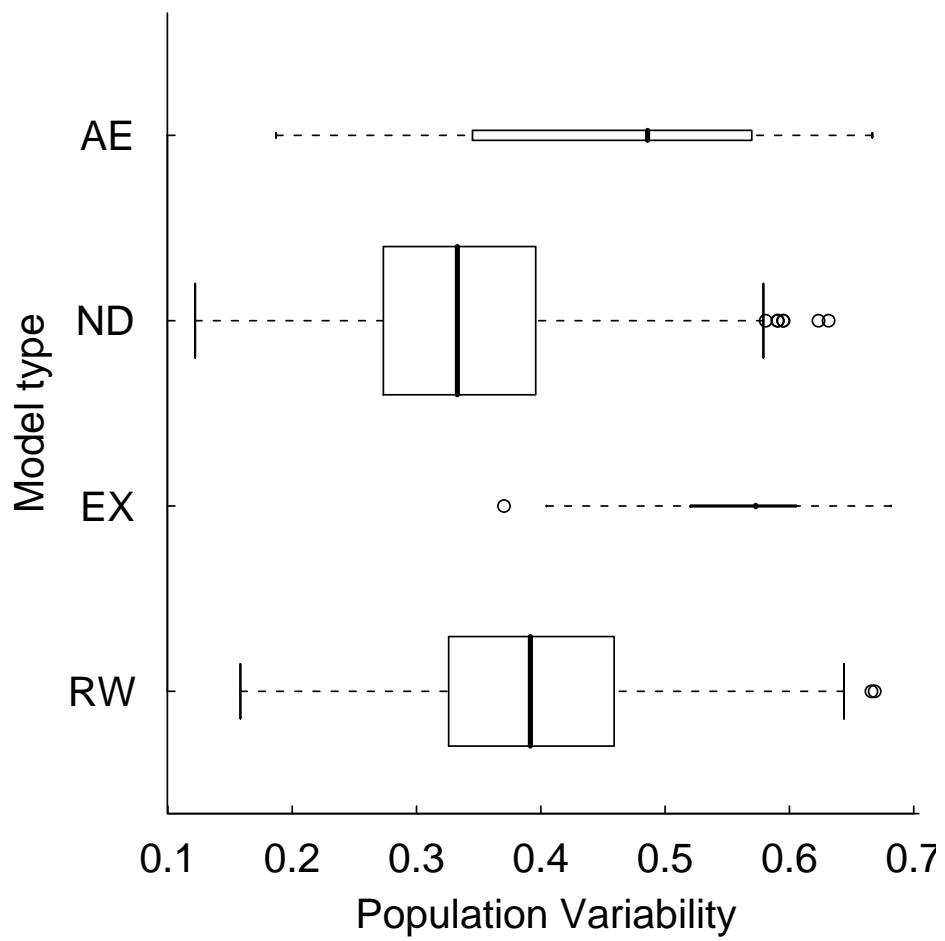


Figure 4.2: (a) Empirical support ( $wAIC_c$ ) for four population growth models as a function of time series (TS) variation using TS simulated from a demographic Allee effect model. The negative density feedback (ND; red curve) and random walk (RW; green curve) models showed relationships in line with predictions (see text). The demographic Allee effect (AE; blue curve) model showed no relationship with TS variation, while the exponential growth (EX; yellow curve) model increased with TS variation.



(b)

Figure 4.2: (b) Top-ranked models as a function of TS variation. Bar width is proportional to the number of top-ranked models. ND and RW showed a pattern of top-ranked models as predicted. EX and AE models, however, had more top-ranked models in highly variable TS than predicted.

for the demographic Allee effect model, followed by the negative density feedback model (Table 4.1). This suggests the presence of a demographic Allee effect and negative density feedback in their population growth dynamics, as predicted. Examination of the plot suggests that a higher proportion of the smallest populations decreased rather than increased in subsequent years (Figure 4.3c), a dynamic indicative of a strong demographic Allee effect. The common pipistrelle dataset, on the other hand, changed from supporting the random walk model to revealing highest empirical support for the exponential growth model (Table 4.1). This suggests both that the method of combining multiple time series is unlikely to spuriously produce the demographic Allee effect signal and that combining multiple time series might help in detecting population growth dynamics other than demographic Allee effects. Importantly, the demographic Allee effect was also observable in the simulated time series dataset (Table 4.1). This suggests that combining multiple time series allows us to ‘refind’ the generating demographic Allee effect in highly variable time series.

**Table 4.1:**  $wAIC_C$  support for each of the four population growth models measured from single time series (TS) and multiple combined TS. The datasets used were roost count TS for the common and soprano pipistrelle in the UK, and a dataset of TS simulated to imitate the length and variation of the pipistrelle TS.

| <b>Dataset</b>      | <b>Single TS</b> |       |       |       | <b>Multiple TS</b> |       |       |       |
|---------------------|------------------|-------|-------|-------|--------------------|-------|-------|-------|
|                     | RW               | EX    | RL    | RA    | RW                 | EX    | RL    | RA    |
| Common pipistrelle  | 0.666            | 0.135 | 0.166 | 0.033 | 0.008              | 0.044 | 0.400 | 0.548 |
| Soprano pipistrelle | 0.686            | 0.134 | 0.166 | 0.014 | 0.215              | 0.688 | 0.077 | 0.020 |
| Simulated           | 0.696            | 0.152 | 0.136 | 0.016 | 0.000              | 0.000 | 0.000 | 0.999 |

Model abbreviations are: RW, random walk; EX, exponential growth; RL, negative density feedback; RA, negative density feedback with a demographic Allee effect.

## 4.4 Discussion

In this study we aimed to: (i) Show that detection of demographic Allee effects in individual population time series would be confounded by the high variation required to ensure the population reached the small sizes where demographic Allee effects act. (ii) Develop a statistical procedure that combines qualitative changes of population size over multiple time series to overcome the high variation masking the demographic Allee effect signal.

We predicted that individual population time series would show support for different population growth dynamics as a function of their variation. More specifically, we predicted that time series with a demographic Allee effect would rarely exhibit it because the high variation required for the population to reach the small size where the demographic Allee effect acts will mask it. Rather, we predicted that negative density feedback would dominate in low variation time series, switching to random walk as their variation increases (Figure 4.1). Our findings supported our predictions. Low variation time series showed highest empirical support for the negative density feedback model, switching to the random walk model as time series variation increased (Figure 4.2). Furthermore, this relationship was also evident in the number of top-ranked negative density feedback and random walk models (Figure 4.2). We are not the first to observe such a

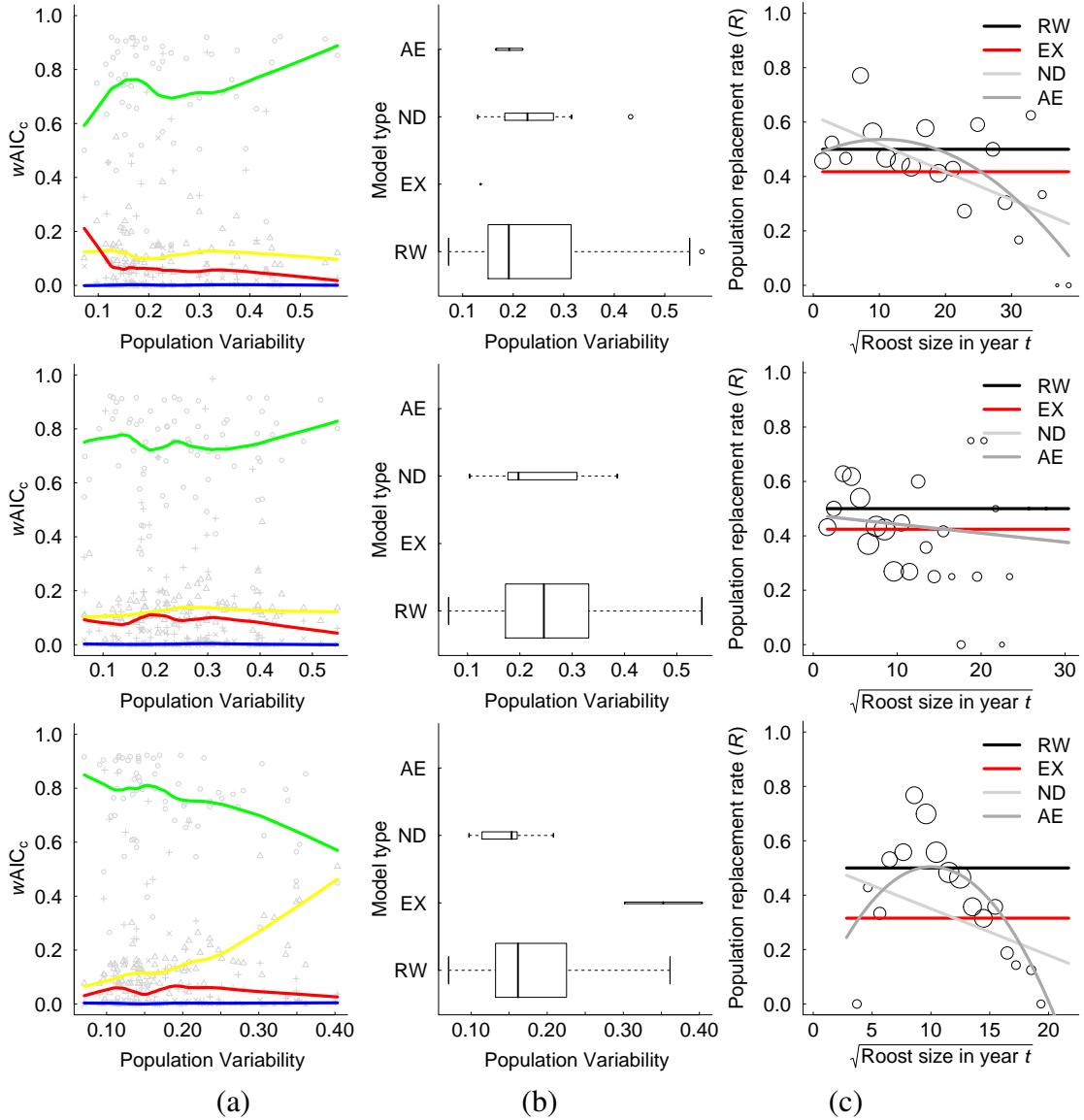


Figure 4.3: (a) Empirical support ( $w\text{AIC}_c$ ) for each model fitted to single time series (TS) as a function of TS variation, (b) the number of single TS in which each model was top-ranked as a function of TS variation (where bar width is proportional to the number of top-ranked models), and (c) each model fitted to multiple combined TS. The top two rows are for soprano and common pipistrelle datasets, respectively. The third row is a dataset of TS simulated from Equation 4.1 to mimic the NBMP datasets.

relationship. Hanski (1990) speculated that, assuming the existence of a stable equilibrium point, a population time series exhibiting strong regulation would show less variation than a time series exhibiting weaker regulation. On the other hand, the negative density feedback model formulation we used here is restricted to detecting direct linear negative density feedback and will fail to detect delayed or non-linear negative density feedback (Turchin 2003).

Empirical support for the demographic Allee effect model was consistently low and unrelated to time series variation (Figure 4.2). Gregory et al. (2010) used a similar model set to examine the support for demographic Allee effects in 1198 real individual population time series. They showed that empirical support for demographic Allee effects increased with decreasing time series variation. Their time series were, however, of varying lengths and their variation was measured using the coefficient of variation (Gregory et al. 2010). Here, we used Population Variability to measure time series variation because it is less biased by time series length and non-Gaussian behaviours (Heath 2006). Shorter time series tend to be less variable as measured by the coefficient of variation simply because they are shorter (Vucetich et al. 2000). Here, we controlled for time series length by keeping it constant and found no relationship between time series variation and empirical support for demographic Allee effects. Our finding suggests that the increasing empirical support for demographic Allee effects with decreasing time series variation observed by Gregory et al. (2010) might be an artefact of time series length. We predict that repeating their analysis measuring time series variation using Population Variability will cause this spurious trend to disappear. Indeed, we found that the highest incidence of top-ranked demographic Allee effect models was among high variation time series (Figure 4.2).

Demographic Allee effects are characterised by an unstable threshold  $A$  and so should be observed in time series declining towards or increasing away from  $A$  (e.g., declining due to habitat loss or increasing due to translocation; Sæther et al. 1996). To examine this possibility, we included the exponential growth model in our model set that fits a constant trend in population growth, whether increasing or decreasing (Brook and Bradshaw 2006). We found that empirical support for this model increased with increasing time series variation (Figure 4.2), and the time series with highest variation had top-ranked exponential growth models (Figure 4.2). This relationship has been the subject of several studies that generally confirm that time series exhibiting deterministic trends have higher variation (e.g., Lande et al. 2003). Recalculating the empirical support excluding the exponential growth model caused only minor changes in the empirical support and number of top-ranked demographic Allee effect models (Table 4.2). This suggests that detection of demographic Allee effects is not constrained to time series trending towards or away from  $A$ . When searching for demographic Allee effects, early recommendations advised disregarding time series that did not include time series observations less than 10% (Fowler and Baker 1991) or 15% (Sæther et al. 1996) of the maximum time series observation. Such recommendations suggest that demographic Allee effects are characterised by trends or sudden changes in population size. Our results, however, suggest that these recommendations are too conservative and might result in underestimating or failing to detect a demographic Allee effect.

Overall, our findings suggest that detection of demographic Allee effects will be particularly challenging in individual time series because the signal will be masked by the high variation required to ensure the population reached the small sizes where demographic Allee effects act. The failure to detect a demographic Allee effect in a highly variable population might result in its unforeseen extinction, particularly as demographic stochasticity increases as populations decline to extinction (Fagan and Holmes 2006). To better detect demographic Allee effects in high variation time series, we developed a procedure based on combining multiple time series (Tobin et al. 2007) and tested it on three highly variable time series datasets: the UK soprano

and common pipistrelle roost count surveys from the Bat Conservation Trust's National Bat Monitoring Programme (NBMP). Further, we applied this statistical procedure to a dataset of time series generated from an demographic Allee effect model to mimic the NBMP datasets. We showed that fitting models to individual time series resulted in almost complete empirical support for the random walk model in all datasets. When using the multiple time series statistical procedure, however, the demographic Allee effect model was the top-ranked model in the soprano and NBMP mimic datasets (Table 4.1).

Using the statistical procedure we present here, we were able to overcome the problems of high variation in population time series and 'refind' the generating demographic Allee effect that proved elusive in individual time series analyses. But at what cost? Tobin et al. (2007) developed their method of combining multiple time series using tens of thousands of moth traps. One of the main reasons we chose the NBMP datasets to illustrate our procedure was their size: we managed to extract 82 and 63 time series of length  $n \geq 7$  from the NBMP common and soprano pipistrelle datasets, respectively. So will the high data requirement of this procedure render it inaccessible? We do not think so. One of the principle advantages of this procedure is its capacity to incorporate very short time series, i.e., any time series with population size in year  $t > 0$  and at least two sequential observations can be incorporated. Throughout the analyses presented in this study, we used only time series  $n \geq 7$  to ensure a valid comparison of individual and multiple time series analyses. This constraint resulted in dropping over 20 time series from both NBMP datasets that the statistical procedure could have otherwise accommodated. Compare this to Myers et al. (1995) who regarded 102 of 128 (or 80%) of their long (15+ years) time series unsuitable for model-fitting analyses to detect depensation. It seems clear to us that through its capacity to accommodate short and highly variable time series, this procedure has an important advantage over conventional individual time series analyses, particularly when seeking to detect demographic Allee effects that are likely to occur in short, extinction-prone time series (Vucetich et al. 2000).

Our statistical procedure is highly extensible and might be useful to detect other population growth dynamics, perhaps in individual long time series or in metapopulations. While reducing the quantitative information in a time series to a string of qualitative changes might appear wasteful, doing so circumvents many of the problems believed to complicate detection of population growth dynamics. For example, measurement error can produce a spurious negative relationship between population size and population growth rate (Freckleton et al. 2006), and such measurement error might be systematically different depending on the size of the censused population (Holmes and Fagan 2002). On the other hand, the existence of a deterministic trend ought to be correctly identified using this method. For example, the common pipistrelle is believed to be declining in the UK (Bat Conservation Trust 2009), a trend that our procedure identified using only a subset of the entire dataset (Figure 4.3). Furthermore, we see no reason why this method could not be used for long individual time series. The time series need only contain sufficient unique population observations to create 7 data bins each containing  $> 1$  observations to satisfy the minimum model-fitting requirements (Brook and Bradshaw 2006). Similarly, the qualitative nature of this procedure means that it could accommodate time series from disparate metapopulation data provided that metapopulation dynamics are not due to completely unrelated drivers. For example, Hanski et al. (1991) showed how different predators drove 3- and 5-year rodent prey population cycles in southern Fennoscandia and northern Lapland, respectively. On the other hand, the loss of information in converting a quantitative to a qualitative measure means that this method might not characterise the strength of a population dynamic. Rather, it will be limited to detecting population growth dynamics (relative to others).

## References

- Barratt, E., R. Deaville, T. Burland, M. Bruford, G. Jones, P. Racey, and R. Wayne. 1997. DNA answers the call of pipistrelle bat species. *Nature* **387**:138.
- Barrowman, N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecological Applications* **13**:784–793.
- Bat Conservation Trust, 2009. the National Bat Monitoring Programme - Annual Report 2008. Technical report, Bat Conservation Trust . URL [http://www.bats.org.uk/pages/nbmp\\_reports.html](http://www.bats.org.uk/pages/nbmp_reports.html).
- Berryman, A. A. 2003. On principles, laws and theory in population ecology. *Oikos* **103**:695–701.
- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**:1445 – 1451.
- Burland, T. M., and J. Worthington Wilmer. 2001. Seeing in the dark: molecular approaches to the study of bat populations. *Biological Reviews* **76**:389–409.
- Corbet, G. B., and S. Harris. 1991. the Handbook of British Mammals. Blackwell.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**:405–410.
- Davidson-Watts, I., and G. Jones. 2006. Differences in foraging behaviour between *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825). *Journal of Zoology* **268**:55–62.
- Dennis, B., W. P. Kemp, and M. L. Taper. 1998. Joint density dependence. *Ecology* **79**:426–441.
- Fagan, W. F., and E. E. Holmes. 2006. Quantifying the extinction vortex. *Ecology Letters* **9**:51 – 60.
- Fowler, C., and J. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. *Reports to the International Whaling Commission* **41**:545–554.
- Fox, D., and J. Ridsdill-Smith. 1995. Tests for density dependence revisited. *Oecologia* **103**:435–443.
- Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters* **11**:756–770.
- Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. Census error and the detection of density dependence. *Journal of Animal Ecology* **75**:837–851.
- Gascoigne, J., L. Berec, S. Gregory, and F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* **51**:355–372.

- Gerber, L. R., and R. Hilborn. 2001. Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Review* **31**:131–150.
- Gregory, S., C. Bradshaw, B. Brook, and F. Courchamp. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology* –:–.
- Gregory, S. D., and F. Courchamp. 2010. Safety in numbers: establishing a link between predator-driven Allee effects and population extinction. *Journal of Animal Ecology* –:–.
- Hanski, I. 1990. Density Dependence, Regulation and Variability in Animal Populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **330**:141–150.
- Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* **60**:353–367.
- Heath, J. P. 2006. Quantifying temporal variability in population abundances. *Oikos* **115**:573–581.
- Holmes, E. E., and W. F. Fagan. 2002. Validating population viability analysis for corrupted data sets. *Ecology* **83**:2379–2385.
- Holyoak, M., and S. R. Baillie. 1996. Factors influencing detection of density dependence in British birds: II. Longevity and population variability. *Oecologia* **108**:54–63.
- Izenman, A. 1991. Recent developments in nonparametric density estimation. *Journal of the American Statistical Association* **86**:205–224.
- Johnson, D. M., A. M. Liebhold, P. C. Tobin, and O. N. Bjornstad. 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature* **444**:361–363.
- Kramer, A., B. Dennis, A. Liebhold, and J. Drake. 2009. the evidence for Allee effects. *Population Ecology* **51**:341–354.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**:911–927.
- Lande, R., S. Engen, and B. E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.
- Langton, S., N. Aebischer, and P. Robertson. 2002. The estimation of density dependence using census data from several sites. *Oecologia* **133**:466–473.
- Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierachic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1976–1984.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenburg. 1995. Population-dynamics of exploited fish stocks at low population-levels. *Science* **269**:1106–1108.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. Technical report, , Vienna, Austria.

- Sæther, B. E., T. H. Ringsby, and E. Roskaft. 1996. Life history variation, population processes and priorities in species conservation: Towards a reunion of research paradigms. *Oikos* **77**:217–226.
- Shelton, P. A., and B. P. Healey. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1521–1524.
- Speakman, J. R., R. E. Stone, and J. L. Kerslake. 1995. Temporal patterns in the emergence behaviour of pipistrelle bats, *Pipistrellus pipistrellus*, from maternity colonies are consistent with an anti-predator response. *Animal Behaviour* **50**:1147–1156.
- Spellucci, P. A. 1998. A SQP method for general nonlinear programs using only equality constrained subproblems. *Mathematical Programming* **82**:413–448.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185–190.
- Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjornstad, and A. M. Liebhold. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecology Letters* **10**:36–43.
- Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton Univ. Press.
- Vucetich, J. A., T. A. Waite, L. Qvarnemark, and S. Ibarguen. 2000. Population variability and extinction risk. *Conservation Biology* **14**:1704–1714.
- Walsh, A. L., C. Catto, T. Hutson, P. Racey, P. Richardson, and S. Langton. 2002. The UK's National Bat Monitoring Programme: Final Report 2001. DEFRA publications.
- Walters, C., and J. F. Kitchell. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:39–50.
- Wang, M. H., and M. Kot. 2001. Speeds of invasion in a model with strong or weak Allee effects. *Mathematical Biosciences* **171**:83–97.

## Appendices

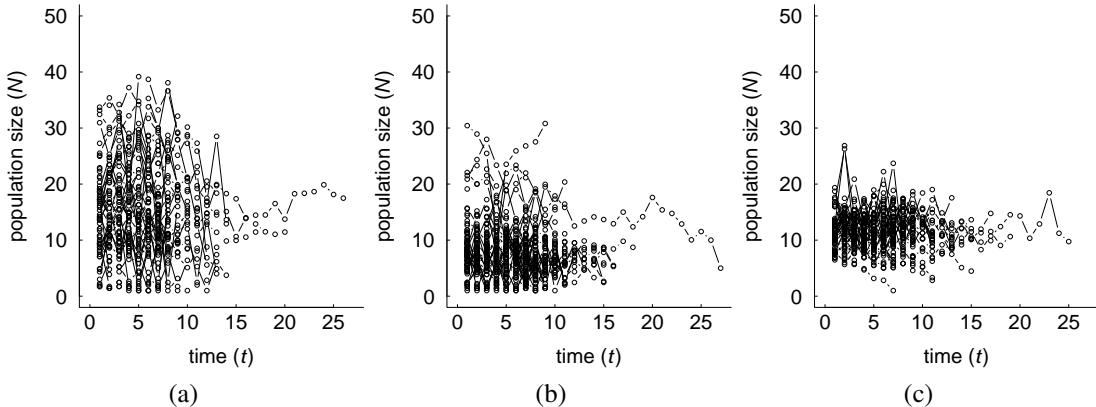


Figure 4.4: Plots showing time series (TS) lengths and amplitudes for (a) soprano pipistrelle, (b) common pipistrelle, and (c) TS simulated from a demographic Allee effect model parameterised to mimic (a) and (b).

Table 4.2: Empirical support ( $wAIC_c$ ) for population growth model sets including and excluding exponential growth (EX) measured from single time series.

|              | RW    | EX    | RL    | RA    |
|--------------|-------|-------|-------|-------|
| Including EX | 0.318 | 0.109 | 0.443 | 0.131 |
| Excluding EX | 0.383 |       | 0.485 | 0.132 |

Model abbreviations are: RW, random walk; EX, exponential growth; RL, negative density feedback; RA, negative density feedback with a demographic Allee effect.

```
### #####
### Population Variability
### #####
### Ref: Heath, J. P., 2006. Quantifying temporal variability in
### population abundances. Oikos 115:573-581.

### This function, PV, is an implementation of PV by Heath (2006) for use
### in R (see www.r-project.org). It has not been tested extensively.
### PV expects a vector of population observations, here denoted P.
### Zero values may be included (although strings of zero values
### cannot as they represent population extirpation) and all time
### series observations, denoted Pi, must be positive. This
### implementation of PV has two options which are, by default,
### withheld:

### <-- Begin function --> ###

PV<-function(P,
  ### (1) comparison.matrix: calling this option will create and
  ### print a design matrix illustrating how all Pi were compared.

  comparison.matrix=FALSE,
  ### (2) loo.pv: calling this option will calculate a measure
  ### of the effect of excluding each Pi, ie., leave-one-out or loo.
  ### This option calculates and prints a leave-one-out statistic

  loo.pv=FALSE,
  ### Additional arguments that can be passed to PV.

  ...){

  ### PV depends on function 'permutations' from package 'gtools'.

  require(gtools)

  ### Preamble variables.

  C.m<-Gd<- 'not requested'
  if(length(P)>45) options(expressions=1e5)

  ### Calculate the absolute differences between all Pi, the
  ### comparison matrix and PV. These calculations are handled
  ### quickly and efficiently using 'permutations' from package
```

```

#### 'gtools' and 'apply' from 'base'.

y<-length(P)
C<-t(permuations(y,2,P, set=FALSE, repeats=FALSE))
if(comparison.matrix)
  Cm<-t(permuations(y,2, set=FALSE, repeats=FALSE))
Num<-abs(apply(C,2,diff))
Denom<-apply(C,2,max)
Diff<-Num/Denom
PV<-mean(Diff)

### Calculate leave-one-out 'pv' statistic. The calculation proceeds
### by defining a function 'G.fn' which selectively removes absolute
### difference values associated with a specific Pi. The 'G.fn'
### function is then passed to 'sapply' from 'base' to calculate the
### leave-one-out statistic for each Pi.

if(loo.pv){
  G.fn<-function(P,Pi){
    G.m<-matrix(Diff,ncol=y)
    I.m<-matrix(rep(1,(y*(y-1))),ncol=y)
    if(Pi==1){
      I.m[,1]<-I.m[1,]<-NA
    }
    if(Pi==y){
      I.m[,y]<-I.m[(y-1),]<-NA
    }
    if(!Pi%in%c(1,y)){
      I.m[(Pi-1),c(1:Pi)]<-I.m[Pi,c(Pi:y)]<-I.m[,Pi]<-NA
    }
    return(as.numeric(na.omit(as.vector(G.m*I.m))))
  }
  Gd<-colMeans(sapply(1:y,function(Pi)
    G.fn(P,Pi)))
}

### Finally, the results are returned with 'not requested'
### substituted for any options not chosen.

return(list('data'=P,
           'diffs'=Diff,
           'comparison.matrix'=C.m,
           'loo.pv'=Gd,
           'pv'=PV))
}

### <-- End function --> ####

```

# Chapter 5

## Examining evidence for demographic Allee effects in nine UK bat species

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Submitted as: **Gregory, S., K. Haysom, P. Briggs, and F. Courchamp** (*submitted*) Examining evidence for demographic Allee effects in nine UK bat species. *Journal of Applied Ecology*

## Abstract

1. Social species should be susceptible to demographic Allee effects when their populations become too small for social behaviours to be efficient. Using the extensive datasets of the UKs National Bat Monitoring Programme, we assessed this hypothesis by examining the dynamics of nine bat species at summer maternity roosts.
2. For each species, we smoothed roost counts for the influence of weather and annual trends using GAM before measuring the empirical support for three major population dynamics in their roost dynamics. The models were: (i) no growth, (ii) negative density feedback, and (iii) negative density feedback with an Allee effect. We repeated our analyses using roost counts smoothed for weather effects only and unsmoothed roost counts.
3. Four of the nine species (44%) analysed here showed high support for an Allee effect a very high incidence compared to the 1.1% recently emerging from an analysis of 1198 taxonomically diverse species. Soprano pipistrelle, Natterers and the greater and lesser horseshoe bats all revealed higher support for the Allee model over the alternatives, and for the soprano pipistrelle and greater horseshoe bats this result was robust to smoothing of roost counts for an annual trend and weather effects, respectively. The lesser horseshoe bat revealed higher support for an Allee effect only when using original roost counts.
4. Roost counts of all species revealed predictable trends with temperature and precipitation when annual trends were statistically removed; otherwise these trends were counter-intuitive and probably emerged spuriously due to unmeasured factors.
5. Synthesis and applications. Our results support the notion that social species are more susceptible to demographic Allee effects. At an individual species level, our findings necessitate the careful monitoring of bat species affect by Allee effects, particularly at declining roosts that will require early conservation action to prevent their abandonment. Globally, our results suggest that many other social bat - and other - species might be susceptible to demographic Allee effects, and an elevated risk of population extirpation.

**Keywords:** Allee effect, bats, colony, brown long-eared, Daubentons, greater horseshoe, lesser horseshoe, Natterers, noctule, pipistrelle, serotine, population dynamics, roost

## 5.1 Introduction

Over 60 years have passed since W.C. Allee first described the Allee effect as proto-cooperation between individuals to increase individual survival (Allee et al. 1949). At the time, he touted cooperation as the principle factor in the origin of sociality in animals (and humans) and supported his views with a range of pioneering experiments (Courchamp et al. 2008). Today, our understanding of Allee effects is still firmly rooted in the concept of cooperation (Stephens and Sutherland 1999), although over time its definition has changed. Stephens and Sutherland (1999) defined two types of Allee effects: component and demographic. A component Allee effect describes a positive relationship between individual fitness and population size, much the same as Allees original proposal. Experimental and observational evidence of component Allee effects is widespread across animals ranging from invasive gypsy moths *Lymantria dispar* (Johnson et al. 2006) to African wild dogs *Lycaon pictus* (Courchamp et al. 2002). A demographic Allee effect describes a positive relationship between collective individual fitness (usually *per capita* population growth rate) and population size, and - in contrast to component Allee effects - is rarely

observed (Gregory et al. 2010). This discrepancy is untoward given the numerous social animals exhibiting component Allee effects. For example, suricates *Suricata suricatta* cooperate to feed juveniles and detect predators so larger colonies have higher juvenile and adult survival (Clutton-Brock et al. 1999). Indeed, several other cooperative mammal species including Damaland mole-rats *Cryptomys damarensis* (Jarvis et al. 1998), Alpine marmots *Marmota marmota* (Stephens et al. 2002), and desert bighorn sheep *Ovis canadensis* (Mooring et al. 2004) exhibit component Allee effects.

One explanation for the scarce evidence of demographic Allee effects might be that many logical candidate species have not been studied in this context (Courchamp et al. 2008, but see Gascoigne et al. 2009 for alternative explanations). The order Chiroptera is outstanding among mammalian orders because of its widespread sociality (Kerth 2008), making bats logical candidates for Allee effects studies. Some of the social behaviours observed in bats appear to be mutualistic. For example, bats of the suborder Microchiroptera, including the Indiana bat *Myotis sodalis*, cluster when hibernating to minimise energy spent on thermoregulation and water loss (Boyles et al. 2008). Female microchiropteran bats often aggregate in maternity roosts to stabilise pre- and post-parturition roost temperature, which is thought to be important for juvenile development and survival (Dietz and Kalko 2006). Bats in some maternity roosts might number millions, reducing the per capita threat of predation on adults (Petrzelkova and Zukal 2003) and pups (McCracken 1984). Other social behaviours observed in bats appear to be altruistic. For example, allogrooming observed among roost sharing individuals may reduce parasite loads (ter Hofstede and Fenton 2005) or reinforce social bonds (Kerth et al. 2003). Captive groups of the megachiropteran short-tailed fruit bat *Carollia perspicillata* exchange information about food (Ratcliffe and ter Hofstede 2005). Bats in maternity roosts may participate in baby-sitting (Akbar et al. 2006) and even communal juvenile nursing (Wilkinson 1992). Perhaps most famously, vampire bats *Desmodus rotundus* will regurgitate a blood meal for starving conspecifics, whether or not they are kin (Wilkinson 1990).

The existence of such a diverse range of social behaviours in bats suggests they will be vulnerable to a component Allee effect if individuals become too few to cooperate effectively. Few studies have, however, explicitly examined this possibility, and their results are contrasting. Tuttle (1976) showed that pre-flight juvenile cave-dwelling gray bats *Myotis grisescens* raised in larger roosts grew faster than those in smaller roosts, which he attributed to the communal warming effect in larger roosts. A similar situation was recently observed in juvenile Brazilian free-tailed bats *Tadarida brasiliensis*, although the comparison was based on only two roosts (Allen et al. 2009). These findings are suggestive of a component Allee effect but alternative explanations abound. Climate, proximity to foraging grounds, food availability, nutritional condition of the mother, and parasite loads, are just some of the factors which are believed to act independently or synergistically to affect juvenile growth and survival (Kunz and Parsons 2009). In contrast to the mechanisms underpinned by cooperation, most of these alternative mechanisms are driven by intra-specific competition. For example, juvenile survival of long-tailed New Zealand bats *Chalinolobus tuberculatus* was higher in smaller roosts where reproductive female and juvenile bats had higher body condition (O'Donnell 2002a). Numbers of juvenile greater mouse-eared bats *Myotis myotis* were higher in smaller roosts, although, in contrast to Tuttles findings, roost temperature was unrelated to roost size (Zahn 1999).

Whether a component Allee effect will translate to a demographic Allee effect will depend upon the relative strengths of opposing cooperative and competitive mechanisms (Stephens et al. 1999). For example, adult survival of Californian Channel Island foxes *Urocyon littoralis* increased when elevated predation risk was shared among more individuals a component Allee

effect. This component Allee effect was, however, largely offset by increased pup production in smaller populations, presumably due to decreased intra-specific competition (Angulo et al. 2007). In contrast to other mammalian species like the Island fox, however, the breakdown of sociality in bats might have an overwhelmingly negative effect at small population sizes (Stephens and Sutherland 1999), particularly if the species was prone to the cumulative influence of multiple component Allee effects (Berec et al. 2007). If this were true, bat populations would be predisposed to demographic Allee effects. This knowledge would be valuable for a number of reasons. First, it would have intrinsic value as empirical support for demographic Allee effects in social animals, which is remarkably scarce (Gregory et al. 2010). Second, it would be paramount for the effective conservation of bat species believed to have suffered large recent declines that might be susceptible to demographic Allee effects and subsequent population collapse (Stephens and Sutherland 1999). Third, it would allow effective management of local bat populations that provide ecological services, like pollination and seed dispersal, and are key predators of economically important insect species (Hutson et al. 2001).

Here, we use summer maternity roost emergence count data from the Bat Conservation Trusts National Bat Monitoring Programme to assess the empirical support for demographic Allee effects in six United Kingdom microchiropteran bat species. We begin by describing the methods used to collect this dataset and how they minimise common sources of error. We then examine changes in roost counts for empirical support for demographic Allee effects and investigate how our results are affected by neglecting factors thought to influence bat counts. We hypothesise that demographic Allee effects will affect a relatively high proportion of these UK bat species.

## 5.2 Methods

### 5.2.1 Bat roost counts; methods, errors and biases

The National Bat Monitoring Programme (NBMP) was established in 1996 by the Bat Conservation Trust (BCT). It was commissioned as a five-year project to develop and test methods to monitor annual population trends of 7 of the UKs 16 breeding bat species. Statistically defensible trends are now delivered for 11 species, with new techniques being developed for species that were previously difficult to monitor on a wide scale. Three core survey techniques are used: (1) summer maternity roost emergence counts, (2) winter hibernacula counts, and (3) summer foraging field surveys (Walsh et al. 2002). The surveys are carried out across the UK by a network of volunteer surveyors coordinated by BCT staff. Compatible datasets are incorporated into the NBMP from other bat monitoring schemes, e.g., the Robert Stebbings Consultancys National Bat Colony Survey and the Countryside Council for Wales lesser horseshoe colony count, which date back to 1977 and 1993 respectively. We use summer maternity roost emergence counts (hereafter roost counts) in this work for reasons outlined below.

Seven bat species currently targeted for NBMP roost counts are: serotine bat *Eptesicus serotinus*, Natterers bat *Myotis nattereri*, common pipistrelle *Pipistrellus pipistrellus*, soprano pipistrelle *Pipistrellus pygmaeus*, brown long-eared bat *Plecotus auritus*, greater horseshoe bat *Rhinolophus ferrumequinum* and lesser horseshoe bat *Rhinolophus hipposideros*. These species are amenable to roost counts because they form maternity roosts, or single-sex aggregations of breeding female bats, in houses and other man-made structures (Walsh et al. 2002). A number of Daubentons *Myotis daubentonii* and noctule *Nyctalus noctula* maternity roosts in man-made structures are also included in the dataset (due largely to the incorporation of the National Bat Colony Survey data that included roost counts for these species), despite their usual propensity

to roost in trees. This tendency for breeding bats to aggregate in single-sex roosts, taken together with their habitual behaviours (Burland and Worthington Wilmer 2001) and their tendency to emergence from roosts at predictable exits and times (e.g., Speakman et al. 1995, should provide accurate estimates of roost sizes by minimising measurement errors.

To promote complete and consistent data collection, roost count volunteers (hereafter surveyors) receive a survey pack including survey instructions and a standardised proforma with fields for the following data: surveyor name and address, bat species, roost type and location, details of any structural changes to the roost, survey date, bat count, count start time and duration, and, importantly, whether a survey was conducted but no bats were present (see online data forms at <http://www.bats.org.uk/pages/nbmp.html>). In addition, surveyors are asked to choose among predefined categories to describe the prevailing weather and the reason for terminating the count. These metadata permit the NBMP to omit counts which were stopped due to confusing bat behaviour or deteriorating weather conditions, and demonstrate how most roosts are monitored by the same individuals, so minimising the influence of observer error (error due to different surveyors abilities to count bats, Sauer et al. 1994; Table 5.3). Furthermore, the proforma field for recording a zero count, and a freepost service for completed proformae, reduce the probability of missing values in the dataset, even when no bats were observed.

Participation in the NBMP has been considerable (over 1000 surveyors made counts in 2008; Bat Conservation Trust 2009) and two annual pre-parturition roost counts have been made at over 2000 maternity roosts nationwide over 13 years (Figure 5.1). For the analyses that follow, we used only the maximum of these two annual pre-parturition roost counts because it represents the minimum number of bats present in the roost in that year.

### 5.2.2 Roost dynamics and demographic Allee effects

A demographic Allee effect is characterised by an unstable threshold population size (the Allee threshold,  $A$ ) about which *per capita* population growth rate is reduced (Courchamp et al. 1999). Since it is unstable, observations of populations near the Allee threshold will be rare, rendering many datasets insufficient for detecting a demographic Allee effect (Gregory et al. 2010). One conceivable solution to this problem is to examine multiple populations as was recently done for Gypsy moths invading North America (Tobin et al. 2007).

We used smoothed roost counts (see below) to examine annual roost size changes for empirical support for demographic Allee effects using the method developed by Tobin et al. (2007). For each roost we calculated the proportion of roost counts increasing in year  $t + 1$  (hereafter “roost replacement rate”) by dividing the count at roost  $r$  in year  $t + 1$  by the count in year  $t$ . For example, a roost monitored for five consecutive years from 2000 would provide four roost replacement rate values 2000/2001, …, 2004/2005 corresponding to roost counts in 2000, …, 2004. We omitted any roost count pairs for which the count in year  $t$  was 0.

We modelled roost replacement rate as a function of roost count using three models representing (1) random walk (RW), which assumes the roost replacement rate is 50% and all deviance from this is due to random fluctuations in roost size, (2) negative density feedback (ND), which assumes a linear decline in the roost replacement rate as the roost size increases, and (3) negative density feedback with an Allee effect (AE), which assumes roost replacement rate decreases both as the population increases but also as the population declines towards  $A$ . Another major population dynamic model is exponential or Mathusian growth that assumes the population is growing (or declining) at a constant rate. We did not fit this model because we chose to identify and smooth annual trends across roosts before calculating the roost replacement rate (see below). This method better accounted for trends at individual roosts and was consistent with

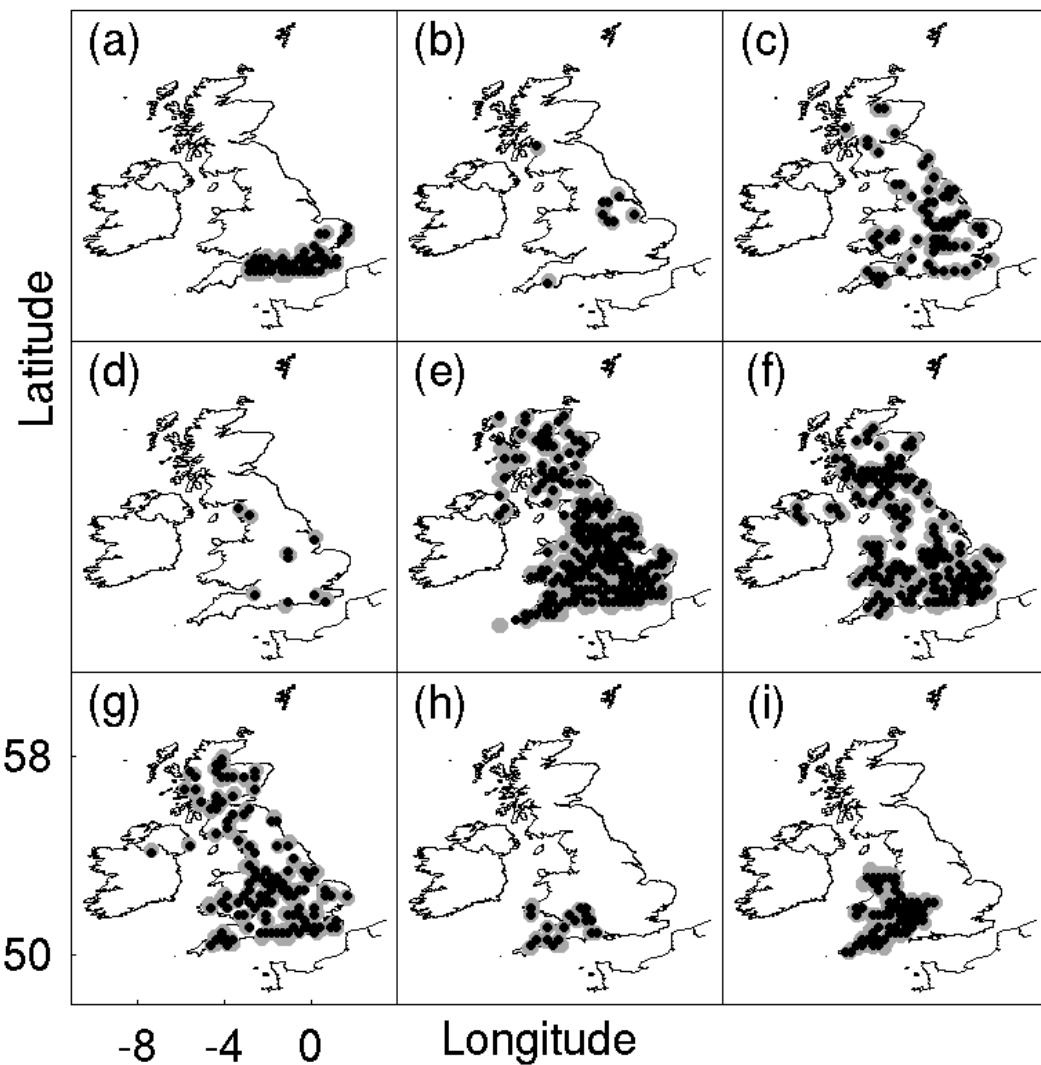


Figure 5.1: Panels (a) to (i) show the distributions of maternity roosts (gray dots) used in these analyses. Bat species are (a) serotine, (b) Daubentons, (c) Natterers, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, (g) brown long-eared, (h) greater horseshoe, and (i) lesser horseshoe. E-OBS grid cells (black dots) used for daily temperature and precipitation measures are overlaid on maternity roost locations.

the methods used by the NBMP but invalidated the use of the exponential growth model. Our decision had a negligible affect our findings (Table 5.4). We square root transformed roost counts to achieve normality and placed them in bins of sizes determined using the Freedman-Diaconis method, preferred for larger sample sizes (Scott 1992). We used the residual error from each model to calculate its Akaike information criterion corrected for small samples ( $AIC_C$ ; Burnham and Anderson 2002). We compared models using their difference in  $AIC_C$  from the top-ranked model ( $\Delta AIC$ ) and calculated their empirical support as an  $AIC_C$  weight ( $wAIC_C$ ) (Burnham and Anderson 2002).

### 5.2.3 Examining prevailing weather and annual trend influences

Despite controlling for various sources of error, the NBMP roost count survey protocol cannot control for (1) prevailing weather at the time of survey, and (2) a bat behaviour variously called “roost philopatry”, “roost fidelity” or conversely “roost lability” that describes the tendency for some bat species to remain faithful to or move regularly between different roosts (Lewis 1995).

Pervailing weather can directly (Scanlon and Petit 2008b), or indirectly through its effect on insect abundance (Scanlon and Petit 2008a), affect numbers of emerging bats, and should be included in analyses of animal counts (Bas et al. 2008). For this reason, the NBMP discourages roost surveys during unfavourable weather, i.e., heavy rain, thick fog or strong winds and requests that surveyors record temperature ( $^{\circ}C$ ) and categorical values for rainfall, cloud cover and wind speed on the NBMP proforma. While routinely collected as part of the NBMP, these data are sometimes missing for earlier surveys. Consequently and for consistency, we used roost locations and count dates to extract 0.25° regular longitude/latitude gridded temperature and precipitation data from the E-OBS datasets developed by the EU-FP6 project ENSEMBLES (Figure 5.1; Haylock et al. 2008). No similar datasets were available for cloud cover and wind speed, which were dropped from further analyses.

Changes in the size of individual roosts might reflect a change in national abundance. They might also, however, be influenced by the movement of bats between roosts (Sauer 2003). Clearly, the latter poses a problem to using roost counts to study roost dynamics that assumes either the fate of all monitored individuals is known, or the units of individuals are closed (i.e., bats show high roost philopatry and return to the same roost annually; Warren and Witter 2002). Since the relative effects of a change in national abundance and movements due to low roost philopatry could not be separated at the individual roost scale, we chose to characterise their combined effect as an annual trend across roosts derived from within roost changes. While this variable was intended to encapsulate density independent changes in roost sizes, due to say human activity or roost philopatry, it is possible it usurps variation due to density feedback changes, including that due to an Allee effect.

We statistically treated roost counts for the influences of prevailing weather and an annual trend. This was done via smoothing applied using Generalized Additive Models (GAM) implemented in the mgcv package (version 1.5-2; Wood 2004) in R (R Development Core Team 2008) and repeated for each species separately. The GAM was:

$$C_{it} = \alpha_i + \beta_t + s(T) + s(P) + \epsilon \quad (5.1)$$

where  $C$  is the count at roost  $r$  in year  $t$ ,  $\alpha$  is the site effect for roost  $r$  and  $\beta$  is the annual effect in year  $t$ .  $s(\bullet)$  is a smoothing function that estimates the functional form of the annual effect and the covariates (Temperature [T] and Precipitation [P]) from the data using cubic regression splines while conditioning on other covariates. Although we assumed a non-linear response of

bats to weather, we investigated this assumption explicitly by modelling the covariables as linear predictors. We examined the explanatory value of T and P by comparing fits omitting one or both (a null intercept model) using an approximation to AIC (Wood 2006) that corrects for over-parameterisation bias (Burnham and Anderson 2002). We repeated these analyses assuming a poisson, quasi-poisson or negative binomial error structure to investigate overdispersion and used a log link function.

Given the possible confounding effect of the annual trend on density feedback detection, we repeated our roost dynamic analyses using roost counts smoothed for prevailing weather and an annual trend (“GAM<sub>WA</sub>”), prevailing weather only (“GAM<sub>W</sub>”) and for unsmoothed roost counts (“Original”). Prevailing weather was considered in all GAM because of its known effects on activity of some bat species (e.g., Rydell 1989).

## 5.3 Results

### 5.3.1 NBMP roost count and E-OBS data summaries

A total of 1356 unique roosts for nine confirmed bat species were examined in this study. Of these, 61.6% were counted annually from the first to last year of their monitoring (including roosts counted once), while one and two annual counts were missed for 16.5 and 8.4% of roosts, respectively (see Figure 5.6). We removed all missing counts for the remaining analyses. Nevertheless, 3836 and 2670 roost counts were made for the common (e) and soprano pipistrelles (f), respectively (Figure 5.2). Fewest roost counts were made for Daubenton’s (b) and noctule (d) bats but these were monitored for relatively long periods (Figure 5.2).

The majority of roost counts were terminated because emergence activity had stopped (51.9%), and fewer than 15% of roost counts were terminated because of confusion, darkness or deteriorated weather (Figure 5.7). Many roost counts (34.4%) were, however, terminated for an unspecified reason, and were hereafter reclassified as terminated because emergence activity had stopped. We removed roost counts terminated because of confusion or deteriorated weather from further analyses. We retained counts terminated due to darkness because most counts, whether specified or not, would have been affected by light levels and retaining these counts maximised our sample sizes.

E-OBS temperature and precipitation data revealed good correspondence with the NBMP data (Figure 5.3). E-OBS temperature values (TE) explained 96.5% of the deviance in the NBMP temperature records (TN; linear model:  $TN = 0 + 0.970 \times TE$ ), and an E-OBS precipitation value of 17.7mm had a 50% probability of being classified in the wet NBMP rainfall category (PN; logistic model:  $p(PN) = 1/(1 + e^{-[-2.756 + 0.154 \times PE]})$ ).

### 5.3.2 Demographic Allee effects in smoothed roost counts

All GAM assuming a negative binomial error structure had substantially lower deviance than those assuming poisson or quasi-poisson errors (Table 5.5), suggesting roost counts were overdispersed. Consequently, negative binomial errors were assumed in all GAM analyses.

Pervailing weather or an annual trend influenced roost counts of eight of nine bat species (Figure 5.4 and Table 5.6). Temperature was retained in fits for five species, including Natterer’s bat (c), soprano pipistrelle (f) and greater horseshoe bat (h), and was associated with an asymptotic non-linear increase in roost counts for all species except the soprano pipistrelle (f), for which the trend decreased above c. 20°C (Figure 5.4). Precipitation, on the other hand, was retained

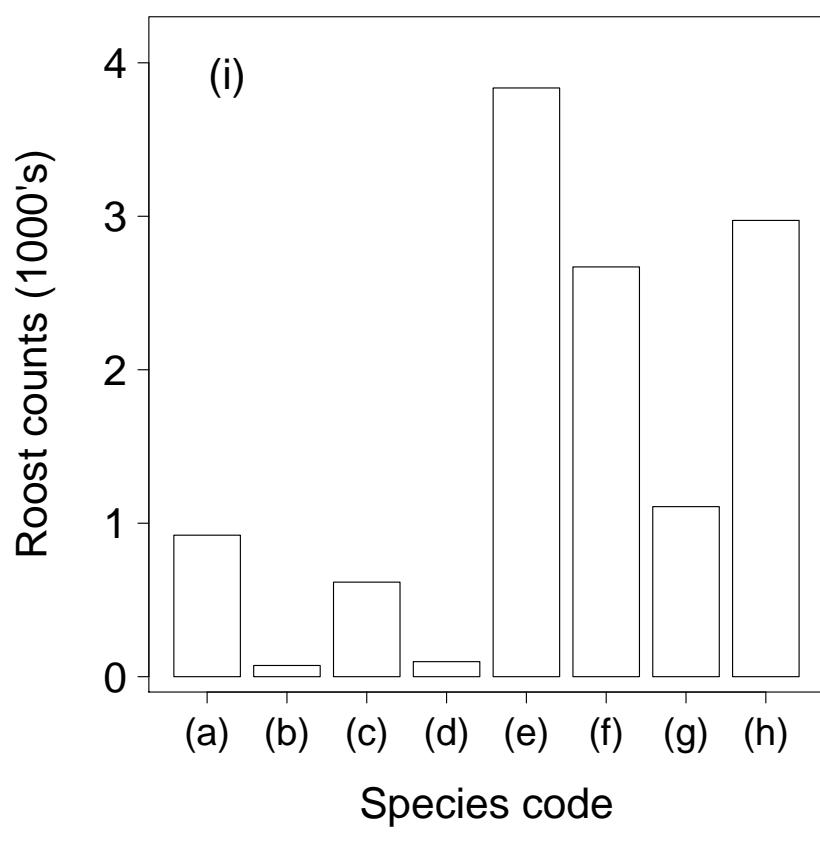
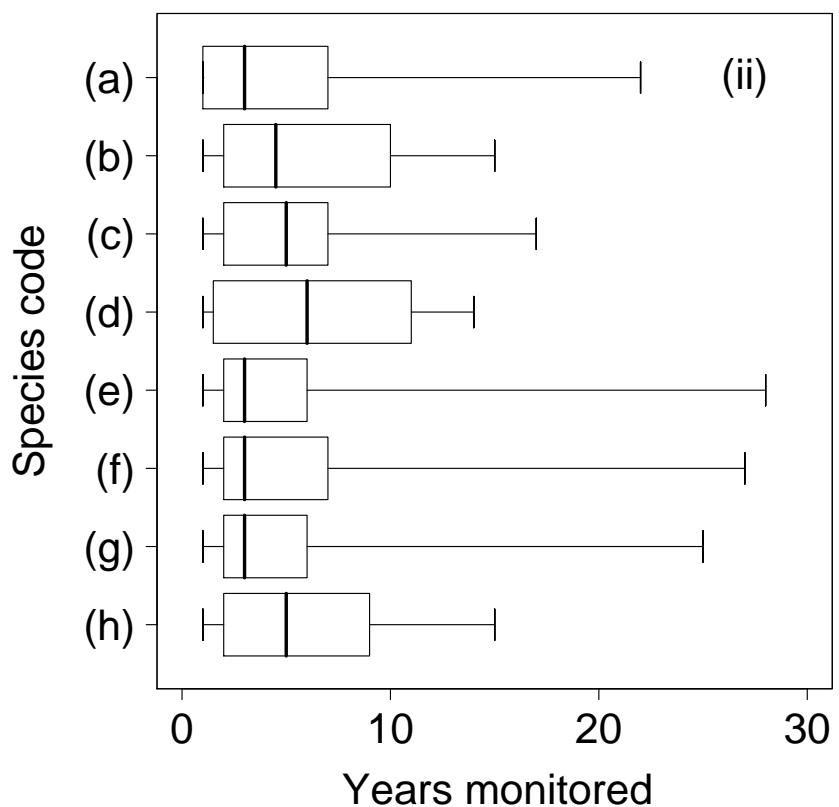


Figure 5.2: Summary plots showing (i) numbers of roost counts in the National Bat Monitoring Programme datasets for each bat species.



(b)

Figure 5.2: (ii) number of years each roost is monitored for each bat species. Bat species are (a) serotine, (b) Daubentons, (c) Natterers, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, (g) brown long-eared, (h) greater horseshoe, and (i) lesser horseshoe.

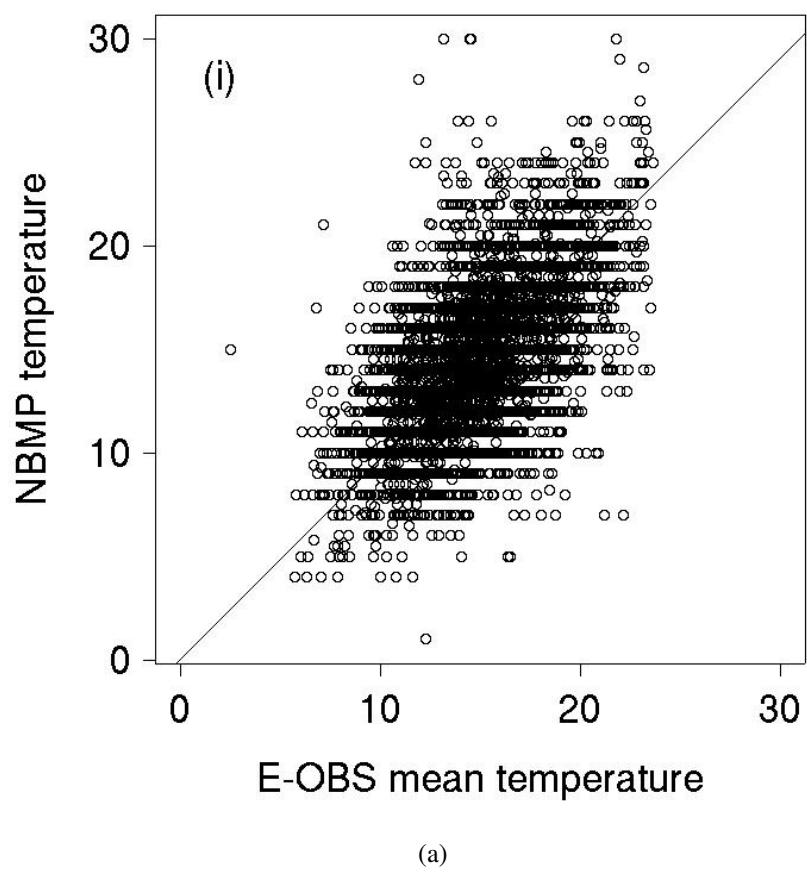


Figure 5.3: Plots showing the (i) linear relationship between the National Bat Monitoring Programme (NBMP) temperature records (TN) and E-OBS temperature values (TE; linear model:  $TN = 0 + 0.970 \times TE$ ).

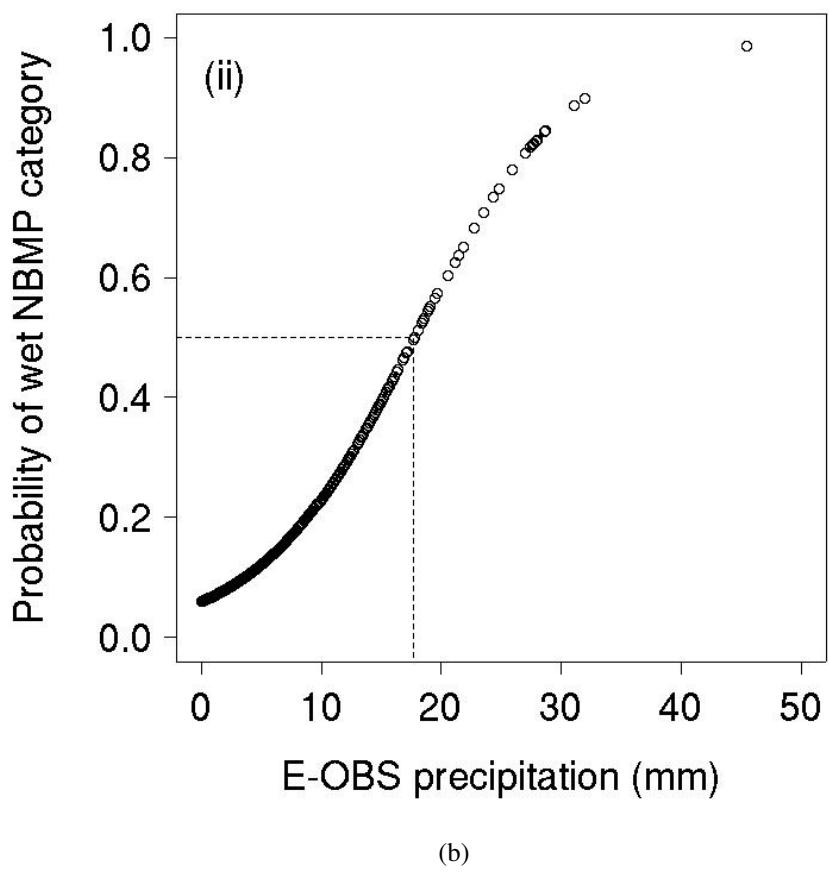


Figure 5.3: (ii) correspondence between collapsed NBMP rainfall records (PN) and E-OBS precipitation values (PE; logistic model:  $p(\text{PN}) = 1/(1 + e^{-[-2.756 + 0.154 \times \text{PE}]})$ ); dashed lines show the E-OBS precipitation value above which the model classified PN in the wet NBMP rain category).

only in the fit for noctule (d) and revealed a non-linear decreasing relationship to roost counts. The annual trend in roost counts was non-linear for most species, despite small net changes in roost counts over the periods monitored (Figure 5.4). Three clear exceptions were the common pipistrelle (e), which revealed a net decrease in roost counts over time, and the horseshoe bats (g and h), which revealed net increases (Figure 5.4). Brown long-eared bat (g) roost counts were unimproved by prevailing weather or annual trend and are discussed further below.

Modelling roost replacement rate calculated from smoothed roost counts revealed empirical support for a demographic Allee effect in Natterer's bat (c), soprano pipistrelle (f) and greater horseshoe (h) bats (Table 5.1, “GAM<sub>WA</sub>”; Figure 5.5). In each case the Allee effect model (AE) had the highest wAIC<sub>C</sub> value, followed by the negative density feedback (ND) model. None of these species showed any empirical support for random fluctuations in roost size described by the random walk model (RW). In contrast, Daubentons (b) and noctule (d) bats showed highest support for random fluctuations in roost size and very little support for a demographic Allee effect. Serotine (a), common pipistrelle (e) and lesser horseshoe (h) bats showed highest support for negative density feedback in roost replacement rate and limited support for a demographic Allee effect (Table 5.1, “GAM<sub>WA</sub>”; Figure 5.5).

### 5.3.3 Neglecting prevailing weather and annual trend

Repeating these analyses with roost counts smoothed for prevailing weather only (i.e., neglecting an annual trend) increased the quantitative support for a demographic Allee effect in the roost dynamics of Natterer's bat (c) and soprano pipistrelles (f) but caused its loss in the greater horseshoe bat (h) (Table 5.1, “GAM<sub>w</sub>”; Figure 5.9). Roost counts of these species showed similar temperature trends with and without smoothing for an annual trend. Greater horseshoe (h) bat roost counts, in addition, revealed a linear trend with precipitation (Figure 5.8). Daubentons bat (b) and common pipistrelle (e), on the other hand, revealed a qualitative change in model support from the random walk model to negative density feedback (Table 5.1, “GAM<sub>w</sub>”; Figure 5.9), and their roost counts changed from increasing to decreasing with increasing temperature (Figure 5.8). Results for the noctule (d) were unchanged and its roost counts varied non-linearly with increasing precipitation. Serotine (a) and lesser horseshoe (i) roost counts were unimproved by prevailing weather when an annual trend was neglected (Table 5.1, “GAM<sub>w</sub>”).

Results changed qualitatively for four species when neglecting the influence of prevailing weather and annual trends on species' roost counts (Table 5.1, compare “GAM<sub>WA</sub>” and “Original”). Lesser horseshoe bats (i) changed support to join greater horseshoe bats (h) in showing highest support for a demographic Allee effect (Table 5.1, “Original”; Figure 5.10). In contrast, Natterer's bat (c) and soprano pipistrelle (f) changed from supporting a demographic Allee effect to random walk and negative density feedback models, respectively (Table 5.1, “Original”; note, however, the soprano pipistrelle showed relatively high support for the Allee effect model). Serotine (a) roost dynamics were unrelated to roost size and supported the random walk model (Table 5.1, “Original”; Figure 5.10).

Finally, brown long-eared bat (g) roost counts were unimproved by prevailing weather or annual trend smoothing. Fitting models using the original roost counts revealed highest support for random walk in its roost replacement rate (Table 5.1, “Original”).

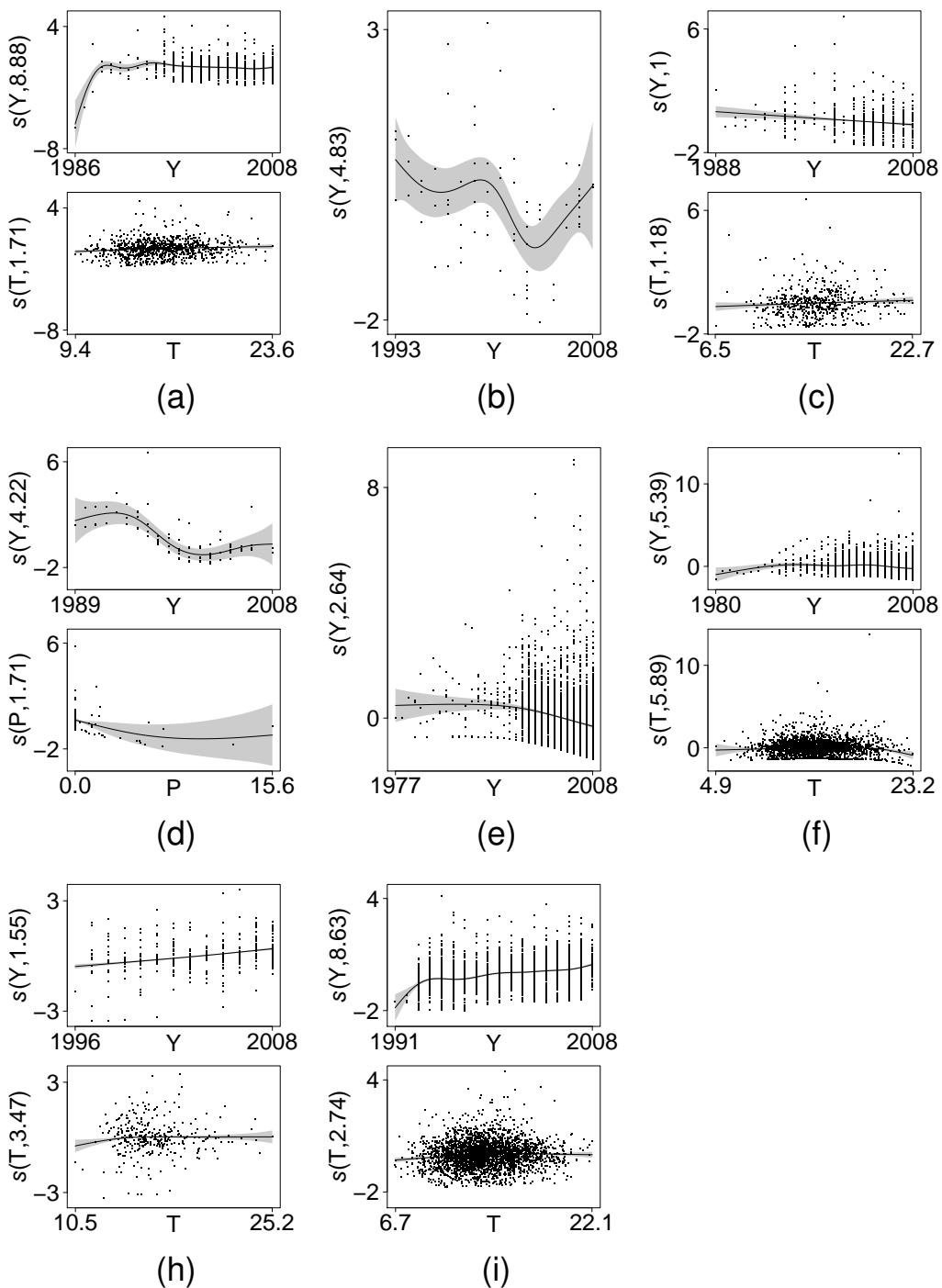


Figure 5.4: GAM smoothing curves for the effects of an annual trend ( $Y$ , years), temperature ( $T$ ,  $^{\circ}$ C) and precipitation ( $P$ , mm) on roost counts.  $s(\bullet)$  on the y-axis is a smoothing function with associated estimated degrees of freedom. Points are residuals and shaded bands represent 95% confidence intervals. Bat species are (a) serotine, (b) Daubentons, (c) Natterers, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, (h) greater horseshoe, and (i) lesser horseshoe. Note: the GAM<sub>WA</sub> model did not explain more deviance than a null intercept model for (g) brown long-eared bat and no plot was generated.

Table 5.1: Empirical support (measured by AICc weights [ $wAICc$ ]) for Random Walk (RW), negative density feedback (ND) and Allee dynamics (AE) in the roost replacement rate for each species. Roost counts were either smoothed for prevailing weather and annual trend ( $GAM_{WA}$ ) or weather only ( $GAM_w$ ), or unsmoothed (Original).  $n$  is the number of observations used to calculate the roost replacement rate.

| Bat species         | code | $GAM_{WA}$ |       |       | $GAM_w$ |      |       | Original |       |      |       |       |       |
|---------------------|------|------------|-------|-------|---------|------|-------|----------|-------|------|-------|-------|-------|
|                     |      | $n$        | RW    | ND    | AE      | $n$  | RW    | ND       | AE    | $n$  | RW    | ND    | AE    |
| Serotine            | (a)  | 380        | 0.102 | 0.702 | 0.197   | -    | -     | -        | -     | 364  | 0.624 | 0.303 | 0.073 |
| Daubenton's         | (b)  | 50         | 0.956 | 0.044 | 0       | 50   | 0.934 | 0.065    | 0.001 | 44   | 0.994 | 0.006 | 0     |
| Natterer's          | (c)  | 233        | 0     | 0.443 | 0.557   | 232  | 0.096 | 0.034    | 0.871 | 219  | 0.926 | 0.067 | 0.008 |
| Noctule             | (d)  | 60         | 0.861 | 0.132 | 0.007   | 59   | 0.073 | 0.918    | 0.009 | 39   | 0.999 | 0.001 | 0     |
| Common pipistrelle  | (e)  | 1439       | 0     | 0.726 | 0.274   | 1438 | 0.794 | 0.162    | 0.044 | 1329 | 0.411 | 0.468 | 0.121 |
| Soprano pipistrelle | (f)  | 984        | 0     | 0.41  | 0.589   | 984  | 0.078 | 0.09     | 0.833 | 940  | 0.008 | 0.517 | 0.475 |
| Brown long-eared    | (g)  | -          | -     | -     | -       | -    | -     | -        | -     | 439  | 0.84  | 0.136 | 0.024 |
| Greater horseshoe   | (h)  | 163        | 0     | 0.487 | 0.513   | 163  | 0.966 | 0.031    | 0.003 | 161  | 0.359 | 0.154 | 0.487 |
| Lesser horseshoe    | (i)  | 1213       | 0     | 0.819 | 0.181   | -    | -     | -        | -     | 1209 | 0     | 0.076 | 0.923 |

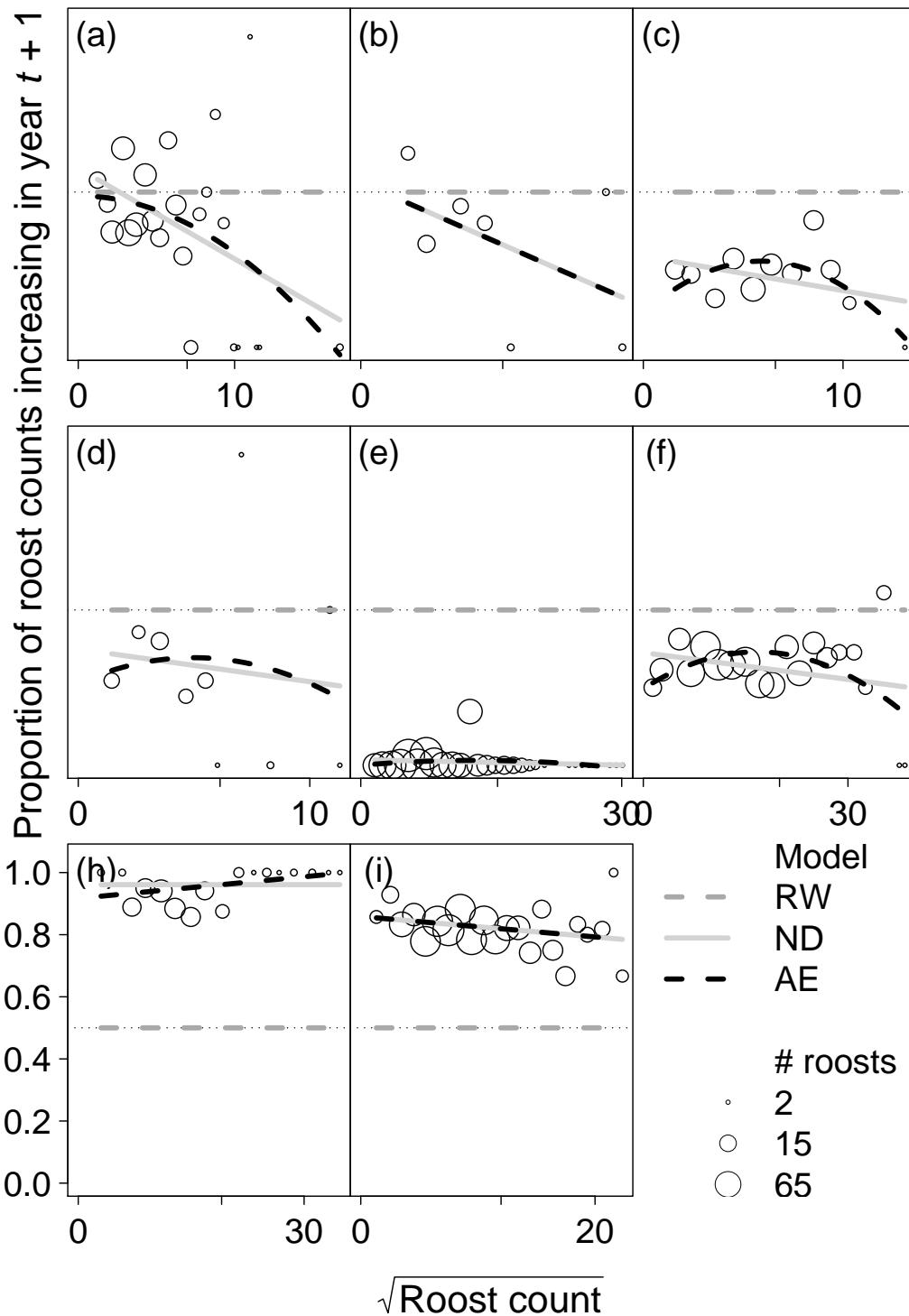


Figure 5.5: Individual species plots showing random walk (RW), negative density feedback (ND) and Allee dynamics (AE) model fits for roost replacement rate as a function of  $\sqrt{\text{roost size}}$ . Roost replacement rate calculated from roost counts smoothed for prevailing weather and annual trend effects ( $\text{GAM}_{\text{WA}}$ ). Bat species are (a) serotine, (b) Daubentons, (c) Natterers, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, (h) greater horseshoe, and (i) lesser horseshoe. Note: the  $\text{GAM}_{\text{WA}}$  model did not explain more deviance than a null intercept model for (g) brown long-eared bat and no plot was generated.

## 5.4 Discussion

Evidence of demographic Allee effects is uncommon in populations of animals and plants (Gregory et al. 2010). Social animals, however, might be predisposed to demographic Allee effects when their populations become too small for social behaviours to be effective (Stephens and Sutherland 1999). We examined the roost dynamics of bats considered highly social mammals that form single sex breeding colonies (Kerth 2008) for empirical evidence of demographic Allee effects. We found that four of the nine species studied (44.4%) showed higher support for a demographic Allee effect than for negative density feedback or density independent roost dynamics: Natterers bat, soprano pipistrelle, and the greater and lesser horseshoe bats. These results were, however, dependent on the influences of prevailing weather and an annual trend on roost counts.

### 5.4.1 Influences of prevailing weather and annual trend

Roost counts are assumed to be an adequate measure of the number of bats present at any particular time and to quantify changes in roost size between years (e.g., Link and Sauer 1998). Several authors have evaluated roost counts as a measure of the number of bats present. For example, O'Donnell (2002b) found good correspondence between counts of emerging bats, interior counts of roosting bats, and numbers of bats trapped at emergence. He found no effect of temperature or rain on the numbers of bats emerging from a single cave and advocated roost counts as a robust measure of roost size. Here, however, results using roost counts collected by the NBMP (and related programmes) at numerous locations over a wide geographical scale suggest that most species are sensitive to both prevailing weather and an annual trend (Table 5.1).

Roost counts of all species except the brown long-eared bat were amenable to smoothing for temperature, precipitation or an annual trend (compared to a null intercept model; Table 5.6). When smoothed together with an annual trend, roost counts generally increased with increasing temperature and were generally unaffected by precipitation. Similar relationships have been observed in activity patterns of a number of other bat species (we assume activity patterns are closely related to emergence patterns). Rydell (1989) found breeding northern bat *Eptesicus nilssoni* activity to increase with minimum temperature (but drop non-linearly at low [ $< 9^{\circ}\text{C}$ ] temperatures) and to be unaffected by moderate precipitation. Scanlon and Petit (2008b) reported similar findings for a variety of Australian bat species, and hypothesized the relationships were underpinned by activity patterns of their insect prey (Scanlon and Petit 2008a). Finally, O'Donnell (2000) analyzed extensive New Zealand long-tailed bat activity data that increased with temperature and insect activity.

Neglecting the influence of an annual trend on roost counts had no qualitative effect on the result for Natterers bat or soprano pipistrelle, suggesting that annual trends were not influential in these species and detection of a demographic Allee effect in their roost dynamics was robust. In contrast, neglecting annual trends in greater horseshoe bats caused a loss of all density feedback signals in its roost replacement rate. A similar finding was observed in the common pipistrelle, which also revealed a tendency for roost counts to decrease with increasing temperature. These findings highlight that (1) although weather variables might affect animal activity and should be incorporated into monitoring programmes (Bas et al. 2008), they can also usurp variation in roost counts due to unmeasured variables leading to spurious findings (Bennetts et al. 1999), and (2) annual trends differ between species and can qualitatively change findings drawn from roost counts, particularly if populations are declining when negative density feedback models might be inappropriate (Stephens et al. 2002).

Although our findings attach high importance to considering annual trends, we are not able to define their precise meanings. Although they capture changes in nationwide abundance, they might also encapsulate roost size changes due to movements between roosts (roost philopatry). We were interested to know the extent to which this behaviour might influence the annual trends for each species and so summarised the current knowledge of roost philopatry for each species in Table 5.2. We found that intra-annual roost philopatry was generally high among all species except common pipistrelle that showed low roost philopatry in radio-tracking studies (Davidson-Watts and Jones 2006). These findings are complemented by analyses of roost switching behaviour (movement of all bats from one roost to another) done by the BCT (Bat Conservation Trust 2008) and suggest that differences in common pipistrelle roost dynamics might be influenced by low roost philopatry behaviour. Indeed, the NBMP guard against this by estimating trends derived from roost counts together with trends calculated from winter hibernacula counts and summer foraging field surveys, and suggest that roost counts might not derive highly robust trends for common pipistrelles (Bat Conservation Trust 2009).

Neglecting the influence of both prevailing weather and annual trends on roost counts (i.e., using the original roost counts) resulted in detection of qualitatively different roost dynamics for four species (Table 5.1, compare “GAM<sub>WA</sub>” and “Original”). These included the Natterer’s bat that no longer supported the demographic Allee effect model. On the other hand, the using unsmoothed roost counts revealed a demographic Allee effect in lesser horseshoe roost dynamics (alongside the closely related greater horseshoe bat) and further emphasises its existence in soprano pipistrelle bat. Given our finding that prevailing weather and annual trends influence roost counts of most species, neglecting them and using unsmoothed roost counts is counter-intuitive. Nevertheless, the cautious view might be to consider the lesser horseshoe bat susceptible to Allee effects until proven otherwise.

#### **5.4.2 Empirical support of demographic Allee effects**

So, did we detect demographic Allee effects in Natterers, soprano pipistrelle and greater and lesser horseshoe bats? We believe the empirical support for the Allee effect model emerging from this meta-analysis of a large sample of maternity roosts provides a strong case for expecting demographic Allee effects in the roost dynamics of these species. This conclusion is supported by knowledge of their roosting behaviour; maternity roosts of three these species are, on average, large compared to the other species examined. From the NBMP data, the mean maximum annual roost count for soprano pipistrelles was 365.68 individuals and was higher than for all other species analysed here. Greater horseshoe bats were formed the next largest roosts, consisting on average of 274.89 individuals. Lesser horseshoe bats had the fourth highest value (after Daubentons bats) at 136.69 individuals. The Natterers bat, on the other hand, gathered in smaller groups of 61.98 individuals, which was higher than for brown long-eared and serotine bats. Given the costs associated with forming large groups (e.g., increased parasite loads; Lourenco and Palmeirim 2007), there should be substantial fitness benefits for individuals to remain a group member a component Allee effect. If this is true, and these large groups are occasionally perturbed to smaller sizes, then the existence of a demographic Allee effect is a distinct possibility (Stephens and Sutherland 1999).

Using similar statistical techniques, Tobin et al. (2007) found empirical support for a demographic Allee effect in invasive Gypsy moth populations in northeast USA. While their findings were highly convincing, they have since focussed on trying to determine the exact mechanism underpinning the demographic Allee effect (i.e., the component Allee effect; e.g., Tcheslavskaja et al. 2002). Therefore, rather than state the existence of a demographic Allee effect in these bat

Table 5.2: Summary information on roost philopatry in the nine bat species included in this study. Intra-annual philopatry is either “strong” (majority of bats loyal to the same roost throughout the duration of the study) or “weak” and measured using either radio-tracking (RT) or capture-mark-recapture (CMR). Evidence of inter-annual philopatry is given as “yes” or “no” and is usually based on CMR. A hyphen (-) indicates missing information.

| <b>Bat species</b>  | <b>code</b> | <b>Intra-annual</b> |               | <b>Inter-</b> | <b>Source</b>   |
|---------------------|-------------|---------------------|---------------|---------------|---|
|                     |             | <b>Level</b>        | <b>Method</b> | <b>annual</b> |   |
| Serotine            | (a)         | Strong              | RT            | -             | Catto et al. 1996   |
|                     |             | Strong              | CMR           | Yes           | Harbusch and Racey 2006 <sup>(1)</sup>                              |
| Daubenton's         | (b)         | Weak                | RT            | Yes           | Senior et al. 2005  |
|                     |             | Strong              | RT            | Yes           | Ngamprasertwong et al. 2008 <sup>(2)</sup>                          |
| Natterer's          | (c)         | Weak                | RT            | -             | Kapfer et al. 2008 <sup>(3)</sup>                                   |
|                     |             | Strong              | CMR           | Yes           | Smith and Racey 2005, P. Smith <i>pers comm</i> <sup>(4)</sup>      |
|                     |             | Strong              | CMR           | Yes           | Rivers et al. 2006 <sup>(5)</sup>                                   |
| Noctule             | (d)         | Strong              | RT            | Yes           | Mackie and Racey 2007, I. Mackie <i>pers comm</i> <sup>(7)</sup>    |
| Common pipistrelle  | (e)         | Weak                | RT            | -             | Davidson-Watts and Jones 2006                                       |
| Soprano pipistrelle | (f)         | Strong              | RT            | -             | Davidson-Watts and Jones 2006                                       |
|                     |             | Strong              | CMR           | Yes           | Park et al. 1998 <sup>(8)</sup>                                     |
| Brown long-eared    | (g)         | Strong              | CMR           | Yes           | Entwistle et al. 2000   |
|                     |             | Strong              | CMR           | Yes           | Park et al. 1998  |
| Greater horseshoe   | (h)         | Strong              | RT            | Yes           | Rossiter et al. 2002  |
| Lesser horseshoe    | (i)         | Strong              | RT            | Yes           | Bontadina et al. 2002, F. Bontadina <i>pers comm</i> <sup>(9)</sup> |
|                     |             | Strong              | RT            | -             | Knight 2006   |

(1) assumed measured by CMR but possibly non-individual measures; study undertaken in Germany

(2) unpublished CMR data reveals high inter-annual philopatry in Scotland

(3) study undertaken in Belgium

(4) unpublished CMR data suggest high inter-annual philopatry

(5) study of bat box use

(6) study used a subset of the dataset analysed by Rivers et al. (2006)

(7) unpublished CMR data suggest high inter-annual philopatry

(8) phonic type confirmed posthoc as 55 kHz from 13 individuals

(9) unpublished CMR data reveals high inter-annual philopatry in two roosts in Switzerland

species, we conclude that our study provides strong support for their existence but this should be confirmed using replicated experiments (Turchin 2003).

### **5.4.3 Management recommendations**

We detected strong evidence for the existence of a demographic Allee effect in the roost dynamics of 44.4% of the bat species we analyzed. Over 1100 species of bat have been described worldwide (Simmons 2005). If our finding could be linearly extrapolated to bat species worldwide, it would amount to over 488 species with possible demographic Allee effects, a remarkably high incidence. Although not a direct comparison because they used a single population time series per species, Gregory et al. (2010) recently reported the existence of a demographic Allee effect in 13 of 1198 (1.1%) taxonomically diverse species examined. The large disparity between these figures might be attributed to the widespread sociality in bat species (Kerth 2008). On the other hand, the probability that 488 bat species will exhibit a demographic Allee effect might be small and is likely to remain unknown.

Nevertheless, bat species worldwide are becoming threatened with extinction due to various human activities (Mickleburgh et al. 2002) and are being nominated as biodiversity indicators worldwide (Jones et al. 2009). If a bat species exhibits a demographic Allee effect and is locally declining, then individuals will suffer reduced fitness as the group size declines and will either disperse to join another group or perish (Stephens and Sutherland 1999). Such density dependent dispersal would in turn hasten the decline of existing groups and might lead to a population collapse (Courchamp et al. 1999). With this possibility in mind, we recommend that UK populations of Natterers bat, soprano pipistrelle and the greater and lesser horseshoe bats, and populations of social species in general, continue to be legally protected (themselves and their roosts) and the focus of careful monitoring. Only thorough such careful monitoring will we be able to identify declines in these species sufficiently early to trigger conservation action to prevent their population collapse due to demographic Allee effects.

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## References

- Akbar, Z., A. Zubaid, G. McCracken, and T. Kunz. 2006. Functional and evolutionary ecology of bats. Oxford University Press, USA.
- Allee, W. C., O. Emerson, T. Park, and K. Schmidt. 1949. Principles of animal ecology. Saunders.
- Allen, L. C., C. S. Richardson, G. F. McCracken, and T. H. Kunz. 2009. Birth size and postnatal growth in cave- and bridge-roosting Brazilian free-tailed bats. *Journal of Zoology* **280**:8–16.
- Angulo, E., G. W. Roemer, L. Berec, J. Gascoigne, and F. Courchamp. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**:1082–1091.
- Bas, Y., V. Devictor, J.-P. Moussus, and F. Jiguet. 2008. Accounting for weather and time-of-day parameters when analysing count data from monitoring programs. *Biodiversity and Conservation* **17**:3403–3416.
- Bat Conservation Trust, 2008. The National Bat Monitoring Programme - Annual Report 2007. Technical report, Bat Conservation Trust . URL [http://www.bats.org.uk/pages/nbmp\\_reports.html](http://www.bats.org.uk/pages/nbmp_reports.html).
- Bat Conservation Trust, 2009. The National Bat Monitoring Programme - Annual Report 2008. Technical report, Bat Conservation Trust . URL [http://www.bats.org.uk/pages/nbmp\\_reports.html](http://www.bats.org.uk/pages/nbmp_reports.html).
- Bennetts, R., W. Link, J. Sauer, and P. Sykes Jr. 1999. Factors influencing counts in an annual survey of Snail Kites in Florida. *The Auk* **116**:316–323.
- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. *Trends in Ecology & Evolution* **22**:185–191.
- Bontadina, F., H. Schofield, and B. Naef Daenzer. 2002. Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *Journal of Zoology* **258**:281–290.
- Boyles, J. G., J. J. Storm, and V. Brack. 2008. Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. *Functional Ecology* **22**:632–636.
- Burland, T. M., and J. Worthington Wilmer. 2001. Seeing in the dark: molecular approaches to the study of bat populations. *Biological Reviews* **76**:389–409.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York.
- Catto, C. M. C., A. M. Hutson, P. A. Racey, and P. J. Stephenson. 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology* **238**:623–633.
- Clutton-Brock, T. H., D. Gaynor, G. M. McIlrath, A. D. C. MacColl, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, and P. N. M. Brotherton. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* **68**:672–683.

- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**:405–410.
- Courchamp, F., G. S. A. Rasmussen, and D. W. Macdonald. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology* **13**:20–27.
- Davidson-Watts, I., and G. Jones. 2006. Differences in foraging behaviour between *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825). *Journal of Zoology* **268**:55–62.
- Dietz, M., and E. K. V. Kalko. 2006. Seasonal changes in daily torpor patterns of free-ranging female and male Daubenton's bats (*Myotis daubentonii*). *Journal of Comparative Physiology B* **176**:223–231.
- Entwistle, A. C., P. A. Racey, and J. R. Speakman. 2000. Social and population structure of a gleaning bat, *Plecotus auritus*. *Journal of Zoology* **252**:11–17.
- Gascoigne, J., L. Berec, S. Gregory, and F. Courchamp. 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology* **51**:355–372.
- Gregory, S., C. Bradshaw, B. Brook, and F. Courchamp. 2010. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology* –:–.
- Harbusch, C., and P. A. Racey. 2006. The sessile serotine: the influence of roost temperature on philopatry and reproductive phenology of *Eptesicus serotinus* (Schreber, 1774) (Mammalia: Chiroptera). *Acta Chiropterologica* **8**:213–229.
- Haylock, M. R., N. Hofstra, A. M. G. Klein Tank, E. J. Klok, P. D. Jones, and M. New. 2008. A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *Journal of Geophysical Research-Atmospheres* **113**:D20119.
- Hutson, A., S. Mickleburgh, and P. Racey. 2001. Microchiropteran bats: global status survey and conservation action plan. World Conservation Union.
- Jarvis, J. U. M., N. C. Bennett, and A. C. Spinks. 1998. Food availability and foraging by wild colonies of Damaraland mole-rats (*Cryptomys damarensis*): implications for sociality. *Oecologia* **113**:290–298.
- Johnson, D. M., A. M. Liebold, P. C. Tobin, and O. N. Bjornstad. 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature* **444**:361–363.
- Jones, G., D. Jacobs, T. Kunz, M. Willig, and P. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* **8**:93–115.
- Kapfer, G., T. Rigot, L. Holsbeek, and S. Aron. 2008. Roost and hunting site fidelity of female and juvenile Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) (Chiroptera: Vespertilionidae). *Mammalian Biology* **73**:267–275.
- Kerth, G. 2008. Causes and consequences of sociality in bats. *Bioscience* **58**:737–746.

- Kerth, G., B. Almasi, N. Ribi, D. Thiel, and S. Lüpold. 2003. Social interactions among wild female Bechstein's bats (*Myotis bechsteinii*) living in a maternity colony. *Acta ethologica* **5**:107–114.
- Knight, T., 2006. The use of landscape features and habitats by the lesser horseshoe bat (*Rhinolophus hipposideros*). Ph.D. thesis, University of Bristol.
- Kunz, T. H., and S. Parsons, editors. 2009. Ecological and behavioral methods for the study of bats. Johns Hopkins University Press.
- Lewis, S. E. 1995. Roost fidelity of bats - a review. *Journal of Mammalogy* **76**:481–496.
- Link, W., and J. Sauer. 1998. Estimating population change from count data: application to the North American Breeding Bird Survey. *Ecological Applications* **8**:258–268.
- Lourenco, S. I., and J. M. Palmeirim. 2007. Can mite parasitism affect the condition of bat hosts? Implications for the social structure of colonial bats. *Journal of Zoology* **273**:161–168.
- Mackie, I. J., and P. A. Racey. 2007. Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): Implications for conservation. *Biological Conservation* **140**:70–77.
- McCracken, G. F. 1984. Communal nursing in mexican free-tailed bat maternity colonies. *Science* **223**:1090–1091.
- Mickleburgh, S., A. Hutson, and P. Racey. 2002. A review of the global conservation status of bats. *Oryx* **36**:18–34.
- Mooring, M. S., T. A. Fitzpatrick, T. T. Nishihira, and D. D. Reisig. 2004. Vigilance, predation risk, and the Allee effect in desert bighorn sheep. *Journal of Wildlife Management* **68**:519–532.
- Ngamprasertwong, T., I. J. Mackie, P. A. Racey, and S. B. Piertney. 2008. Spatial distribution of mitochondrial and microsatellite DNA variation in Daubenton's bat within Scotland. *Molecular Ecology* **17**:3243–3258.
- O'Donnell, C. F. J. 2000. Cryptic local populations in a temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand. *Animal Conservation* **3**:287–297.
- O'Donnell, C. F. J. 2002a. Timing of breeding, productivity and survival of long-tailed bats *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae) in cold-temperate rainforest in New Zealand. *Journal of Zoology* **257**:311–323.
- O'Donnell, C. F. J. 2002b. Variability in numbers of long-tailed bats (*Chalinolobus tuberculatus*) roosting in Grand Canyon Cave, New Zealand: implications for monitoring population trends. *New Zealand Journal of Zoology* **29**:273–284.
- Park, K. J., E. Masters, and J. D. Altringham. 1998. Social structure of three sympatric bat species (Vespertilionidae). *Journal of Zoology* **244**:379–389.
- Petrzelkova, K. J., and J. Zukal. 2003. Does a live barn owl (*Tyto alba*) affect emergence behavior of serotine bats (*Eptesicus serotinus*)? *Acta Chiropterologica* **5**:177–184.

- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. Technical report, , Vienna, Austria.
- Ratcliffe, J. M., and H. M. ter Hofstede. 2005. Roosts as information centres: social learning of food preferences in bats. *Biology Letters* **1**:72–74.
- Rivers, N. M., R. K. Butlin, and J. D. Altringham. 2006. Autumn swarming behaviour of Natterer's bats in the UK: Population size, catchment area and dispersal. *Biological Conservation* **127**:215–226.
- Rossiter, S., G. Jones, R. Ransome, and E. Barratt. 2002. Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Behavioral Ecology and Sociobiology* **51**:510–518.
- Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. *Oecologia* **80**:562–565.
- Sauer, J. R., 2003. A critical look at national monitoring programs for birds and other wildlife species. Pages 119–126 in Monitoring trends in bat populations of the United States and Territories: Problems and Prospects, Information and Technology Report USGS/BRD/ITR-2003-0003. Fort Collins, CO: U.S. Geological Survey.
- Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer differences in the North-American Breeding Bird Survey. *Auk* **111**:50–62.
- Scanlon, A., and S. Petit. 2008a. Biomass and biodiversity of nocturnal aerial insects in an Adelaide City park and implications for bats (Microchiroptera). *Urban Ecosystems* **11**:91–106.
- Scanlon, A. T., and S. Petit. 2008b. Effects of site, time, weather and light on urban bat activity and richness: considerations for survey effort. *Wildlife Research* **35**:821–834.
- Scott, D., editor. 1992. Multivariate density estimation: theory, practice, and visualization. John Wiley.
- Senior, P., R. K. Butlin, and J. D. Altringham. 2005. Sex and segregation in temperate bats. *Proceedings of The Royal Society B: Biological Sciences* **272**:2467–2473.
- Simmons, N., 2005. Order Chiroptera. Pages 312–529 in D. E. Wilson and D. A. M. Reeder, editors. *Mammal species of the world: a taxonomic and geographic reference*. Johns Hopkins University Press.
- Smith, P. G., and P. A. Racey. 2005. The itinerant Natterer: physical and thermal characteristics of summer roosts of *Myotis nattereri* (Mammalia : Chiroptera). *Journal of Zoology* **266**:171–180.
- Speakman, J. R., R. E. Stone, and J. L. Kerslake. 1995. Temporal patterns in the emergence behaviour of pipistrelle bats, *Pipistrellus pipistrellus*, from maternity colonies are consistent with an anti-predator response. *Animal Behaviour* **50**:1147–1156.
- Stephens, P. A., F. Frey Roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology* **71**:343–361.

- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution* **14**:401–405.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185–190.
- Tcheslavskiaia, K., C. C. Brewster, and A. A. Sharov. 2002. Mating success of gypsy moth (Lepidoptera : Lymantriidae) females in Southern Wisconsin. *Great Lakes Entomologist* **35**:1–7.
- ter Hofstede, H. M., and M. B. Fenton. 2005. Relationships between roost preferences, ectoparasite density, and grooming behaviour of neotropical bats. *Journal of Zoology* **266**:333–340.
- Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjornstad, and A. M. Liebhold. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecology Letters* **10**:36–43.
- Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton Univ. Press.
- Tuttle, M. D. 1976. Population ecology of the gray bat (*Myotis grisescens*): factors influencing growth and survival of newly volant young. *Ecology* **57**:587–595.
- Walsh, A. L., C. Catto, T. Hutson, P. Racey, P. Richardson, and S. Langton. 2002. The UK's National Bat Monitoring Programme: Final Report 2001. DEFRA publications.
- Warren, R. D., and M. S. Witter. 2002. Monitoring trends in bat populations through roost surveys: methods and data from *Rhinolophus hipposideros*. *Biological Conservation* **105**:255–261.
- Wilkinson, G. 1990. Food sharing in vampire bats. *Scientific American*. **262**:64–70.
- Wilkinson, G. 1992. Communal nursing in the evening bat, *Nycticeius humeralis*. *Behavioral Ecology and Sociobiology* **31**:225–235.
- Wood, S. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association* **99**:673–686.
- Wood, S. 2006. Generalized additive models: an introduction with R. CRC Press.
- Zahn, A. 1999. Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. *Journal of Zoology* **247**:275–280.

## Appendices

Table 5.3: Number of observer for roosts of each species. The 50% quantile is equivalent to the median.

| Bat species         | code | Quantiles (%) |    |    |    |     |
|---------------------|------|---------------|----|----|----|-----|
|                     |      | 0             | 25 | 50 | 75 | 100 |
| Serotine            | (a)  | 1             | 1  | 1  | 1  | 4   |
| Daubenton's         | (b)  | 1             | 1  | 1  | 1  | 2   |
| Natterer's          | (c)  | 1             | 1  | 1  | 1  | 3   |
| Noctule             | (d)  | 1             | 1  | 1  | 1  | 2   |
| Common pipistrelle  | (e)  | 1             | 1  | 1  | 1  | 3   |
| Soprano pipistrelle | (f)  | 1             | 1  | 1  | 1  | 4   |
| Brown long-eared    | (g)  | 1             | 1  | 1  | 1  | 2   |
| Greater horseshoe   | (h)  | 1             | 1  | 1  | 2  | 3   |
| Lesser horseshoe    | (i)  | 1             | 1  | 1  | 2  | 3   |
| All                 |      | 1             | 1  | 1  | 1  | 4   |

Table 5.4: Empirical support (measured by AICc weights [wAICc]) for Random Walk (RW), exponential growth (EX), negative density feedback (ND) and Allee dynamics (AE) in the roost replacement rate for each species. Roost counts were either smoothed for weather ( $GAM_w$ ), or unsmoothed (Original).  $n$  is the number of observations used to calculate the roost replacement rate. These models were not fit to roost counts smoothed for an annual trend because EX fits such a trend and fitting both models would produce misleadingly high support for EX. Note the results for the greater horseshoe bat.

| Bat species         | code | $GAM_w$ |       |       |       |       | Original |       |       |       |       |
|---------------------|------|---------|-------|-------|-------|-------|----------|-------|-------|-------|-------|
|                     |      | $n$     | RW    | EX    | ND    | AE    | $n$      | RW    | EX    | ND    | AE    |
| Serotine            | (a)  | -       | -     | -     | -     | -     | 364      | 0.306 | 0.509 | 0.149 | 0.036 |
| Daubenton's         | (b)  | 50      | 0.815 | 0.128 | 0.057 | 0.001 | 44       | 0.837 | 0.158 | 0.005 | 0     |
| Natterer's          | (c)  | 232     | 0.092 | 0.037 | 0.033 | 0.838 | 219      | 0.694 | 0.25  | 0.05  | 0.006 |
| Noctule             | (d)  | 59      | 0.057 | 0.226 | 0.71  | 0.007 | 39       | 0.912 | 0.088 | 0.001 | 0     |
| Common pipistrelle  | (e)  | 1438    | 0.592 | 0.254 | 0.121 | 0.033 | 1329     | 0.187 | 0.545 | 0.213 | 0.055 |
| Soprano pipistrelle | (f)  | 984     | 0.075 | 0.04  | 0.086 | 0.8   | 940      | 0.008 | 0.011 | 0.511 | 0.47  |
| Brown long-eared    | (g)  | -       | -     | -     | -     | -     | 439      | 0.605 | 0.279 | 0.098 | 0.017 |
| Greater horseshoe   | (h)  | 163     | 0.791 | 0.18  | 0.025 | 0.003 | 161      | 0.222 | 0.381 | 0.095 | 0.301 |
| Lesser horseshoe    | (i)  | -       | -     | -     | -     | -     | 1209     | 0     | 0     | 0.076 | 0.923 |

Table 5.5: Table to show better Negative Binomial deviances.

| Bat species         | Poisson    | quasi-Poisson | negative binomial |
|---------------------|------------|---------------|-------------------|
| Serotine            | 3574.912   | 3623.078      | 870.170           |
| Daubenton's         | 515.904    | 873.913       | 95.124            |
| Natterer's          | 4340.382   | 4514.050      | 686.182           |
| Noctule             | 1035.318   | 1306.762      | 100.681           |
| Common pipistrelle  | 101714.710 | 102104.803    | 6254.561          |
| Soprano pipistrelle | 153724.185 | 154800.079    | 4601.952          |
| Brown long-eared    | 5866.483   | 5918.607      | 953.542           |
| Greater horseshoe   | 9581.131   | 10077.213     | 626.852           |
| Lesser horseshoe    | 38555.279  | 38722.926     | 1938.085          |

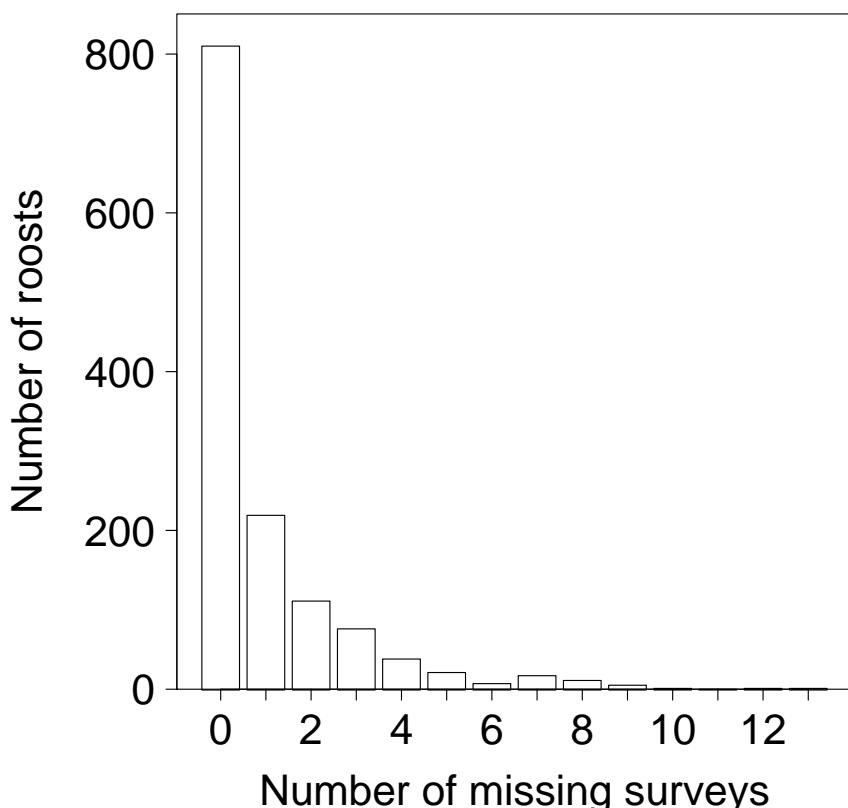


Figure 5.6: A barchart showing the number of roosts with different numbers of missing counts.

**Table 5.6:** GAM<sub>WA</sub> results for all species. Models are ordered by their  $\Delta\text{AIC}$  where the best model has  $\Delta\text{AIC} = 0$ . Model parameters are:  $\alpha$  is the site effect for roost  $r$ ,  $\beta$  is the time effect for year  $t$ , T and P are site and year specific measures of temperature and precipitation, and  $s()$  is a smooth term calculated by cubic splines. See Methods for further details.

| Bat species         | Model   | deviance | df     | AIC      | $\Delta\text{AIC}$ |
|---------------------|---|----------|--------|----------|--------------------|
| Serotine            | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 871.95   | 118.59 | 6245.87  | 0.000              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 873.74   | 117.88 | 6246.24  | 0.368              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 870.17   | 119.67 | 6246.26  | 0.382              |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 872.08   | 118.87 | 6246.55  | 0.680              |
|                     | $\alpha_r + s(\beta_t)$                         | 884.80   | 116.89 | 6255.33  | 9.455              |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 882.12   | 118.37 | 6255.60  | 9.721              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 883.14   | 117.88 | 6255.65  | 9.773              |
|                     | $\alpha_r + 1$                                  | 1115.96  | 108.00 | 6255.65  | 9.780              |
|                     | $\alpha_r + \beta_t$                            | 922.42   | 109.00 | 6277.16  | 31.287             |
|                     | $\alpha_r + s(\beta_t)$                         | 97.45    | 14.83  | 706.85   | 0.000              |
| Daubenton's         | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 96.36    | 15.92  | 708.64   | 1.791              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 96.37    | 15.78  | 708.72   | 1.869              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 96.37    | 15.78  | 708.72   | 1.869              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 96.88    | 15.75  | 708.77   | 1.923              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 95.12    | 16.91  | 710.50   | 3.647              |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 95.72    | 16.71  | 710.66   | 3.812              |
|                     | $\alpha_r + \beta_t$                            | 118.52   | 11.00  | 715.15   | 8.300              |
|                     | $\alpha_r + 1$                                  | 122.33   | 10.00  | 717.95   | 11.102             |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 679.25   | 79.18  | 4546.81  | 0.000              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 679.78   | 79.00  | 4546.85  | 0.035              |
| Natterer's          | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 686.18   | 80.99  | 4547.40  | 0.583              |
|                     | $\alpha_r + s(\beta_t)$                         | 688.88   | 78.00  | 4548.21  | 1.400              |
|                     | $\alpha_r + \beta_t$                            | 688.88   | 78.00  | 4548.21  | 1.400              |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 682.99   | 80.00  | 4548.60  | 1.789              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 690.64   | 79.00  | 4550.15  | 3.332              |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 681.07   | 83.23  | 4551.33  | 4.519              |
|                     | $\alpha_r + 1$                                  | 689.73   | 77.00  | 4556.99  | 10.176             |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 98.83    | 16.93  | 751.99   | 0.000              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 100.68   | 17.98  | 753.02   | 1.027              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 100.29   | 16.09  | 753.79   | 1.800              |
| Noctule             | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 101.88   | 17.22  | 754.57   | 2.577              |
|                     | $\alpha_r + s(\beta_t)$                         | 101.77   | 15.18  | 754.79   | 2.801              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 102.51   | 16.30  | 755.61   | 3.617              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 102.51   | 16.30  | 755.61   | 3.617              |
|                     | $\alpha_r + \beta_t$                            | 124.53   | 12.00  | 765.28   | 13.286             |
|                     | $\alpha_r + 1$                                  | 198.83   | 11.00  | 792.33   | 40.341             |
|                     | $\alpha_r + s(\beta_t)$                         | 6251.48  | 399.64 | 35053.27 | 0.000              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 6247.19  | 400.61 | 35053.62 | 0.354              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 6247.23  | 400.79 | 35053.74 | 0.470              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 6251.11  | 400.65 | 35054.98 | 1.708              |
| Common pipistrelle  | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 6246.73  | 401.62 | 35055.26 | 1.993              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 6254.56  | 401.86 | 35063.17 | 9.902              |
|                     | $\alpha_r + \beta_t$                            | 6272.14  | 398.00 | 35068.41 | 15.143             |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 6270.68  | 400.65 | 35074.55 | 21.282             |
|                     | $\alpha_r + 1$                                  | 6278.47  | 397.00 | 35121.59 | 68.322             |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 4602.59  | 303.28 | 29793.37 | 0.000              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 4601.95  | 304.83 | 29794.51 | 1.140              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 4632.99  | 298.57 | 29808.94 | 15.568             |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 4634.08  | 299.55 | 29810.62 | 17.251             |
|                     | $\alpha_r + s(\beta_t)$                         | 4642.59  | 297.60 | 29811.00 | 17.628             |
| Soprano pipistrelle | $\alpha_r + s(\beta_t) + P_{rt}$                | 4644.22  | 298.59 | 29812.94 | 19.576             |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 4643.97  | 298.91 | 29813.05 | 19.678             |
|                     | $\alpha_r + \beta_t$                            | 4694.91  | 293.00 | 29849.88 | 56.516             |
|                     | $\alpha_r + 1$                                  | 4836.13  | 292.00 | 29921.97 | 128.600            |
|                     | $\alpha_r + 1$                                  | 1291.63  | 147.00 | 8013.68  | 0.000              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 953.54   | 161.41 | 8037.74  | 24.054             |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 960.95   | 158.59 | 8039.51  | 25.829             |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 964.11   | 157.37 | 8040.23  | 26.543             |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 971.00   | 155.65 | 8043.68  | 29.998             |
|                     | $\alpha_r + s(\beta_t)$                         | 973.45   | 154.54 | 8043.89  | 30.209             |
| Brown long-eared    | $\alpha_r + s(\beta_t) + T_{rt}$                | 971.58   | 155.48 | 8043.92  | 30.236             |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 969.68   | 156.60 | 8044.24  | 30.559             |
|                     | $\alpha_r + \beta_t$                            | 987.77   | 148.00 | 8045.14  | 31.462             |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 630.66   | 29.02  | 3750.22  | 0.000              |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 626.85   | 30.06  | 3750.28  | 0.054              |
|                     | $\alpha_r + \beta_t$                            | 634.95   | 25.00  | 3750.58  | 0.353              |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 629.95   | 27.71  | 3751.51  | 1.286              |
|                     | $\alpha_r + s(\beta_t)$                         | 637.95   | 25.38  | 3752.09  | 1.863              |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 635.39   | 26.36  | 3752.90  | 2.679              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 635.39   | 26.36  | 3752.90  | 2.679              |
| Greater horseshoe   | $\alpha_r + s(\beta_t) + T_{rt}$                | 630.41   | 33.21  | 3755.26  | 5.038              |
|                     | $\alpha_r + 1$                                  | 597.38   | 24.00  | 3819.54  | 69.317             |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt})$             | 1907.88  | 277.38 | 28504.45 | 0.000              |
|                     | $\alpha_r + s(\beta_t) + T_{rt} + P_{rt}$       | 1916.90  | 276.63 | 28511.98 | 7.533              |
|                     | $\alpha_r + s(\beta_t) + T_{rt}$                | 1919.53  | 275.61 | 28512.56 | 8.119              |
|                     | $\alpha_r + s(\beta_t) + P_{rt}$                | 1930.83  | 275.38 | 28523.41 | 18.963             |
|                     | $\alpha_r + s(\beta_t)$                         | 1934.32  | 274.30 | 28524.73 | 20.282             |
|                     | $\alpha_r + \beta_t$                            | 1951.09  | 267.00 | 28526.91 | 22.460             |
|                     | $\alpha_r + s(\beta_t) + s(T_{rt}) + s(P_{rt})$ | 1938.09  | 278.42 | 28536.75 | 32.300             |
|                     | $\alpha_r + s(\beta_t) + s(P_{rt})$             | 1965.22  | 275.38 | 28557.79 | 53.349             |
| Lesser horseshoe    | $\alpha_r + 1$                                  | 3302.09  | 266.00 | 28681.66 | 177.216            |
|                     |   |          |        |          |                    |

**Table 5.7:** GAM<sub>W</sub> results for all species. Models are ordered by their  $\Delta\text{AIC}$  where the best model has  $\Delta\text{AIC} = 0$ . Model parameters are:  $\alpha$  is the site effect for roost  $r$ , T and P are site and year specific measures of temperature and precipitation, and  $s()$  is a smooth term calculated by cubic splines. See Methods for further details.

| Bat species         | Model                              | deviance | df     | AIC      | $\Delta\text{AIC}$ |
|---------------------|------------------------------------|----------|--------|----------|--------------------|
| Serotine            | $\alpha_r + 1$                     | 1115.96  | 108.00 | 6255.65  | 0.000              |
|                     | $\alpha_r + s(T_{rt})$             | 916.25   | 110.16 | 6273.30  | 17.647             |
|                     | $\alpha_r + T_{rt}$                | 919.47   | 109.00 | 6274.21  | 18.559             |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 915.02   | 111.34 | 6274.45  | 18.793             |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 918.57   | 110.00 | 6275.31  | 19.653             |
|                     | $\alpha_r + s(P_{rt})$             | 925.53   | 109.48 | 6281.23  | 25.575             |
|                     | $\alpha_r + P_{rt}$                | 926.61   | 109.00 | 6281.35  | 25.691             |
| Daubenton's         | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 93.86    | 18.09  | 711.54   | 0.000              |
|                     | $\alpha_r + s(P_{rt})$             | 98.32    | 17.32  | 711.84   | 0.303              |
|                     | $\alpha_r + 1$                     | 122.33   | 10.00  | 717.95   | 6.412              |
|                     | $\alpha_r + T_{rt}$                | 122.32   | 11.00  | 718.29   | 6.752              |
|                     | $\alpha_r + s(T_{rt})$             | 122.32   | 11.00  | 718.29   | 6.752              |
|                     | $\alpha_r + P_{rt}$                | 119.60   | 11.00  | 719.04   | 7.500              |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 119.65   | 12.00  | 719.54   | 7.995              |
| Natterer's          | $\alpha_r + s(T_{rt})$             | 681.84   | 78.00  | 4556.74  | 0.000              |
|                     | $\alpha_r + T_{rt}$                | 681.85   | 78.00  | 4556.74  | 0.000              |
|                     | $\alpha_r + 1$                     | 689.73   | 77.00  | 4556.99  | 0.249              |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 688.51   | 79.72  | 4557.50  | 0.756              |
|                     | $\alpha_r + s(P_{rt})$             | 695.05   | 78.64  | 4558.33  | 1.586              |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 685.69   | 79.00  | 4558.36  | 1.625              |
|                     | $\alpha_r + P_{rt}$                | 692.59   | 78.00  | 4558.82  | 2.082              |
| Noctule             | $\alpha_r + s(P_{rt})$             | 130.60   | 19.71  | 761.29   | 0.000              |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 124.65   | 25.52  | 761.29   | 0.006              |
|                     | $\alpha_r + P_{rt}$                | 142.79   | 12.00  | 772.34   | 11.054             |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 140.78   | 13.00  | 773.88   | 12.591             |
|                     | $\alpha_r + s(T_{rt})$             | 150.18   | 12.00  | 775.55   | 14.260             |
|                     | $\alpha_r + T_{rt}$                | 150.18   | 12.00  | 775.55   | 14.260             |
|                     | $\alpha_r + 1$                     | 198.83   | 11.00  | 792.33   | 31.047             |
| Common pipistrelle  | $\alpha_r + T_{rt}$                | 6261.54  | 398.00 | 35114.99 | 0.000              |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 6259.95  | 399.00 | 35116.47 | 1.484              |
|                     | $\alpha_r + 1$                     | 6278.47  | 397.00 | 35121.59 | 6.602              |
|                     | $\alpha_r + P_{rt}$                | 6276.46  | 398.00 | 35122.91 | 7.925              |
|                     | $\alpha_r + s(P_{rt})$             | 6270.47  | 401.36 | 35123.32 | 8.329              |
|                     | $\alpha_r + s(T_{rt})$             | 6272.00  | 398.00 | 35125.45 | 10.458             |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 6278.97  | 398.00 | 35133.30 | 18.312             |
| Soprano pipistrelle | $\alpha_r + s(T_{rt})$             | 4780.06  | 297.78 | 29894.69 | 0.000              |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 4797.80  | 297.79 | 29910.94 | 16.249             |
|                     | $\alpha_r + T_{rt}$                | 4811.81  | 293.00 | 29912.40 | 17.704             |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 4812.23  | 294.00 | 29914.15 | 19.453             |
|                     | $\alpha_r + 1$                     | 4836.13  | 292.00 | 29921.97 | 27.274             |
|                     | $\alpha_r + P_{rt}$                | 4836.97  | 293.00 | 29923.98 | 29.289             |
|                     | $\alpha_r + s(P_{rt})$             | 4985.73  | 291.00 | 30066.96 | 172.269            |
| Brown long-eared    | $\alpha_r + 1$                     | 1291.63  | 147.00 | 8013.68  | 0.000              |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 968.96   | 154.03 | 8038.39  | 24.707             |
|                     | $\alpha_r + s(P_{rt})$             | 974.32   | 151.60 | 8038.88  | 25.198             |
|                     | $\alpha_r + s(T_{rt})$             | 983.36   | 149.35 | 8043.43  | 29.747             |
|                     | $\alpha_r + T_{rt}$                | 988.47   | 148.00 | 8045.84  | 32.158             |
|                     | $\alpha_r + P_{rt}$                | 988.48   | 148.00 | 8045.85  | 32.163             |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 987.00   | 149.00 | 8046.37  | 32.687             |
| Greater horseshoe   | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 585.22   | 30.07  | 3812.35  | 0.000              |
|                     | $\alpha_r + s(T_{rt})$             | 590.45   | 29.03  | 3812.93  | 0.575              |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 585.94   | 26.00  | 3818.28  | 5.932              |
|                     | $\alpha_r + T_{rt}$                | 590.46   | 25.00  | 3818.38  | 6.031              |
|                     | $\alpha_r + 1$                     | 597.38   | 24.00  | 3819.54  | 7.187              |
|                     | $\alpha_r + P_{rt}$                | 594.37   | 25.00  | 3820.16  | 7.807              |
|                     | $\alpha_r + s(P_{rt})$             | 594.38   | 25.06  | 3820.21  | 7.854              |
| Lesser horseshoe    | $\alpha_r + 1$                     | 3302.09  | 266.00 | 28681.66 | 0.000              |
|                     | $\alpha_r + s(T_{rt}) + s(P_{rt})$ | 2181.73  | 270.82 | 28765.19 | 83.525             |
|                     | $\alpha_r + s(T_{rt})$             | 2185.41  | 269.87 | 28766.96 | 85.298             |
|                     | $\alpha_r + T_{rt} + P_{rt}$       | 2200.34  | 268.00 | 28778.16 | 96.497             |
|                     | $\alpha_r + T_{rt}$                | 2207.89  | 267.00 | 28783.71 | 102.049            |
|                     | $\alpha_r + P_{rt}$                | 2251.14  | 267.00 | 28826.96 | 145.297            |
|                     | $\alpha_r + s(P_{rt})$             | 2262.87  | 267.00 | 28838.69 | 157.024            |

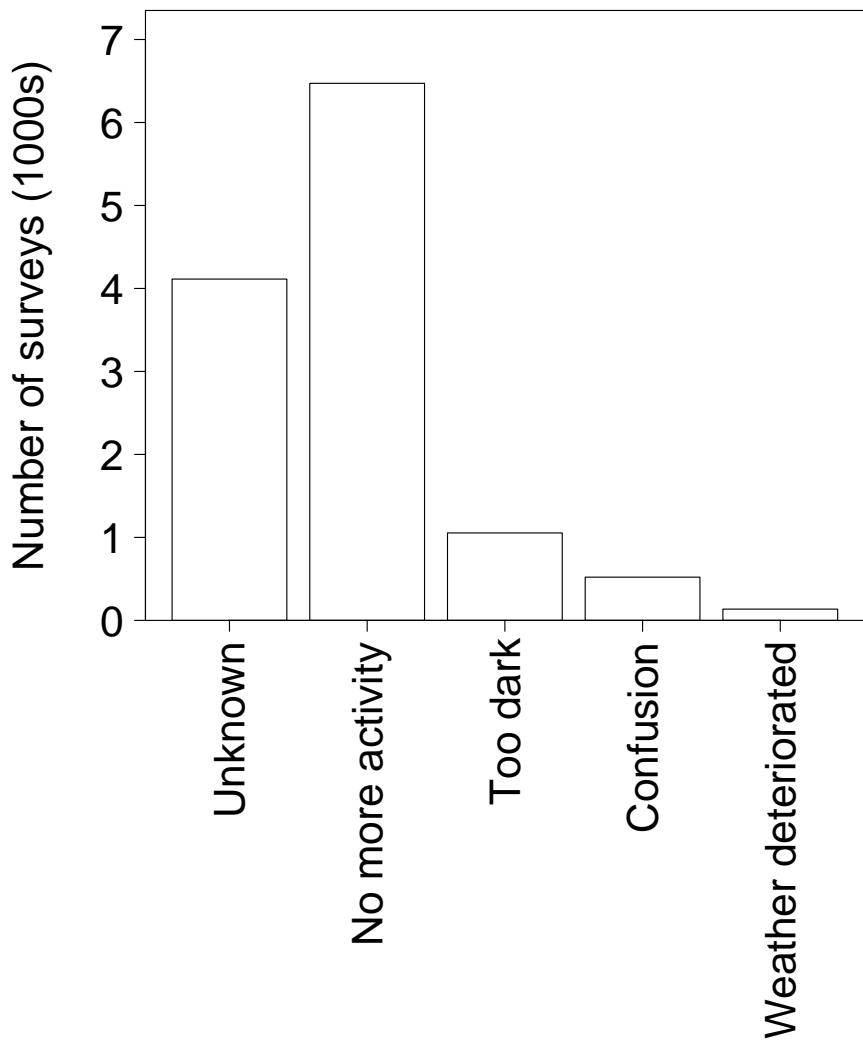


Figure 5.7: A barchart showing the reasons given for terminating roost counts.

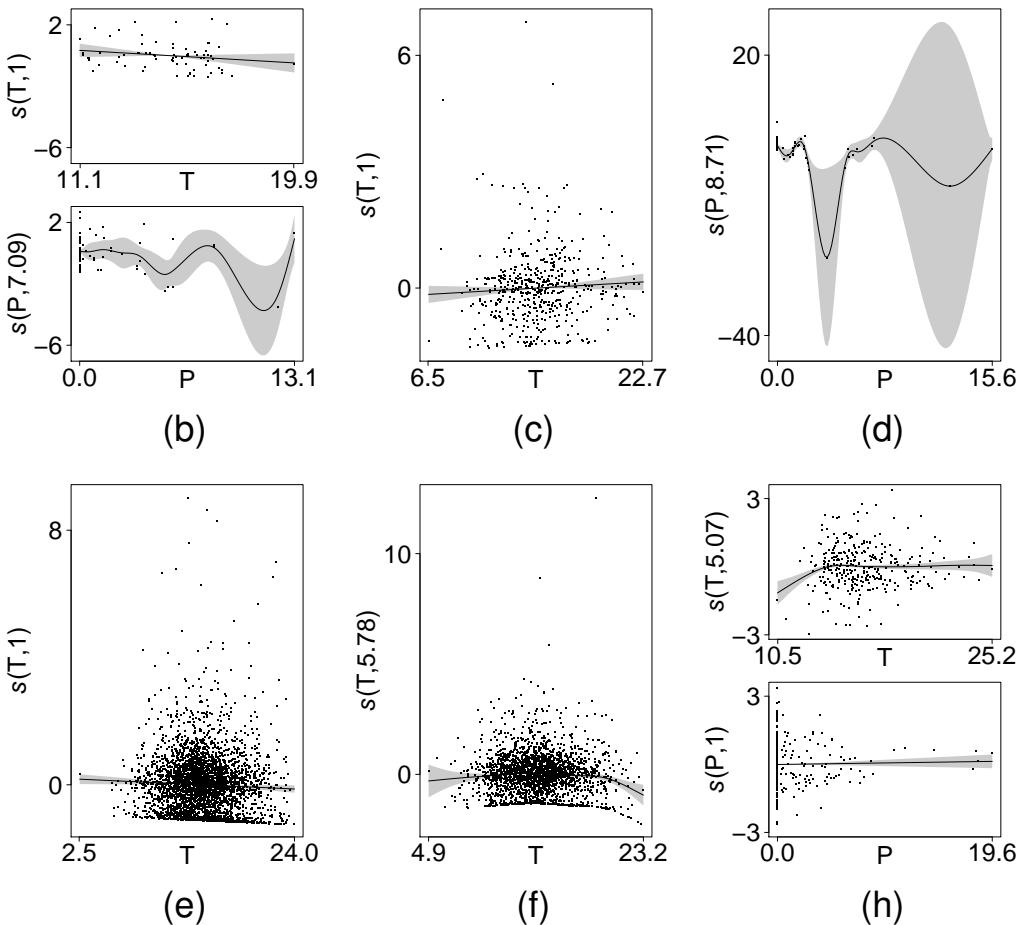


Figure 5.8: GAM smoothing curves for the effects of temperature ( $T$ , °C) and precipitation ( $P$ , mm) on roost counts.  $s(\bullet)$  on the y-axis is a smoothing function with associated estimated degrees of freedom. Points are residuals and shaded bands are 95% confidence intervals. Bat species are (b) Daubenton's, (c) Natterer's, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, and (h) greater horseshoe. Note: the  $\text{GAM}_w$  model did not explain more deviance than a null intercept model for (a) serotine, (g) brown long-eared, and (i) lesser horseshoe and no plots were generated.

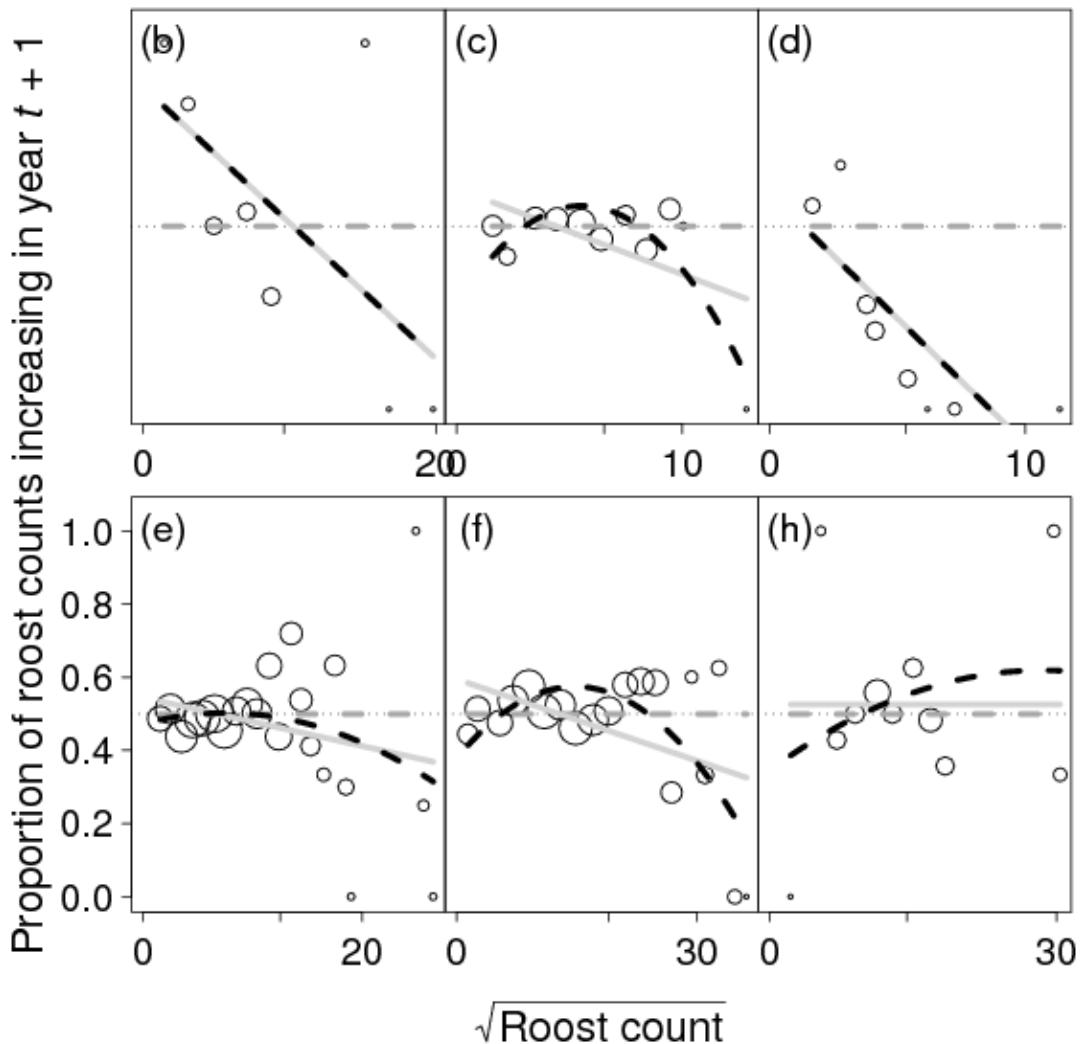


Figure 5.9: Individual species plots showing random walk (RW), negative density feedback (ND) and Allee dynamics (AE) model fits for roost replacement rate as a function of  $\sqrt{\text{roost size}}$ . Roost replacement rate calculated from roost counts (i) smoothed for prevailing weather effects ( $\text{GAM}_w$ ). Bat species are (a) serotine, (b) Daubenton's, (c) Natterer's, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, (g) brown long-eared, (h) greater horseshoe, and (i) lesser horseshoe. Note: the  $\text{GAM}_w$  model did not explain more deviance than a null intercept model for the (a), (g), (i) and no plots were generated. Legend in Figure 5.5.

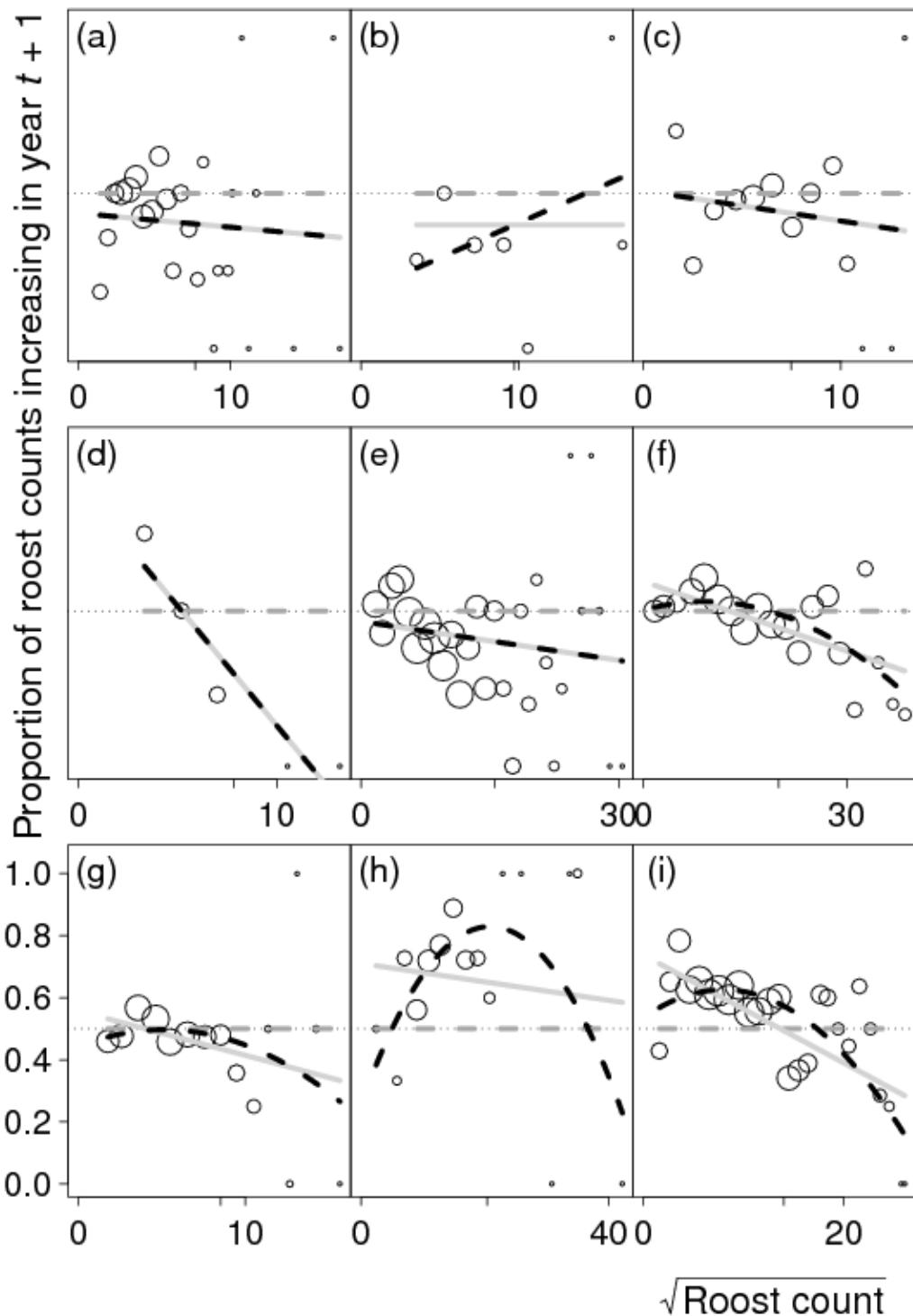


Figure 5.10: Individual species plots showing random walk (RW), negative density feedback (ND) and Allee dynamics (AE) model fits for roost replacement rate as a function of  $\sqrt{\text{roost size}}$ . Roost replacement rate calculated from roost counts (ii) with no smoothing (Original). Bat species are (a) serotine, (b) Daubenton's, (c) Natterer's, (d) noctule, (e) common pipistrelle, (f) soprano pipistrelle, (g) brown long-eared, (h) greater horseshoe, and (i) lesser horseshoe. Note: the  $\text{GAM}_w$  model did not explain more deviance than a null intercept model for the (a), (g), (i) and no plots were generated. Legend in Figure 5.5.

# **Chapter 6**

## **General discussion**

## **6.1 Thesis aims and objectives: a reminder**

The principle aim of this thesis was to quantify the empirical support for demographic Allee effects and then refine the statistical methods used to detect them. I confronted this by setting four objectives, each of which was the motivation or question to one of the four preceding thesis chapters. The objectives were to: (i) Review the concept and empirical evidence for Allee effects and use this as a platform to speculate about the commonness of demographic Allee effects in natural populations. (ii) Examine a large sample of taxonomically diverse populations for empirical evidence of demographic Allee effects and identify possible biases in the data and methods used to detect them. (iii) Highlight the biases of commonly used model-fitting methods for detecting demographic Allee effects in natural populations and propose an alternative method. And (iv) Use the newly developed method to seek evidence of demographic Allee effects in a group of social species.

Below I will attempt to summarize the findings from these four chapters and show how they have made a valuable contribution to the methods used to detect demographic Allee effects, and our ability to predict when and where demographic Allee effects might occur.

## **6.2 Thesis findings in a (long) paragraph**

Recall that a component Allee effect describes reduced individual fitness at a reduced population size and can, under certain conditions, manifest as reduced population growth at reduced population size - a demographic Allee effect. Assuming no taxonomic or publication bias, my collaborators and I reviewed the Allee effect literature, using the intuitive mate-finding Allee effect mechanism as an example, and found that component Allee effects are common in natural populations but rarely manifest as demographic Allee effects (II). There are myriad reasons for this including benefits accrued from a release from intraspecific competition. However, since so many of todays populations are declining and threatened, we predicted a higher incidence of demographic Allee effects. An analysis of 1198 natural populations failed to support this prediction and we detected a demographic Allee effect in less than 1 in 92 populations. Nevertheless, the analysis also showed a higher likelihood of detecting demographic Allee effects, suggesting problems in the data or methods used to detect them. Analysis of the factors preventing their detection indicated that local climate, measurement error or deterministic trends could all play a role (III). Unfortunately, however, the relationships between these factors are probably too complex to untangle. Rather they are likely to manifest in highly variable time series. We used a simulation study to show that detecting demographic Allee effects in highly variable time series is likely to be challenging. Subsequently, we borrowed from existing time series analysis methods to develop a statistical procedure to better detect demographic Allee effects in highly variable time series, and illustrated its advantage using real datasets (IV). We then applied the new statistical procedure to large datasets collected for nine species of UK social bats and revealed - after controlling for some potentially confounding variables - a demographic Allee effect in 4 of 9 bat species. This reaffirmed our confidence in the new statistical procedure and calls into question the paucity of demographic Allee effects observed in other social species (V).

## 6.3 Three key advances for demographic Allee effects

This thesis contributes three important advances to the field of Allee effects: (i) an advance in the methods used to detect demographic Allee effects, (ii) an advance in the statistical framework used to isolate evidence of demographic Allee effects, and (iii) an advance in our knowledge of which species should exhibit demographic Allee effects. I will expand on each of these in turn below.

### 6.3.1 Advancing demographic Allee effect detection: $R$ or $r$ ?

One of the key messages emerging from this thesis is that population replacement rate ( $R$ ) appears to have important advantages over *per capita* population growth rate ( $r$ ) for identifying population growth dynamics, particularly demographic Allee effects. Population censuses are subject to various practical problems that affect their accuracy (II). For example, population counts are subject to measurement error that can cause spurious detection of population growth dynamics (Shenk et al. 1998). Moreover, smaller populations might be prone to higher levels of measurement error compared to larger populations (Holmes and Fagan 2002) introducing systematic bias, especially in time series exhibiting a demographic Allee effect. Where more than one observer is responsible for recording population censuses, differences between counts might be due to differences in skills between observers - a bias known as observer error (Cunningham et al. 1999).

Such sources of error are endemic to population census techniques and are practically unavoidable. Various approaches have, however, been proposed to overcome them. Perhaps the single best solution would be to measure the magnitude of measurement error for each observer (even if a single observer) or combine observations from different observers (e.g., Cunningham et al. 1999). This has been routinely recommended as part of radio telemetry studies (White and Garrott 1986) and involves measuring each observer's performance in blind and predetermined tests. Unfortunately, this has not been standard practice in population censuses. Rather, a large amount of data has been collected over long periods for which no information on measurement or observer error is known (Freckleton et al. 2006). Although some authors might condemn these data to the data archive in the sky, others consider this wasteful and have suggested alternative solutions including using several populations to improve estimates of density feedback (Dennis et al. 1998; Langton et al. 2002; Barrowman et al. 2003) and various statistical solutions including the use of simulation procedures (Ellner et al. 2002) and state-space models (Dennis et al. 2006).

We advocate using multiple populations to better detect population growth dynamics (III). Rather, however, than adapting analyses to accommodate several population time series as spatial replicates, we advocate using multiple population time series to calculate  $R$ , and use it in subsequent analyses in place of  $r$ . By using  $R$ , we reduce the quantitative annual change in population size to a qualitative value (i.e., 'increased' or 'decreased'; see the schematic of  $R$  calculation in Figure 6.1). This has the desirable effect of removing all variation in counts due to measurement and observer errors. It also, however, removes all other variation including that due to the population growth dynamic itself. Consequently, although this statistical procedure might facilitate distinguishing between different population growth dynamics, it might fail to characterize the 'strength' of the population dynamic.

The decision to use  $R$  or  $r$  will depend upon the aim of the investigation and the quality of the time series available. If the aim is to detect a particular population dynamic using existing data for which there is no assessment of measurement or observer error, then the use of  $R$  is highly

recommended. This is principally because calculation of  $R$  removes the influence of unknown sources of variation but also because  $R$  can include time series with  $\geq 2$  consecutive observations. On the other hand, if the aim is to determine the strength of a particular dynamic from a single and unique long time series, then using  $r$  will be preferable. If using  $r$ , however, it will also be preferable to control for the influence of factors including measurement and observer error, local climate, habitat change, interspecific interactions and migration on population estimates by measuring them alongside population censuses. Even better, a carefully replicated and controlled manipulative experiment should be used (Turchin 2003).

Although in this thesis I extended the use of  $R$  to better detect demographic Allee effects in replicate population time series (III), I believe that  $R$  can be usefully applied to detect other population growth dynamics replicate time series and in metapopulations with unknown levels of migration. These two points are both illustrated by the common pipistrelle *Pipistrellus pipistrellus* analysis in chapter IV. My collaborators and I calculated  $R$  from many common pipistrelles roosts distributed across the UK. Common pipistrelles show low roost site fidelity meaning that individuals move routinely between different roosts (Davidson-Watts and Jones 2006). We fitted a suite of population growth models to  $R$  and found highest support for the negative exponential growth model, suggesting that the common pipistrelle is declining across the UK. This finding accords with recent population trends compiled by the UK's Bat Conservation Trust (BCT) and was confirmed with a General Additive Model (GAM) using the raw population time series (IV). The consensus of these findings suggests that common pipistrelles are declining in the UK, but also that using multiple time series to calculate  $R$  will facilitate detection of population growth dynamics other than demographic Allee effects including, for example, negative density feedback and exponential growth.

### 6.3.2 Advancing demographic Allee effect evidence: multi-model analyses

Measurement and observer error, environmental stochasticity, species interactions and migration are just a few of the factors that might lessen our ability to collect accurate population census data and might therefore complicate detection of population growth dynamics (II; III). Nevertheless, early research on population growth dynamics focused strongly on isolating "statistical density dependence" (*sensu* Dennis and Taper 1994) from such noisy population time series. This usually entailed comparing negative density feedback and random walk population growth model fits calculated using linear regression (e.g., Dennis and Taper 1994). Several such tests were developed during the period from 1980 to 2000, when it appeared that flaws in one test were good justification to develop another. Consequently, we have, at our disposal, a battery of tests to detect 'statistical density dependence' using linear regression (Fox and Ridsdillsmith 1995).

Besides the accuracy of the data used to detect population growth dynamics, the statistical tests frequently employed to detect population growth dynamics have also come under criticism. For example, Freckleton et al. (2006) showed how linear regression techniques could produce spurious negative density feedback signals in density independent data with measurement error. They also, however, stated that non-linear density feedback should not spuriously arise from measurement error because the latter should be strictly linear on a log-log scale (Freckleton et al. 2006). Zeng et al. (1998), however, have shown how using highly dimensional models, such as those parameterised to detect non-linear density feedback, can result in spurious detection of complex population dynamics due to overparameterisation. How to best detect density feedback in population growth dynamics is therefore a subject of ongoing debate (Dennis et al. 2006).

Some researchers opted for a different paradigm to investigate the evidence for density feedback in population growth. They did not aim to demonstrate the existence of 'statistical density

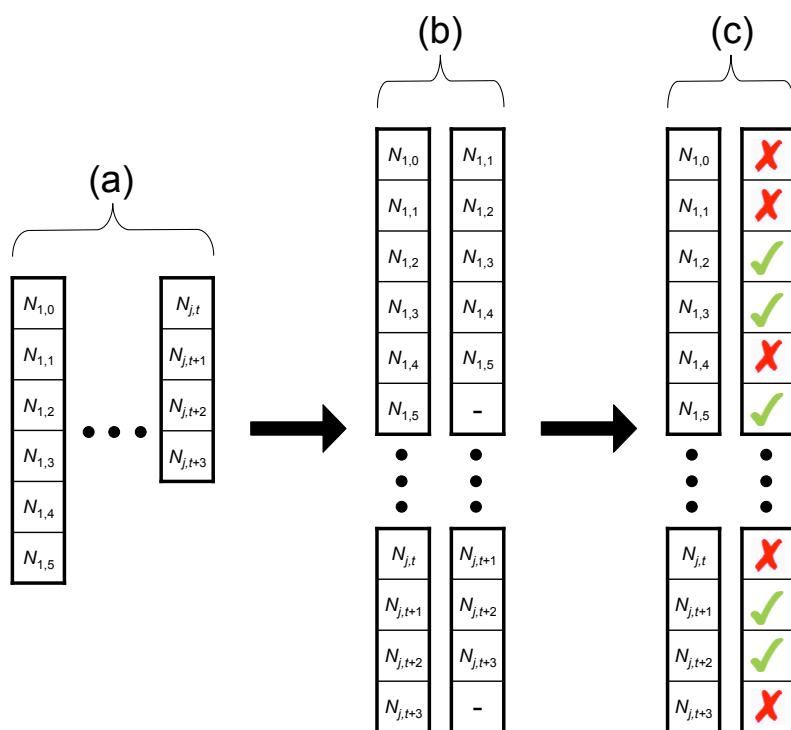


Figure 6.1: A schematic illustrating how to calculate population replacement rate (see also Tobin et al. 2007). (a) Begin with  $j$  time series, each with observations  $N$  taken from time  $t$  to time  $t + i$ . For example, the first observation of the first time series is denoted  $N_{1,0}$ . (b) For each of the  $j$  time series, align  $N_t$  with  $N_{t+1}$  and concatenate the two resulting columns with those calculated for the previous time series. (c) Calculate whether  $N_{t+1}$  increased (tick) or decreased (cross) from the observed population size  $N_t$ .

dependence' but rather aimed to measure the empirical support for the existence of density feedback set against a background of feasible alternative population growth models (e.g., Zeng et al. 1998; Brook and Bradshaw 2006). Empirical support is generally defined as a model's Information Theoretic or Bayesian parameter-adjusted measure of likelihood relative to all other models in the model set (Brook and Bradshaw 2006), although it can be measured using more conventional measures such as  $r^2$  (Coulson et al. 2008).

When measuring the empirical support for a set of population growth dynamics, we must first decide on which models to include in the model set. This is a somewhat subjective exercise and should be dictated by the question we hope to answer. For example, the main question in this thesis has been 'how common are demographic Allee effects?' and required me to compare the support for demographic Allee effects to the support for other 'major' population growth dynamics (i.e., negative density feedback, exponential growth and no growth). Obviously, there will be population growth dynamics that I did not consider. For example, the theta logistic model (also known as the  $\theta$ -logistic model) fits negative density feedback in population growth with an extra parameter ( $\theta$ ) that allows it to take a non-linear concave or convex form (Sæther et al. 2008). Indeed, Sibly et al. (2005) found high support for the concave form of theta-logistic growth in over 5000 time series taken from the Global Population Dynamics Database. Freckleton et al. (2006), on the other hand, question the biological meaning and thus value of including the catchall  $\theta$  parameter.

The model sets used in this thesis generally reflected the model set used by Berryman (2003) in his article developing a general theory of population growth, albeit we used a simpler linear negative density feedback term. As such, the models were all generally special cases of the most complex model: a non-linear model with direct linear negative density feedback and a demographic Allee effect (Courchamp et al. 1999). Consequently, the model set had the desirable quality of quantifying the value of adding terms encapsulating negative density feedback and a demographic Allee effect to describe observed population growth dynamics. This, in turn, allowed us to draw inferences about the commonness of these population growth dynamics in natural populations. Since this represents an aim common to many studies of population growth - from meta-analyses to studies of individual species - we recommend discontinuing the use of 'statistical density dependence' tests (see Fox and Ridsdillsmith 1995 and references therein) and adopting the multi-model Information Theoretic approach used here and elsewhere (Turchin and Taylor 1992; Zeng et al. 1998; Brook and Bradshaw 2006).

Finally, since population growth models including demographic Allee effects are often generalizations of simpler negative density feedback models, we recommend including a demographic Allee effect model in all model sets, even when identifying a demographic Allee effect is not an explicit study aim.

### 6.3.3 Advancing demographic Allee effect knowledge: social species

In this thesis, I developed a statistical procedure to better detect demographic Allee effects using multiple time series and used it to examine evidence of demographic Allee effects in social species - UK bats. The choice to focus on social species was taken because previous theoretical studies have suggested that social behaviours require a minimum number of participants to be efficient, thereby rendering the species susceptible to demographic Allee effects (Courchamp et al. 2008). At a rudimentary level (referred to as "proto-cooperation" by W.C. Allee), social behaviours could include sexual reproduction, predator defense or environmental conditioning (II). More traditionally, however, social behaviours include cooperative breeding, cooperative hunting, huddling for warmth and information sharing (Courchamp et al. 2008).

## Discussion

Using the statistical procedure developed to better detect demographic Allee effects, I found a higher incidence of demographic Allee effects in a selection of social species (IV) compared to a selection of 'random' species (II). Although this comparison might reflect the higher power of the statistical procedure to detect demographic Allee effects, it also suggests that social species might be more prone to them. To disentangle these two possibilities would require collecting and analysing additional time series for the 'random' species analysed in chapter II - a substantial undertaking that could not be achieved within the timeframe of this thesis. Alternatively, a reanalysis of the Bat Conservation Trusts National Bat Monitoring Programme datasets analysed in chapter IV using the techniques employed in chapter II might suffice - another large undertaking, but a possibility nonetheless. Here, however, I will attempt to convince the reader that social species are more prone to demographic Allee effects by outlining the mechanisms by which component Allee effects might arise in a social species, the Kalahari meerkat *Suricata suricatta*.

Meerkats have been the subject of research led by Prof. Tim CluttonBrock for over 15 years. They are strong candidates for exhibiting demographic Allee effects because they are obligate cooperative breeders (Clutton-Brock et al. 1998b) and they forage in groups to protect themselves from predators (Clutton-Brock et al. 1999a). Furthermore, it appears the benefits accrued from these behaviours vary with group size. Meerkats are singular breeders; breeding is monopolised by a single dominant female and subordinate females, or helpers, help raise the dominant female's pups by babysitting and caring, even at their own expense (Scantlebury et al. 2002, but see Russell et al. 2003b). Clutton-Brock et al. (1998b) showed that helpers in smaller groups invest proportionally more time babysitting than helpers in larger groups, offsetting the otherwise reduced reproductive success in smaller groups (Russell et al. 2003a, 2002). Indeed, reduced pup fitness in smaller groups is actively avoided. Although dominant females rarely participate in the care of their offspring (Clutton-Brock et al. 2000; Hodge et al. 2008), they will invest more effort in caring if the helper to pup ratio decreases (Clutton-Brock et al. 2004) thereby ensuring pups maximise their daily weight gain (Clutton-Brock et al. 2001c)). Although at first sight this appears to be a selfish act to maximise their own fitness, it also appears to benefit helpers by promoting larger group sizes (Clutton-Brock et al. 2001c; Russell et al. 2007).

Observations on feeding behaviours also suggest that dominant females and helpers act to promote larger group sizes. It seems that helpers are more likely to feed female pups than males (Brotherton et al. 2001; English et al. 2008) possibly because females are the more philopatric sex and therefore more likely to contribute to group success (Clutton-Brock et al. 2002). This finding is robust to various alternative explanations including relatedness (Clutton-Brock et al. 2001a), the amount of begging (Madden et al. 2009a,b) and the productivity of each individual helper (Hodge et al. 2007). Indeed, Kokko et al. (2001) showed how passive and active group augmentation could be an evolutionary stable strategy, i.e., could maximise long-term fitness of individual group members.

Aside from the benefits of cooperative breeding, meerkats also forage in groups to protect themselves from predators. Clutton-Brock et al. (1999a) showed that predation rates were higher in the Kalahari national park, where predator abundance was high, than in neighbouring ranchland devoid of predators. Moreover, they showed that juvenile mortality was higher in smaller groups both inside and outside the national park. This arises because smaller groups are less vigilant than larger groups. Meerkats forage under the watchful eye of a 'sentinel' - an individual who scans the horizon for predators while others forage (Clutton-Brock et al. 1999c). It is logical that the smaller the group size, the fewer sets of eyes there are to be vigilant for predators and so the higher the risk of predation. This increased predation risk might, however, be offset by sen-

tinels that guard more frequently and for longer periods at the expense of foraging (Clutton-Brock et al. 1999c). In actual fact, it seems that sentinels might assume the task of guarding for their own selfish protection, and only when they have fed sufficiently (Clutton-Brock et al. 1999c). Interestingly, being a sentinel might afford other untoward advantages. Extra-group paternity is likely to be an important factor in stabilizing group sizes as subordinate males seek to maximise their individual fitness (Isvaran and Clutton-Brock 2007). It seems that sentinels are rewarded for their duties with extra opportunities to mate with females (Clutton-Brock et al. 2006; Young et al. 2007) despite the penalties of reduced foraging and pup caring (Young et al. 2005), and probably with females in geographically closer groups (Drewe et al. 2009).

Meerkats are cooperative breeders and cooperate to reduce predation risk but are they really social animals. If we define allo-grooming as a social behaviour, then meerkats can be considered as social. Dominant animals are most likely to be groomed and are more likely to groom other dominants or youngest female subordinates (Kutsukake and Clutton-Brock 2006b). Further, subordinates groom dominants for longer in larger groups (Kutsukake and Clutton-Brock 2010). Although allo-grooming can have direct fitness advantages by reducing shared parasite loads, it seems that grooming in meerkats serves a social role. Meerkats appear to use grooming as a way to express subservience (Madden and Clutton-Brock 2009). Indeed, not only do dominants groom older subordinates less, but they are actively more aggressive to them too (Kutsukake and Clutton-Brock 2006a). But what does grooming have to do with group size? Well, aggression appears to have a long-lasting effect on subordinates (Kutsukake and Clutton-Brock 2008) and is the main way that dominant animals assert their superiority over subordinate animals (Clutton-Brock et al. 2001b). Higher aggression tends to suppress breeding in older subordinate females (O'Riain et al. 2000; Young et al. 2006), and where that doesn't work, infanticide is an alternative option (Clutton-Brock et al. 1998a; Young and Clutton-Brock 2006). Also, if group sizes get too large, then it seems that older subordinates subjected to high levels of aggression are the first to be evicted (Clutton-Brock et al. 2008) and this results in stable group sizes with maximal long-term fitness (Stephens et al. 2005).

Although females can suppress subordinates from breeding and evict them if the group size gets too large, there is little evidence that a breakdown of cooperative behaviours at small group sizes will manifest as a demographic Allee effect. One noteworthy exception was recorded after a period of prolonged low rainfall. There is no doubt that rainfall dictates the availability of food in the Kalahari and this plays a role in meerkat population regulation (Hodge et al. 2008). Interestingly, however, it might also interact with meerkat cooperation and drive demographic Allee effect dynamics. Clutton-Brock et al. (1999b) noted that over 60% of groups went extinct during a long period of drought and few of these returned in the ensuing years. This was because lone emigrants could not successfully find groups without the presence of helpers (Courchamp et al. 1999), perhaps because they were more prone to predation (Courchamp et al. 2000b). In contrast, groups that survived the drought recovered to pre-drought levels, albeit somewhat slowly (Clutton-Brock et al. 1999b). Although not proof of a demographic Allee effect, the meerkat population dynamics were similar to those predicted from models of obligate cooperative breeders with a prescribed demographic Allee effect (Courchamp et al. 1999; Courchamp et al. 2000b).

Here, I have illustrated how social and cooperative behaviours might render species more prone to demographic Allee effects using the Kalahari meerkat as an example. Of course, there are countless other social species of species that are obliged to cooperate. Take, for example, eusocial insects that show the same singular breeder cooperative breeding strategy as the meerkats (Wilson and Hölldobler 2005), or the many microchiropteran bat species that gather for a variety of reasons (Kerth 2008). Many bird species might cooperate to improve foraging: seabirds

that share information on food locations (Schreiber and Burger 2002), or to improve breeding: Arabian babblers *Turdoides squamiceps* and white-fronted bee-eaters *Merops bullockoides* co-operate to raise bigger clutches (Koenig and Dickinson 2004). African wild dogs *Lycaon pictus* exhibit several cooperative behaviours including cooperative hunting, cooperative breeding, and cooperative predator and resource defense (Courchamp et al. 2000a). Interestingly, there is reason to suspect that component Allee effects that might arise from each of these cooperative behaviours will interact in various ways to (generally) intensify their impact on individual fitness (Berec et al. 2007). Although my emphasis here has been on meerkats, it is my hope that the reader can see the wide range of social species that may be prone to demographic Allee effects and to see that the social behaviours they practice are not always facultative but often obligatory to maximise their individual fitness.

## 6.4 Caveats and shortfalls

In this section I will highlight some caveats that could alter the conclusions drawn from this thesis and indicate areas where the thesis might fall short of a comprehensive coverage of demographic Allee effects. I will aim to illustrate some of these points by discussing - in detail - a recent study by Kramer and Drake (2010) that provides a rare and highly commendable experimental illustration of a demographic Allee effect driven by predation.

From the outset, this thesis has focused on analysing population time series for empirical support of demographic Allee effects. I attempted to do this in chapter II using 1198 species' population time series. There are, however, reasons why the conclusions of this chapter might be called into question. First, I used only one of many different ways to fit the population growth models to time series, omitting methods such as Bayesian parameter estimation. Liermann and Hilborn (1997) reanalysed the datasets used by Myers et al. (1995) using a Bayesian approach and reached conflicting conclusions about the commonness of demographic Allee effects. In contrast to Myers et al. (1995), they argued that the existence of demographic Allee effects could not be refuted and recommended that future meta-analyses adopt a Bayesian analytical framework (Liermann and Hilborn 1997). On the other hand, Barrowman et al. (2003) analysed coho salmon *Oncorhynchus kisutch* datasets for evidence of demographic Allee effects using both a frequentist and Bayesian approach and found no discernable difference between their results. Whether I would have reached different conclusions using a Bayesian framework is an open question.

Conclusions from our analyses will be sensitive to our choice of datasets, and although we attempted to use the best and largest datasets we could find, they will have biases. In particular, the 1198 species population time series analysed in chapter II will be biased. The majority of these time series were taken from the Global Population Dynamics Database (GPDD). Sibly et al. (2005) analysed over 4000 GPDD time series (several per species) and suggested that a concave form of negative density dependence was common in natural populations. Peacock and Garshelis (2006), however, highlighted that many of the times series were harvest records and poor substitutes for population censuses because of varying levels of harvesting effort. Although it is difficult to know what proportion of our 1198 time series were harvesting records, it is likely to include the fish datasets which constituted approximately 10% of the datasets. Aside from biases in the methods used to collect these time series, plotting the geographical distribution of the 1198 time series revealed that they were collected primarily in the Northern Hemisphere (Figure 6.2). Since the majority of species in temperate climates are discrete breeders (i.e., they breed at discrete times), we chose to analyse these datasets using discrete population growth models. Had we analysed them assuming continuous growth, the results might have been quite

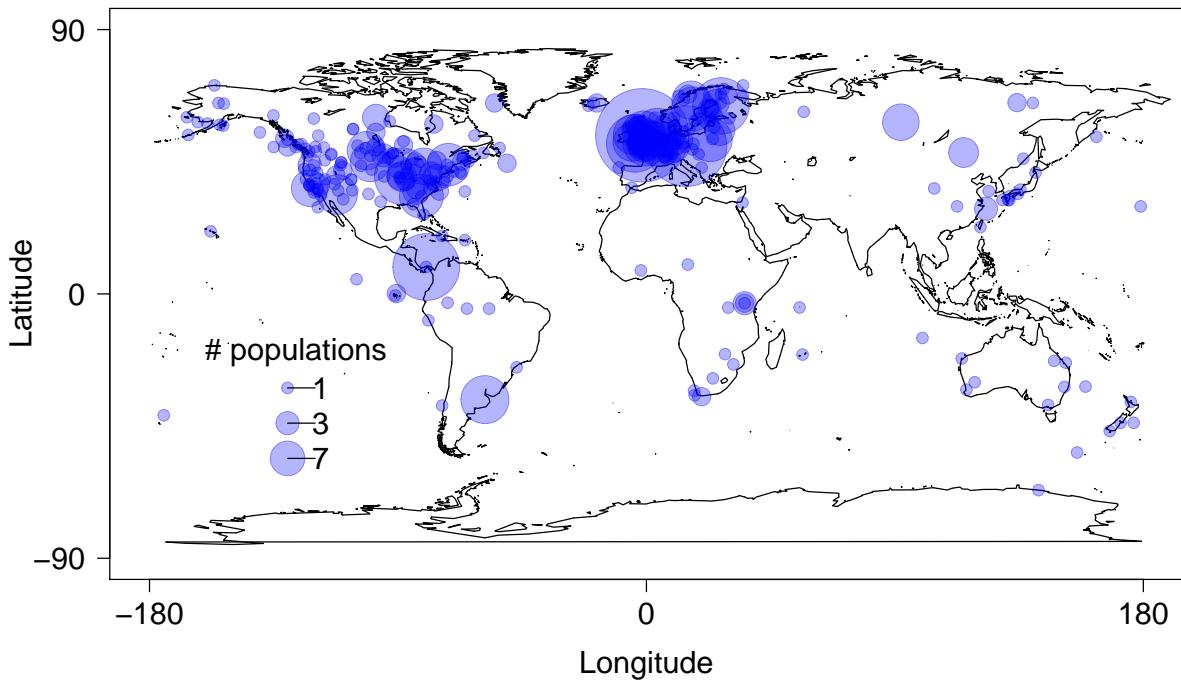


Figure 6.2: Global distribution of the 1198 populations analysed in chapter III. Note that the majority of populations monitored were distributed in the Northern Hemisphere. This suggests using a discrete-time population growth model is appropriate, but, not necessarily for all populations.

different (Getz and Lloyd Smith 2006).

Although the datasets used in chapter II might be biased their collection methods and geographical distribution, the BCT National Bat Monitoring Programme (NBMP) datasets used in chapters III and IV are likely to be robust to these biases. First, they are all collected using a common methodology. Second, they are all collected in the same region of the world - the UK. Indeed, the NBMP was carefully conceived to avoid major sources of bias (Walsh et al. 2002). On the other hand, the NBMP time series are frequently short and might be spatially dependent. Consequently, using individual NBMP time series to parameterise population growth models might give spurious results (Freckleton et al. 2006). Indeed, many of the 1198 time series analysed in chapter II might have been open populations (i.e., populations subject to immigration and emigration) and unsuitable for individual analysis. Unfortunately, overcoming such uncertainty is no menial task: the debate on what constitutes a population is far complicated and so far inconclusive (Camus and Lima 2002). Spatial dependency might be overcome by modelling multiple time series with correlated errors (Dennis et al. 1998; Langton et al. 2002). Alternatively, calculating and modelling  $R$  might also accommodate spatially dependent - and short - time series, although this remains to be investigated and assumes that the drivers of population dynamics are the same for all populations (Hanski et al. 1991).

Besides population time series, there other data types that might be better suited to detecting population growth dynamics such as demographic Allee effects. Coulson et al. (2008) recently showed how data on individual birth and death rates could be used to estimate population growth

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dynamics similarly, or better than, a variety of 'phenomenological' population growth models - demographic models lacking detail on individual demographic processes. Their approach is highly commendable as it attempts to consolidate explicitly the biological processes that might underpin the observed population dynamics. Furthermore, although their data were extensive and very high quality (over 20 years of individual-based data on the insular Soay sheep *Ovis aries* population on Hitra, St. Kilda), similar datasets are being collected for other species (Jones et al. 2008; <http://www.imperial.ac.uk/litsproject/>) and deserve similar attention.

Data derived from carefully designed replicated and controlled manipulative experiments provide the optimal chance of proving (or refuting) the existence of demographic Allee effects and their consequences for reduced and declining populations. For example, Kramer and Drake (2010) recently used replicated and controlled manipulative experiments to demonstrate the existence of a predator-driven demographic Allee effect in laboratory populations of waterfleas *Daphnia magna*. This approach is the single best way to examine the evidence of demographic Allee effect (Turchin 2003). Unfortunately, such data are rare and collecting them anew is costly and will usually be restricted to plants, microorganisms or insects (Kramer et al. 2009).

The study by Kramer and Drake (2010) highlights another shortfall of this thesis: our conclusion that demographic Allee effects might be more common in social species arises from a confounded comparison that fails to acknowledge the existence of other - potentially widespread - Allee effect mechanisms. I concluded from chapter IV that the empirical support for demographic Allee effects from a group of social species was particularly high compared to that found for the 1198 species analysed in chapter II. This fails to consider, however, that the two results were borne of different statistical analyses. Had I analysed the two datasets using the same statistical analyses, the results might have been quite different. Furthermore, concluding that the higher demographic Allee effect evidence in the social species was a consequence of the species' social life-histories ignores recent work suggesting that many non-social species might also be prone demographic Allee effects. To illustrate this, together with the value of using replicated and controlled experiments, I present below a detailed discussion of a recent study of predator-driven Allee effects (Kramer and Drake 2010).

A demographic Allee effect describes a decrease in population growth rate at small population size or low density (Stephens et al. 1999; Figure 6.3a). Despite the increasing numbers of species coming under threat from human activity, evidence for demographic Allee effects is rare (Gregory et al. in press). 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 a large prey (Courchamp et al. 2002). Gascoigne and Lipcius (2004), however, showed that a predator - an extrinsic factor - could induce an Allee effect 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 and Lipcius 2004; Figure 6.3b). 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) showed the existence of a demographic Allee effect 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.

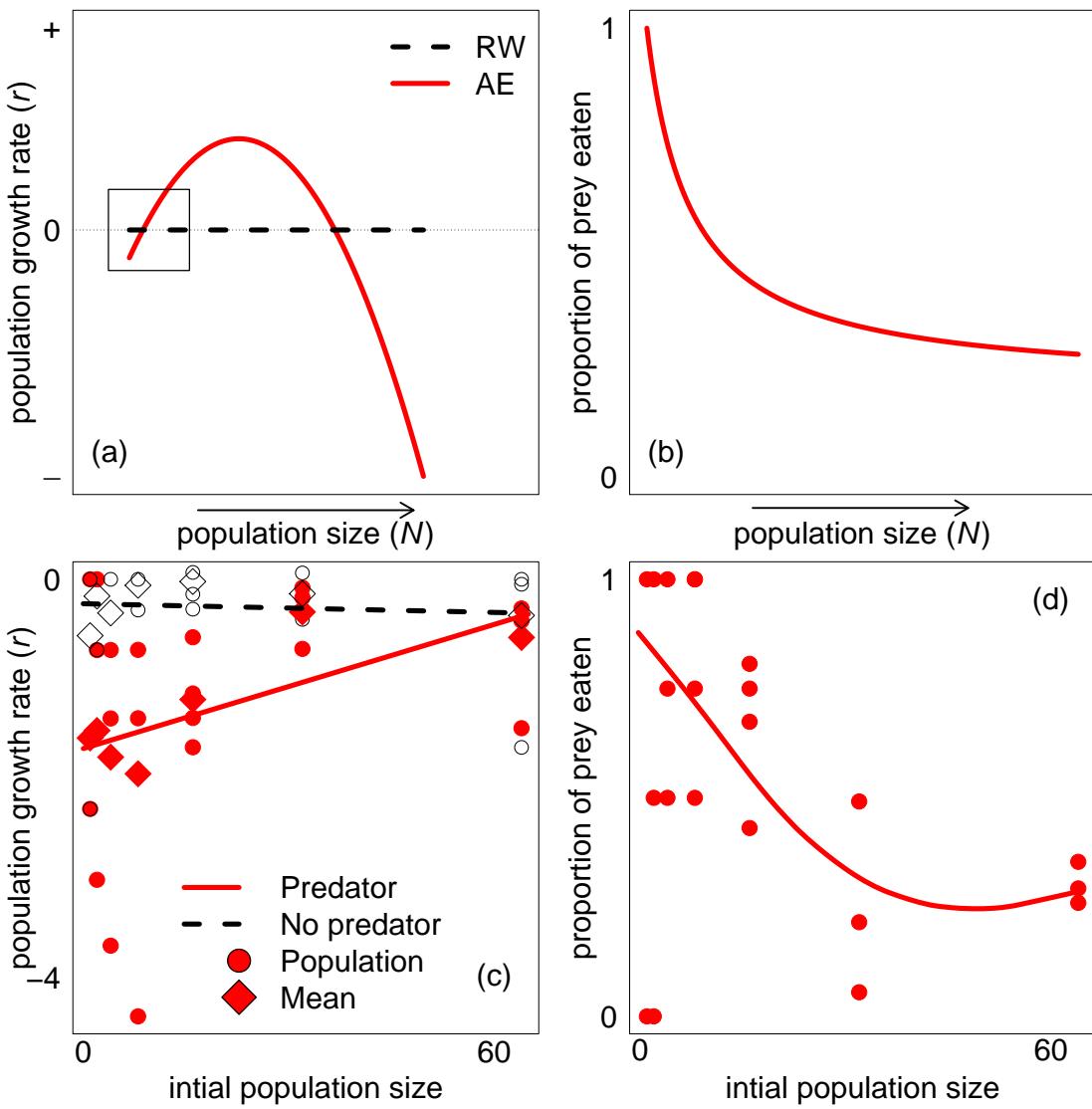


Figure 6.3: (a) a plot to show the shape of a demographic Allee effect (AE) in population growth rate ( $r$ ) in contrast to no growth or random walk (RW). Note how, in contrast to RW,  $r$  with an AE is low and negative at low population size ( $N$ ; see the inset box). (b) a plot to show a Type II predator functional response in prey consumption rate (here shown as proportion of prey consumed to compliment Kramer and Drake (2010)). (c) the predator-driven demographic Allee effect 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 and Drake (2010).

## Discussion

Kramer and Drake (2010) report that predatory midge larvae of the genus *Chaoborus* can induce a demographic Allee effect in water flea *Daphnia magna* populations via a predator-driven Allee effect, and that the demographic Allee effect can speed smaller prey populations to premature extinction. Although not the first demonstration of a predator-driven Allee effect, Kramer and Drake (2010), by using a controlled laboratory experiment with replication, was able to avoid the dilemma of alternative explanations and confirm the existence of a predator-driven Allee effect. As Kramer and Drake (2010) point out, other reported cases of predator-driven Allee effects 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 Allee effect 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 Allee effects can manifest as a demographic Allee effect, and in the case of the Island fox, represented an alternative explanation to a predator-driven Allee effect (Angulo et al. 2007). Indeed, most field-based trials of predator-driven Allee effects will support alternative explanations. Of course, the presence of a type II predator function response needs not translate to a predator-driven Allee effect if predation pressure is insufficient. Moreover, even if induced in a laboratory or an in situ field setting, a predator-driven Allee effect might be too weak to manifest as a demographic Allee effect, as is true of any component Allee effect (Stephens et al. 1999).

Although not the first evidence of a predator-driven demographic Allee effect, Kramer and Drake (2010) do present the first experimental demonstration that this process can precipitate population extinction. They developed a stochastic predator-driven Allee effect model for their *Chaoborus-Daphnia* predator-prey system that predicted a sigmoid prey population extinction probability curve characteristic of a demographic Allee effect (Dennis 1989). Armed with these predictions, they revealed a Type II functional response in *C. trivittatus* predation on different *D. magna* densities (Figure 6.3d) that manifested as a lower population growth rate ( $r$ ) at low prey densities (Figure 6.3c). Indeed, this finding was strengthened by comparison with the control groups (no predators); control group  $r$  was comparatively unchanging across different prey densities, and at highest prey densities was roughly the same as for experimental groups. By comparing observed population extinction probabilities to predictions from their mechanistic model, Kramer and Drake (2010) established a clear link between a predator-driven Allee effect and population extinction due to a demographic Allee effect. This represents the first experimental illustration of a predator-driven Allee effect 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 and 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 Allee effect, it might not easily generalise to any but the shortest of timescales under field conditions. Excessive variation in calculated  $r$  prevented them estimating the Allee threshold ( $A$ ) beneath which  $r$  becomes negative and the population (usually) begins its decent to extinction (a ‘strong’ Allee effect; Wang and 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 Allee effects. This latter case highlights a larger issue in the detection of Allee effects, particularly demographic Allee effects; evolution should act against any mechanism that results in lower individual fitness. Consequently, species should be adapted either to counteract Allee effects or avoid the population sizes at which they act (Courchamp et al. 2008).

The aforementioned reasons alone should illustrate the point that experiments do not always epitomise 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 and 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 Allee effect. 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 and Chesson 2002). Indeed, such events have provided the setting for several predator-driven Allee effect studies including the quokka and island fox (Angulo et al. 2007, Sinclair et al. 1998). Also, humans themselves might be regarded as part of the system - the predator. Human exploitation of natural populations might induce Allee effects including, for example, the highly publicised collapse and failing recovery of the cod fishery off Newfoundland, Canada (Rose and Kulka 1999).

Adding humans to the list of predators doubtless adds numerous examples to the list of predator-driven Allee effects; however, according to a recent literature review of the Allee effect (Kramer et al. 2009) and book (Courchamp et al. 2008) there are relatively few studies published on the subject (Figure 6.4). 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 Allee effects. Prey behaviours like the ‘dilution effect’ might be indicative of a predator-driven Allee effect 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; \* = a wildcard representing a character string of any length) revealed some 73 references - approximately twice the number used in Figure 6.4. Second, we launch a call for more carefully designed *in situ* experiments, such as those by Turchin and Kareiva (1989), to demonstrate the existence of predator-driven Allee effects despite nature’s complexities.

Kramer and Drake (2010) merely (and modestly) hint at the implications of their findings, speculating a higher incidence of demographic Allee effects 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 consider briefly some untoward implications of predator-driven Allee effects 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 fisherman, by removing large predatory fish, freed the crown-of-thorns starfish *Acanthaster planci* from a weak predator-driven Allee effect, which subsequently underwent a population boom with dire consequences for its reef-building coral prey (Dulvy et al. 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 pallasi* 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 and Dill 1997).

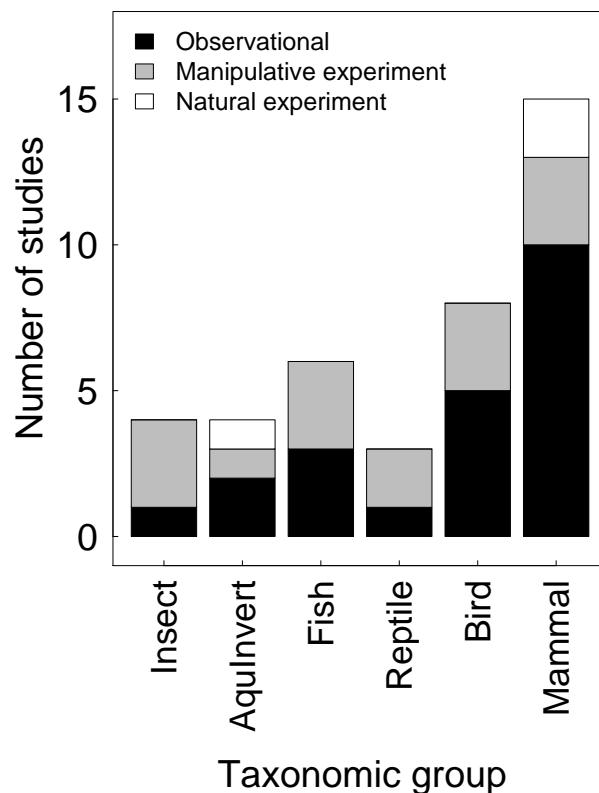


Figure 6.4: A barplot to show the relative numbers of predator-driven Allee effect studies included in a recent review (Kramer et al. 2009) and book (Courchamp et al. 2008) on Allee effects. Studies are categorised by taxonomic group and type of study. Although not a comprehensive treatment of the predator-driven Allee effect 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 Allee effects, 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 aquatic invertebrates (Kramer and Drake 2010) were manipulative experiments done in laboratories. The references used to compile this graphic are presented in Supporting Information.

Kramer and Drake (2010) have closed an important knowledge gap with the experimental demonstration of a predator-driven Allee effect. These results show that despite more than half a century of research into the core processes of the Allee effect, 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 Allee effects could apply to species competing for limited resources, in what might become known as a competition-driven Allee effect.

## 6.5 Conclusion

Studies of demographic Allee effects can be classified as belonging to one of the following categories: meta-analytical, species account, or theoretical development. Leaving aside theoretical developments and focusing on the empirical evidence of demographic Allee effects, we note very few confirmed cases of their existence. Before this thesis we would have attributed this to their unstable nature (recall populations rarely remain at the population sizes where Allee effects should act), problems measuring populations at small and declining sizes (recall that Allee effects are unstable and populations will rarely be observed near them, and such observations are prone to large measurement errors), and problems in statistically detecting them (recall that measurement and observer error, deterministic trends and spatial scales will all complicate statistical analyses).

This thesis has provided a more detailed understanding of the problems associated with statistically detecting demographic Allee effects and has presented a solution to overcome them. Nevertheless, the paucity of confirmed empirical cases of demographic Allee effects is almost certainly still due to their unstable nature, reducing our likelihood of observing them in natural populations. Perhaps then, rather than focusing on statistical methods to detect them, we should focus our efforts on experimenting with replicate populations to uncover the life-histories that predispose a species to exhibit a demographic Allee effect. According to this thesis, social species would be a good place to start...

## 6.6 Why did I do this thesis?

In the introduction to this thesis I posed myself the question: why did I do a thesis on this subject? to which I responded that I wanted to improve our ability to detect demographic Allee effects to facilitate the management of threatened and invasive populations of plants and animals.

So, did I achieve this aim? Yes and no. This thesis does not provide any irrefutable evidence for widespread occurrence, or even the existence, of demographic Allee effects. It does, on the other hand, advance methods we use to detect demographic Allee effects and suggests that social species might be prone to them. As suggested above, the new ideal research path will be to conduct experiments to confirm or refute the widespread occurrence of demographic Allee effects, concentrating on social species. Prime candidates might be eusocial insects. On the other hand, given the difficulties of experimenting with populations of larger animals, and the fact that many of the populations we would want to investigate are reduced and threatened, we should also continue efforts to detect demographic Allee effects, particularly in social species. In this way, we might hope to meet the burden of proof (de Boer 1991) required to demonstrate their existence. At least in the latter aim, I feel that my collaborators and I have made some important advances. Our developments in the methods and knowledge of demographic Allee effect will be useful to detect and predict where and when they might occur. Now, I urge others to use these advances in

the quest to understand demographic Allee effects and to identify them in declining populations thereby enabling us to implement management before they descend into the extinction vortex.

## **6.7 Perspectives**

I hope this discussion has highlighted the value of this thesis and the advances it contributes to the study of demographic Allee effects. Besides highlighting its advances, however, I am sure that this discussion has also highlighted a number of areas where this thesis falls short of providing a complete answer to some burning questions. Personally, I see clearly two questions particularly emerging from this thesis.

### **6.7.1 Are social species really more prone to demographic Allee effects?**

Chapter IV of this thesis concluded that social species might be prone to demographic Allee effects because they require a minimum number of participants to cooperate effectively. Given their tendency to be dispersed in geographically proximate groups, I believe that data on social species will be amenable to the analyses presented in chapter IV and analysing such datasets will begin to provide weight to the argument that social species are prone to demographic Allee effects. Indeed, this could be extended to a large multi-species factorial meta-analysis of time series data with degree of sociality included as a factor. I have not done this for want of time but it is something I hope to do in the near future.

### **6.7.2 Are there other contexts in which *R* could be useful?**

In Chapters II and IV I demonstrate how the method pioneered by Tobin et al. (2007) can be analysed in an Information theoretic multi-model framework to better detect demographic Allee effects in multiple time series (refer back to chapters III and IV for details). Although I only really used this to detect demographic Allee effects, I see no particular reason why it should not be equally applicable to detecting other major (direct and simple) population growth dynamics. Namely, I see no reason why it could not be used to detect, or distinguish between, random walk, exponential growth and direct linear negative density feedback. Each one of the battery of test conceived to detect these dynamics has been found to perform poorly relative to another (Fox and Ridsdillsmith 1995). Perhaps *R* will prove a robust method for detecting these dynamics?

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## **References**

- Angulo, E., G. W. Roemer, L. Berec, J. Gascoigne, and F. Courchamp. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**:1082–1091.

- Barrowman, N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecological Applications* **13**:784–793.
- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. *Trends in Ecology & Evolution* **22**:185–191.
- Berryman, A. A. 2003. On principles, laws and theory in population ecology. *Oikos* **103**:695–701.
- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* **87**:1445–1451.
- Brotherton, P., T. Clutton-Brock, M. O’Riain, D. Gaynor, L. Sharpe, R. Kansky, and G. McIlrath. 2001. Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology* **12**:590–599.
- Camus, P., and M. Lima. 2002. Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population concepts. *Oikos* **97**:433–438.
- Clutton-Brock, T., P. Brotherton, M. O’Riain, A. Griffin, D. Gaynor, R. Kansky, L. Sharpe, and G. McIlrath. 2001a. Contributions to cooperative rearing in meerkats. *Animal Behaviour* **61**:705–710.
- Clutton-Brock, T., P. Brotherton, M. O’Riain, A. Griffin, D. Gaynor, L. Sharpe, R. Kansky, M. Manser, and G. McIlrath. 2000. Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**:301–305.
- Clutton-Brock, T., P. Brotherton, A. Russell, M. O’Riain, D. Gaynor, R. Kansky, A. Griffin, M. Manser, L. Sharpe, G. McIlrath, T. Small, A. Moss, and S. Monfort. 2001b. Cooperation, control, and concession in meerkat groups. *Science* **291**:478–481.
- Clutton-Brock, T., P. Brotherton, R. Smith, G. McIlrath, R. Kansky, D. Gaynor, M. O’Riain, and J. Skinner. 1998a. Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**:2291–2295.
- Clutton-Brock, T., D. Gaynor, R. Kansky, A. MacColl, G. McIlrath, P. Chadwick, P. Brotherton, J. O’Riain, M. Manser, and J. Skinner. 1998b. Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**:185–190.
- Clutton-Brock, T., D. Gaynor, G. McIlrath, A. MacColl, R. Kansky, P. Chadwick, M. Manser, J. Skinner, and P. Brotherton. 1999a. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology* **68**:672–683.
- Clutton-Brock, T., A. MacColl, P. Chadwick, D. Gaynor, R. Kansky, and J. Skinner. 1999b. Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. *African Journal of Ecology* **37**:69–80.
- Clutton-Brock, T., M. O’Riain, P. Brotherton, D. Gaynor, R. Kansky, A. Griffin, and M. Manser. 1999c. Selfish sentinels in cooperative mammals. *Science* **284**:1640–1644.

## *Discussion*

- Clutton-Brock, T., A. Russell, and L. Sharpe. 2004. Behavioural tactics of breeders in cooperative meerkats. *Animal Behaviour* **68**:1029–1040.
- Clutton-Brock, T., A. Russell, L. Sharpe, P. Brotherton, G. McIlrath, S. White, and E. Cameron. 2001c. Effects of helpers on juvenile development and survival in meerkats. *Science* **293**:2446–2449.
- Clutton-Brock, T., A. Russell, L. Sharpe, A. Young, Z. Balmforth, and G. McIlrath. 2002. Evolution and development of sex differences in cooperative behavior in meerkats. *Science* **297**:253–256.
- Clutton-Brock, T. H., S. J. Hodge, and T. P. Flower. 2008. Group size and the suppression of subordinate reproduction in Kalahari meerkats. *Animal Behaviour* **76**:689–700.
- Clutton-Brock, T. H., S. J. Hodge, G. Spong, A. F. Russell, N. R. Jordan, N. C. Bennett, L. L. Sharpe, and M. B. Manser. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature* **444**:1065–1068.
- Coulson, T., T. H. G. Ezard, F. Pelletier, G. Tavecchia, N. C. Stenseth, D. Z. Childs, J. G. Pilkington, J. M. Pemberton, L. E. B. Kruuk, T. H. Clutton-Brock, and M. J. Crawley. 2008. Estimating the functional form for the density dependence from life history data. *Ecology* **89**:1661–1674.
- Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press.
- Courchamp, F., T. Clutton Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**:405–410.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 2000a. Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. *Animal Conservation* **3**:277–285.
- Courchamp, F., B. Grenfell, and T. Clutton-Brock. 2000b. Impact of natural enemies on obligately cooperative breeders. *Oikos* **91**:311–322.
- Courchamp, F., G. S. A. Rasmussen, and D. W. Macdonald. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behavioral Ecology* **13**:20–27.
- Cunningham, R., D. Lindenmayer, H. Nix, and B. Lindenmayer. 1999. Quantifying observer heterogeneity: a comparison of observers and observation methods. *Australian Journal of Ecology* **24**:270–277.
- Davidson-Watts, I., and G. Jones. 2006. Differences in foraging behaviour between *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825). *Journal of Zoology* **268**:55–62.
- Dennis, B. 1989. Allee effects: population growth, critical density and the chance of extinction. *Natural Resource Modeling* **3**:481–538.
- Dennis, B., W. P. Kemp, and M. L. Taper. 1998. Joint density dependence. *Ecology* **79**:426–441.

- Dennis, B., J. M. Ponciano, S. R. Lele, M. L. Taper, and D. F. Staples. 2006. Estimating density dependence, process noise, and observation error. *Ecological Monographs* **76**:323–341.
- Dennis, B., and M. L. Taper. 1994. Density-dependence in time-series observations of natural-populations - estimation and testing. *Ecological Monographs* **64**:205–224.
- Drewe, J. A., J. R. Madden, and G. P. Pearce. 2009. The social network structure of a wild meerkat population: 1. Inter-group interactions. *Behavioral Ecology and Sociobiology* **63**:1295–1306.
- Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7**:410–416.
- Ellner, S., Y. Seifu, and R. Smith. 2002. Fitting population dynamic models to time-series data by gradient matching. *Ecology* **83**:2256–2270.
- English, S., H. P. Kunc, J. R. Madden, and T. H. Clutton-Brock. 2008. Sex differences in responsiveness to begging in a cooperative mammal. *Biology Letters* **4**:334–337.
- Fox, D. R., and J. Ridsdillsmith. 1995. Tests for density-dependence revisited. *Oecologia* **103**:435–443.
- Freckleton, R. P., A. R. Watkinson, R. E. Green, and W. J. Sutherland. 2006. Census error and the detection of density dependence. *Journal of Animal Ecology* **75**:837–851.
- Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. *Journal of Applied Ecology* **41**:801–810.
- Getz, W. M., and J. O. Lloyd Smith. 2006. Comment on "On the Regulation of Populations of Mammals, Birds, Fish, and Insects" I. *Science* **311**:1100a.
- Gregory, S., C. Bradshaw, B. Brook, and F. Courchamp. in press. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology* **-:-**.
- Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology* **60**:353–367.
- Hodge, S. J., T. P. Flower, and T. H. Clutton-Brock. 2007. Offspring competition and helper associations in cooperative meerkats. *Animal Behaviour* **74**:957–964.
- Hodge, S. J., A. Manica, T. P. Flower, and T. H. Clutton-Brock. 2008. Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology* **77**:92–102.
- Holmes, E. E., and W. F. Fagan. 2002. Validating population viability analysis for corrupted data sets. *Ecology* **83**:2379–2385.
- Isvaran, K., and T. Clutton-Brock. 2007. Ecological correlates of extra-group paternity in mammals. *Proceedings of the Royal Society B-Biological Sciences* **274**:219–224.
- Jones, O. R., J.-M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P. Bize, J. Brommer, A. Charmantier, M. Charpentier, T. Clutton-Brock, F. S. Dobson, M. Festa-Bianchet, L. Gustafsson, H. Jensen, C. G. Jones, B.-G. Lillandt, R. McCleery, J. Merila, P. Neuhaus, M. A. C. Nicoll, K. Norris, M. K. Oli, J. Pemberton, H. Pietiainen, T. H. Ringsby,

## *Discussion*

- A. Roulin, B.-E. Saether, J. M. Setchell, B. C. Sheldon, P. M. Thompson, H. Weimerskirch, E. J. Wickings, and T. Coulson. 2008. Senescence rates are determined by ranking on the fast-slow life-history continuum. *Ecology Letters* **11**:664–673.
- Kerth, G. 2008. Causes and consequences of sociality in bats. *Bioscience* **58**:737–746.
- Koenig, W., and J. Dickinson. 2004. *Ecology and evolution of cooperative breeding in birds*. Cambridge Univ Pr.
- Kokko, H., R. Johnstone, and T. Clutton-Brock. 2001. The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**:187–196.
- Kramer, A., B. Dennis, A. Liebhold, and J. Drake. 2009. The evidence for Allee effects. *Population Ecology* **51**:341–354.
- Kramer, A. M., and J. M. Drake. 2010. Experimental demonstration of population extinction due to a predator–driven Allee effect. *Journal of Animal Ecology* –:–.
- Kutsukake, N., and T. Clutton-Brock. 2006a. Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats *Suricata suricatta*. *Behavioral Ecology and Sociobiology* **59**:541–548.
- Kutsukake, N., and T. H. Clutton-Brock. 2006b. Social functions of allogrooming in cooperatively breeding meerkats. *Animal Behaviour* **72**:1059–1068.
- Kutsukake, N., and T. H. Clutton-Brock. 2008. Do meerkats engage in conflict management following aggression? Reconciliation, submission and avoidance. *Animal Behaviour* **75**:1441–1453.
- Kutsukake, N., and T. H. Clutton-Brock. 2010. Grooming and the value of social relationships in cooperatively breeding meerkats. *Animal Behaviour* **79**:271–279.
- Langton, S., N. Aebsicher, and P. Robertson. 2002. The estimation of density dependence using census data from several sites. *Oecologia* **133**:466–473.
- Liermann, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierachic Bayesian meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1976–1984.
- Madden, J. R., and T. H. Clutton-Brock. 2009. Manipulating grooming by decreasing ectoparasite load causes unpredicted changes in antagonism. *Proceedings of the Royal Society B-Biological Sciences* **276**:1263–1268.
- Madden, J. R., H.-J. P. Kunc, S. English, M. B. Manser, and T. H. Clutton-Brock. 2009a. Do meerkat (*Suricata suricatta*) pups exhibit strategic begging behaviour and so exploit adults that feed at relatively high rates? *Behavioral Ecology and Sociobiology* **63**:1259–1268.
- Madden, J. R., H. P. Kunc, S. English, M. B. Manser, and T. H. Clutton-Brock. 2009b. Calling in the gap: competition or cooperation in littermates' begging behaviour? *Proceedings of the Royal Society B-Biological Sciences* **276**:1255–1262.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenburg. 1995. Population-dynamics of exploited fish stocks at low population-levels. *Science* **269**:1106–1108.

- O'Riain, M., N. Bennett, P. Brotherton, G. McIlrath, and T. Clutton-Brock. 2000. Reproductive suppression and inbreeding avoidance in wild populations of co operatively breeding meerkats (*Suricata suricatta*). *Behavioral Ecology and Sociobiology* **48**:471–477.
- Peacock, E., and D. L. Garshelis. 2006. Comment on "On the Regulation of Populations of Mammals, Birds, Fish, and Insects" IV. *Science* **313**:45a.
- Rose, G., and D. Kulka. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:118–127.
- Russell, A., P. Brotherton, G. McIlrath, L. Sharpe, and T. Clutton-Brock. 2003a. Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology* **14**:486–492.
- Russell, A., T. Clutton-Brock, P. Brotherton, L. Sharpe, G. McIlrath, F. Dalerum, E. Cameron, and J. Barnard. 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats *Suricata suricatta*. *Journal of Animal Ecology* **71**:700–709.
- Russell, A., L. Sharpe, P. Brotherton, and T. Clutton-Brock. 2003b. Cost minimization by helpers in cooperative vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* **100**:3333–3338.
- Russell, A. F., A. J. Young, G. Spong, N. R. Jordan, and T. H. Clutton-Brock. 2007. Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society B-Biological Sciences* **274**:513–520.
- Sæther, B. E., S. Engen, V. Grotan, T. Bregnballe, C. Both, P. Tryjanowski, A. Leivits, J. Wright, A. P. Møller, M. E. Visser, and W. Winkel. 2008. Forms of density regulation and (quasi-) stationary distributions of population sizes in birds. *Oikos* **117**:1197–1208.
- Scantlebury, M., A. Russell, G. McIlrath, J. Speakman, and T. Clutton-Brock. 2002. The energetics of lactation in cooperatively breeding meerkats *Suricata suricatta*. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269**:2147–2153.
- Schreiber, E., and J. Burger. 2002. Biology of Marine Birds. *Marine Turtle Newsletter* **97**:744pp.
- Sharpe, F., and L. Dill. 1997. The behavior of Pacific herring schools in response to artificial humpback whale bubbles. *Canadian Journal of Zoology* **75**:725–730.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* **17**:170–176.
- Shenk, T. M., G. C. White, and K. P. Burnham. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological Monographs* **68**:445–463.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the Regulation of Populations of Mammals, Birds, Fish, and Insects. *Science* **309**:607–610.
- Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**:564–575.

- Stephens, P., A. Russell, A. Young, W. Sutherland, and T. Clutton-Brock. 2005. Dispersal, eviction, and conflict in meerkats (*Suricata suricatta*): An evolutionarily stable strategy model. *American Naturalist* **165**:120–135.
- Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185–190.
- Tobin, P. C., S. L. Whitmire, D. M. Johnson, O. N. Bjornstad, and A. M. Liebhold. 2007. Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecology Letters* **10**:36–43.
- Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton Univ. Press.
- Turchin, P., and P. Kareiva. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology* **70**:1008–1016.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* **73**:289–305.
- Walsh, A. L., C. Catto, T. Hutson, P. Racey, P. Richardson, and S. Langton. 2002. The UK's National Bat Monitoring Programme: Final Report 2001. DEFRA publications.
- Wang, M. H., and M. Kot. 2001. Speeds of invasion in a model with strong or weak Allee effects. *Mathematical Biosciences* **171**:83–97.
- White, G., and R. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. *The Journal of Wildlife Management* **50**:509–513.
- Wilson, E., and B. Hölldobler. 2005. Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences* **102**:13367.
- Young, A., A. Carlson, and T. Clutton-Brock. 2005. Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour* **70**:829–837.
- Young, A. J., A. A. Carlson, S. L. Monfort, A. F. Russell, N. C. Bennett, and T. Clutton-Brock. 2006. Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the United States of America* **103**:12005–12010.
- Young, A. J., and T. Clutton-Brock. 2006. Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters* **2**:385–387.
- Young, A. J., G. Spong, and T. Clutton-Brock. 2007. Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society B-Biological Sciences* **274**:1603–1609.
- Zeng, Z., R. M. Nowierski, M. L. Taper, B. Dennis, and W. P. Kemp. 1998. Complex population dynamics in the real world: Modeling the influence of time-varying parameters and time lags. *Ecology* **79**:2193–2209.

## 6.8 Appendices

### Appendix A: A list of the predator-driven Allee effect studies that were used to compile Figure 6.4.

- Allee, W. C., O. Emerson, T. Park, and K. Schmidt. 1949. Principles of animal ecology. Saunders.
- Angulo, E., G. W. Roemer, L. Berec, J. Gascoigne, and F. Courchamp. 2007. Double Allee effects and extinction in the island fox. *Conservation Biology* **21**:1082–1091.
- Aukema, B. H., and K. F. Raffa. 2004. Does aggregation benefit bark beetles by diluting predation? Links between a group-colonisation strategy and the absence of emergent multiple predator effects. *Ecological Entomology* **29**:129–138.
- Austad, S. N., and K. N. Rabenold. 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolored wren. *Behavioral Ecology and Sociobiology* **17**:19–27.
- Berg, Å., T. Lindberg, and K. G. Källebrink. 1992. Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. *Journal of Animal Ecology* **61**:469–476.
- Berger, K. M., and M. M. Conner. 2008. Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. *Ecological Applications* **18**:599–612.
- Birkhead, T. R. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *Journal of Animal Ecology* **46**:751–764.
- Calvert, W. H., L. E. Hedrick, and L. P. Brower. 1979. Mortality of the Monarch butterfly (*Danaus-plexippus L*) - avian predation at 5 overwintering sites in Mexico. *Science* **204**:847–851.
- Capurro, A. F., M. Gatto, and G. Tosi. 1997. Delayed and inverse density dependence in a chamois population of the Italian Alps. *Ecography* **20**:37–47.
- Clutton Brock, T. H., D. Gaynor, G. M. McIlrath, A. D. C. MacColl, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, and P. N. M. Brotherton. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal Of Animal Ecology* **68**:672–683.
- Cuthbert, R. 2002. The role of introduced mammals and inverse density-dependent predation in the conservation of Hutton's shearwater. *Biological Conservation* **108**:69–78.
- DeVito, J. 2003. Metamorphic synchrony and aggregation as antipredator responses in American toads. *Oikos* **103**:75–80.
- Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecology Letters* **7**:410–416.

## *Discussion*

- Eckrich, C. E., and D. W. Owens. 1995. Solitary versus arribada nesting in the olive ridley sea turtles (*Lepidochelys olivacea*): a test of the predator-satiation hypothesis. *Herpetologica* **51**:349–354.
- Foster, W. A., and J. E. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**:466–467.
- Harcourt, R. 1992. Factors affecting early mortality in the South American Fur Seal (*Arotocephalus australis*) in Peru - density-related effects and predation. *Journal of Zoology* **226**:259–270.
- Kenward, R. E. 1978. Hawks and doves - factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology* **47**:449–460.
- Kramer, A., and J. Drake. 2010. Experimental demonstration of population extinction due to a predator-driven Allee effect. *Journal of Animal Ecology* **-**:**-**.
- Malcolm, J. R., and K. Marten. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology* **10**:1–13.
- Moehlman, P. D. 1979. Jackal helpers and pup survival. *Nature* **277**:382–383.
- Mooring, M. S., T. A. Fitzpatrick, T. T. Nishihira, and D. D. Reisig. 2004. Vigilance, predation risk, and the Allee effect in desert bighorn sheep. *Journal of Wildlife Management* **68**:519–532.
- Mumme, R. 1992. Do helpers increase reproductive success? *Behavioral Ecology and Sociobiology* **31**:319–328.
- Oro, D., A. Martinez Abrain, M. Paracuellos, J. C. Nevado, and M. Genovart. 2006. Influence of density dependence on predator-prey seabird interactions at large spatio-temporal scales. *Proceedings of the Royal Society B* **273**:379–383.
- Rangeley, R. W., and D. L. Kramer. 1998. Density-dependent antipredator tactics and habitat selection in juvenile pollock. *Ecology* **79**:943–952.
- Rasa, O. 1989. The costs and effectiveness of vigilance behaviour in the dwarf mongoose: Implications for fitness and optimal group size. *Ethology Ecology & Evolution* **1**:265–282.
- Rood, J. 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour* **39**:566–572.
- Rosenzweig, M. L., Z. Abramsky, and A. Subach. 1997. Safety in numbers: Sophisticated vigilance by Allenby's gerbil. *Proceedings of the National Academy of Sciences* **94**:5713–5715.
- Sandin, S. A., and S. W. Pacala. 2005. Fish aggregation results in inversely density-dependent predation on continuous coral reefs. *Ecology* **86**:1520–1530.
- Schradin, C. 2000. Confusion effect in a reptilian and a primate predator. *Ethology* **106**:691–700.

- Serrano, D., D. Oro, U. Esperanza, and J. L. Tella. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *American Naturalist* **166**:E22–E31.
- Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**:564–575.
- Stoner, A. W., and M. Ray. 1993. Aggregation dynamics in juvenile Queen conch (*Strombus gigas*) - population-structure, mortality, growth, and migration. *Marine Biology* **116**:571–582.
- Turchin, P., and P. Kareiva. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology* **70**:1008–1016.
- Turesson, H., and C. Bronmark. 2004. Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. *Journal of Fish Biology* **65**:363–375.
- Ward, D., K. Nislow, and C. Folt. 2008. Predators reverse the direction of density dependence for juvenile salmon mortality. *Oecologia* **156**:515–522.
- White, J. W. 2007. Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality. *Ecology Letters* **10**:1054–1065.
- Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* **144**:257–267.
- Wood, C. C. 1987. Predation of juvenile Pacific salmon by the Common merganser (*Mergus-merganser*) on Eastern Vancouver Island .1. Predation during the seaward migration. *Canadian Journal Of Fisheries And Aquatic Sciences* **44**:941–949.