Bats and Allee effects: When social behaviours go batty

As social species that cooperate to improve their fitness, bats should be prone to 'Allee effects', or a breakdown in social behaviour in small groups with a detrimental cost for individual – and possibly population – fitness. But what are Allee effects? And what is the evidence that they will affect bats?

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Over 70 years have passed since Warder Clyde Allee published his 'proto-cooperation' idea in his seminal book Animal Aggregations (Allee 1931), an idea that would later become known as the 'Allee effect'. Despite those 70 years, many readers – whether interested laypeople or trained population biologists – are probably now scratching their heads and asking what is an Allee effect? And why are they important for bats? Well, you'd be forgiven if you were because the Allee effect is elusive, both by repute and by its very nature.

When first described in 1931, the Allee effect was presented as a mechanism involving cooperation to boost population growth. At the time, however, population biologists were too infatuated with the processes limiting growth in large populations to take interest in processes impacting small populations. Consequently, the term 'Allee effect' scarcely appeared in the scientific literature until 1985 when Michael A. Soulé highlighted how ecological processes may become disrupted during animal and plant population declines. Since then, the number of articles published on the subject has increased dramatically, particularly after 1999 when two key studies were published back-to-back in the journal *Trends in Ecology & Evolution* (Figure 1).

The slow uptake of the Allee effect concept is owing, in part, to its meandering name. It

Group formation in bats may ensure that a minimum number participate in social behaviours. Falling numbers may make foraging, or finding a partner, more difficult.

began life as 'proto-cooperation', and then 'Allee's principle', before the term 'Allee effect' was coined. Sadly, it also has many synonyms, including 'inverse density dependence', 'under crowding' and even 'depensation' in the fisheries literature. Each of these synonyms has its merits and drawbacks but their existence certainly complicates the task of locating Allee effect studies in biological literature.

Fortunately these complications need not deter the reader from pursuing an understanding of all things Allee effect – as we have done the hard work for you. The aim of this short review is to answer your questions using a few instructive examples, before focusing on the evidence for Allee effects in bats, which could be ideal model taxa for exploring these phenomena.

What is an Allee effect?

Despite complicating the task of finding Allee effect studies, the range of synonyms for an Allee effect does convey a general notion of what defines it – a positive relationship between 'fitness[1]' and population size[2]. Consider, for example, the term 'positive density dependence'. Most readers will be familiar with the term 'negative density dependence' as meaning a decrease in fitness with an increase in population size. An Allee effect is an increase in fitness with an increase in population size, or vice versa; a decrease in fitness with a decrease in population size.

Perhaps the best way to describe an Allee effect is with the aid of graphs. Two types of Allee effects are currently recognised: component and demographic. Newfoundland cod might suffer both types of Allee effect (Anderson and Rose 2001) and provide a convenient example to illustrate these different types.

A component Allee effect describes, for example, how individuals might have difficulties accomplishing normal tasks, such as finding a sexual partner, when the cod population is reduced. It follows that as the population gets smaller, fewer eggs are fertilised and the individual fitness of each cod is reduced (Figure 2a). Component Allee effects can affect individual fitness through a wide range of mechanisms. A few well-studied examples include the reduced ability of smaller groups of African wild dogs *Lycaon pictus* to capture prey, or, in smaller groups of pigeons, the lower chance of spotting and avoiding predators.

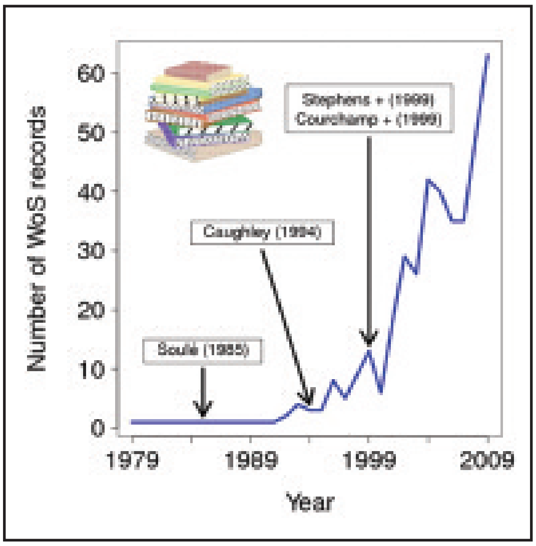

Figure 1: ISI Web of Science records from 1900-2009 with the term 'Allee effect' appearing in either their topic or title. Data downloaded on 14 June 2010. Citations are: Soulé, M.A. (1985) BioScience, 35, 27-34; Caughley, G. (1994) *Journal of Animal Ecology*, 63, 215-244; Stephens, P.A. & Sutherland, W.J. (1999) *Trends in Ecology & Evolution*, 14, 401-405; Courchamp et al, (1999) *Trends in Ecology & Evolution*, 14, 405-410.

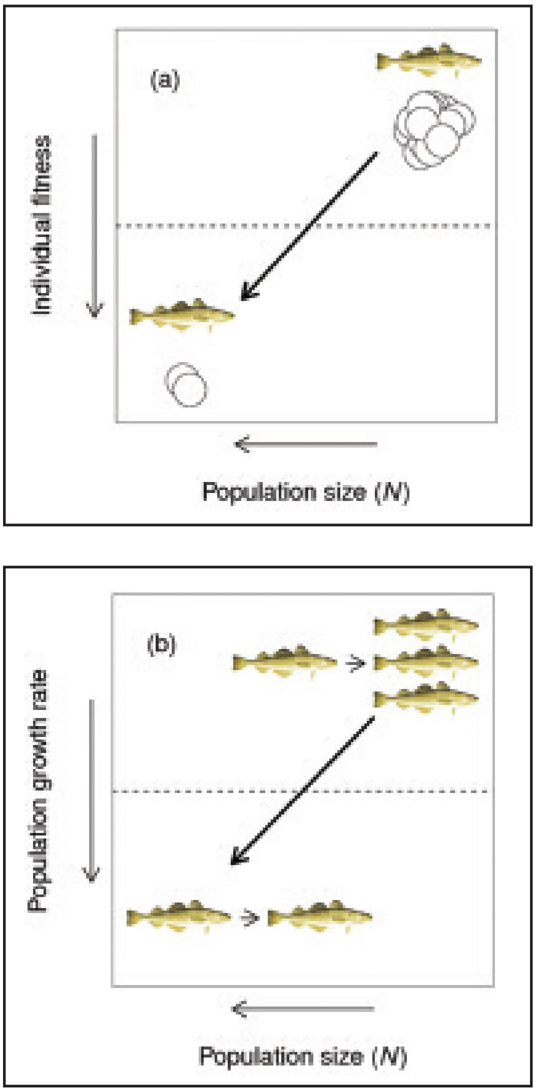

Figure 2: Graphs illustrating (a, left) component and (b, below left) demographic Allee effects in Newfoundland cod *Gadus morhua*. (a) The fitness of each individual – illustrated here as the number of eggs produced per individual – decreases with decreasing population size. (b) The population growth rate – i.e. the number of reproducing adults produced per individual – decreases with decreasing population size.

A demographic Allee effect is when a component Allee effect manifests as a change in population size. In the Newfoundland cod, the decreased number of fertilised eggs at reduced population size (the component Allee effect) can result in fewer codling hatching and surviving to recruitment. Consequently,

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[1] Fitness is used here loosely to include surrogates of fitness, such as reproduction and survival.

[2] This notion applies equally for population density.

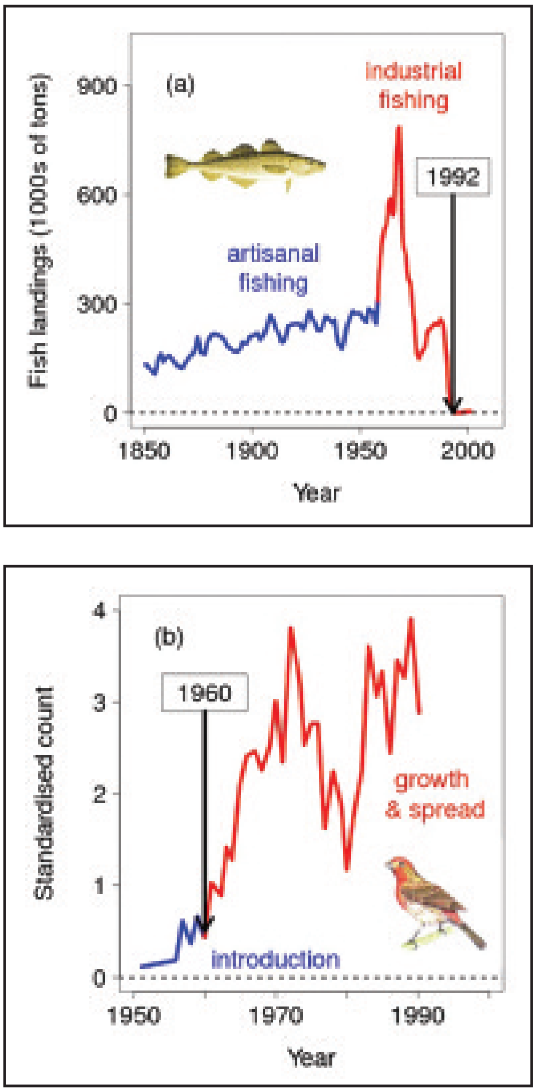

Figure 3: Graphs illustrating (a, right) the Newfoundland cod decline after the change in fishing practice from artisanal to industrial that caused the population to crash in 1992, and (b, below right) the house finch population explosion in 1960, 10 years after it was introduced to New York City. Both the cod crash and finch explosion could have been caused by Allee effects.

the population will be smaller in the following year, which again results in even fewer codling hatching, and so on (Figure 2b).

Demographic Allee effects are driven by component Allee effects and so can also be caused by a wide range of mechanisms. Unlike component Allee effects, however, demographic Allee effects are uncommon, perhaps because a component Allee effect that influences one measure of fitness (e.g. decreased reproduction) might be compensated by a change in another (e.g. increased survival).

Although, the Allee effect appears only to impact individuals and populations negatively, it can positively impact individuals and populations if the population is increasing. Consider how, if individuals in a reduced population of a social species cooperate, then each could increase its individual fitness as the population size increases. For example, meerkats cooperate to babysit pups, thereby protecting them from predation. If there are too few individuals in a group, then adults must either babysit but starve, or forage but increase the risk of losing their pups to predators. As the group size increases, however, there are sufficient individuals to take turns babysitting.

Are Allee effects important?

A common misunderstanding is that Allee effects affect small populations *per se*. This is not strictly true since some populations have been small throughout their history and evolved mechanisms to cope with their small size. For example, some large animals such as cheetahs living in low-resource habitats might have large home ranges and small and sparse populations. Rather, Allee effects will affect populations that are reduced in size compared to their natural (equilibrium) state. These populations will have been reduced to sizes to which they are not adapted, although may still comprise hundreds of thousands of individuals.

The number of reduced animal and plant populations is at an historical high, largely due to human activities. At one extreme, humans have overexploited many populations and destroyed their habitat driving them to reduced size (*Threatened* species). At the other extreme, humans accidentally or deliberately release reduced populations of exotic animals and plants to areas otherwise beyond their normal geographic distribution (*Introduced* species).

Allee effects can affect both *Threatened* species (such as Newfoundland cod) and *Introduced* species (for example, house finches). Following the change in fishing practice from artisanal to industrial in the late 1950s, the landings of Newfoundland cod increased dramatically. Unfortunately, and unbeknown to the fishermen, the cod population was unable to sustain such high fishing pressure and, by 1992, had all but disappeared (Figure 3a). Despite a moratorium on cod fishing and international protection, the population has failed to recover, perhaps because there are too few individuals remaining to breed successfully and rebuild stocks – an example of both a component and demographic Allee effect (Anderson and Rose 2001).

House finches were introduced in New York Central Park in the early 1950s and the population scarcely grew for the first 10 years. In 1960, however, the population began to increase dramatically, albeit with large fluctuations in population size (Figure 3b). A retrospective analysis revealed an Allee effect in the finch population and suggested that the rate of reproduction in the initial introduced population was too low to permit their spread (Veit and Lewis 1996).

Alas, the increasing number of reduced populations and the rate at which they are being reduced might mean that Allee effects will play an increasingly important role in the extinction of many of the world's animal and plant populations.

Allee effects in bats

Almost a quarter of all 1100 bat species are globally threatened with extinction meaning that many bat populations will be reduced and prone to Allee effects. Bats are also highly social animals and many colonies show 'fission-fusion' dynamics, or frequent splitting and merging of colony subunits (Kerth 2008). The sociobiological reasons for fission-fusion dynamics are not known but are thought to include maintaining individual social, and perhaps kinship, bonds. An alternative explanation, however, might be that group formation ensures a minimum number of individuals participate in social behaviours to maximise individual fitness – an Allee effect.

Social behaviours and group size

Several temperate bat species have been the subject of studies to understand the reasons for fission-fusion dynamics. Kerth and König (1999) studied maternity colonies (groups of females that congregate to breed) of Bechstein's bat *Myotis bechsteinii* in deciduous forests in Germany using a combination of individual marking, genetic analyses and video surveillance of roosting boxes. They confirmed fission-fusion dynamics but found that related individuals did not associate. Rather, they observed that lactating mothers tended to associate. Similarly, patterns of association among big brown bats *Eptesicus fuscus* (Metheny *et al.* 2008) and northern long-eared bats *Myotis septentrionalis* (Patriquin *et al.* 2010) are not predominately among close kin, suggesting that the benefits of grouping to individual fitness might be sufficient to explain the fission-fusion dynamics. Relatedness of colony members, however, is high in some species. For example, colonies of Greater horseshoe bats *Rhinolophus ferrumequinum* show strong matrilineal structure and female relatives forage together (Rossiter *et al.* 2002).

Many studies have hypothesised that bats congregate for thermoregulation and that this behaviour catalyses juvenile development. Growth and development in juvenile Brazilian free-tailed bats *Tadarida brasiliensis* (Allen *et al.* 2010) and greater mouse-eared bats *Myotis myotis* (Zahn 1999) is fastest at warm roost sites. Juvenile gray bats *Myotis grisescens* raised in larger roosts grew faster than those in smaller roosts, which Tuttle (1976) attributed to the communal warming effect in larger roosts.

Willis and Brigham (2007) found that the presence of big brown bats increased tree roost temperatures by up to 7°C, and that roost temperature, and consequent individual energy savings, was positively correlated to the number of bats present. These findings are suggestive of a component Allee effect but alternative explanations include climate, proximity to foraging grounds and food availability. In no case to date, however, has a link been confirmed between faster juvenile development at higher temperature and higher temperatures resulting from being in a larger group – a necessary step to identify a potential component Allee effect.

Some bat species might also benefit from social foraging. Food resources are often ephemeral and patchily distributed, and can be located more easily if several animals search for them. Once located, the resources (e.g. insects in swarms) can be superabundant, and hence no competition occurs between foragers. Velvety free-tailed bats *Molossus molossus* from the same colony forage together more frequently than expected by chance (Dechmann *et al.* 2010), and bats may also transfer information about feeding sites among colony members (Wilkinson 1992). For example, Greater spear-nosed bats *Phyllostomus hastatus* emit social calls to recruit and co-ordinate foraging with unrelated group members (Wilkinson and Boughman 1998). Fringe-lipped bats *Trachops cirrhosus* transmit novel associations between prey cues (frog calls) and prey quality (palatability) via social learning (Page and Ryan 2006). Benefits of social foraging and information transfer are likely to be dependent on group size, and might be compromised if colony size decreases.

The above examples illustrate just a few social behaviours in bats (others are reviewed

Figure 4: Female lesser horseshoe bats *Rhinolophus hipposideros* clustered together in a roost in Wales. There are many possible reasons why bats gather in groups including for better thermoregulation, and information sharing. Photo: Gareth Jones.

in Kerth 2008). To our knowledge, however, the benefits of these behaviours have neither been compared or contrasted across groups of different sizes, nor linked to individual fitness. It is therefore an open question as to whether any of these other behaviours might also conceal component, and perhaps a demographic, Allee effect.

Demographic responses to reduced group size

There have been few demographic studies of bats and this is partly because it is difficult to count them. Bats are nocturnal, secretive and volant; characteristics that are not conducive to conventional monitoring techniques. In addition, many bats are small bodied, so monitoring individuals using transponders (passive or radio) is difficult. Perhaps unsurprisingly, there have been no studies of the demographic consequences of component Allee effects in bats.

Despite the difficulties involved in studying bat populations, there are some indications that bat groups might have a lower limit on the number of members required to persist. For example, individual bats might advertise their presence to encourage other individuals to join them. A recent experimental study has shown how noctules *Nyctalus noctula* broadcast their presence actively to passing conspecifics, possibly to attract roost mates and reap the benefits that accrue from increased colony size (Ruczynski *et al.* 2007).

Future directions

The existence of a demographic Allee effect indicates the existence of a component Allee effect, itself the result of a specific mechanism. In the past, the search for demographic Allee effects has proceeded by identifying a mechanism and extrapolating to its demographic consequences. A more productive approach, however, might be to reverse this procedure: to isolate a demographic Allee effect and then to confirm the existence of an underlying mechanism. This approach would, however, suffer from the disadvantage that demographic Allee effects are notoriously difficult to detect.

Figure 5: A noctule bat *Nyctalus noctula* calling to other passing noctule bats to join it in an experimental tree hole roost. Such behaviour strongly implies that it is beneficial to share a roost with conspecifics, and suggests that failure to find a conspecific to share the roost will be to the detriment of the lone noctule. Photo: Ireneusz Ruczyński.

The detection of demographic Allee effects is sensitive to the data analysed. Roost count data can be distorted by 'noise' factors such as roost switching, prevailing weather conditions and roost accessibility, limiting our confidence in any patterns we detect. Furthermore, detection of demographic Allee effects is likely to require observing roosts of a wide range of different sizes and over several consecutive years.

At first impression, the extensive data required to study demographic Allee effects in bat populations would appear to be prohibitive. There are, however, possible solutions. The first is to use statistical procedures developed for sparse and poor data (Schaub *et al.* 2007), although these are computer intensive. Another alternative to overcome poor data quality might be to use it to derive qualitative, rather than quantitative, measures about population dynamics. Finally, we could construct individual-based models to predict population changes and compare them to observed population changes to examine evidence for demographic Allee effects (Federico *et al.* 2008).

A second appealing solution is to use data (such as from national monitoring surveys) from a large number of roosts. By using large amounts of data, we are better able to estimate patterns that emerge over many consecutive measurements, thereby reducing the effect of 'noise'. In the UK, the Bat Conservation Trust (BCT) has been running the National Bat Monitoring Programme (NBMP) in collaboration with the Countryside Council for Wales, Natural England and the Robert Stebbings Consultancy since 1996 (Bat Conservation Trust 2009). At the time of writing, over 1000 volunteers have helped to count bats at over 2000 roosts nationwide.

The BCT currently uses the NBMP data to derive statistically defensible national trends for 11 of the UK's 16 breeding bat species. The NBMP data could also, however, be used to look at bat population dynamics at roosts as a function of the roost size, i.e. to search for demographic Allee effects. Although this could be done for individual roosts, the aforementioned data problems suggest that we

The nocturnal nature of bats makes counting them difficult – there have been no studies of demographic Allee effects in bats.

ought to approach the problem from a meta-analytical perspective, i.e. combining data for multiple roosts in the same analysis. Executed correctly, such an approach might provide strong evidence for the existence of demographic Allee effects in bat species.

Detection of a demographic Allee effect would signal vulnerability to roost decline and allow conservation managers to better target conservation efforts, such as mitigating disturbance, at particular bat species. It does not, however, confirm that the demographic Allee effect arises from social behaviours. Bats are susceptible to component Allee effects unrelated to sociality, including, for example, genetic Allee effects.

Genetic drift (the random change in genetic diversity by chance) is stronger in small populations, resulting in reduced genetic diversity. Small populations are also subject to increased levels of inbreeding, resulting in reduced average heterozygosity, and a higher chance of deleterious alleles appearing in the population. These routes to reduced genetic diversity might reduce individual fitness, and consequently result in demographic Allee effects. For example, the effects of a range of phenotypic, phenological and genetic factors influencing survival in greater horseshoe bats were investigated by Rossiter *et al.* (2001). The only factor affecting the likelihood of survival was a measure of outbreeding based on a range of gene loci, suggesting that genetic Allee effects could potentially be profound in small bat populations.

To confirm a detected demographic Allee effect, one should identify the underlying component Allee effect(s). Knowledge of the mechanism would both help to halt roost declines and, importantly, help us understand the demographic consequences of sociality in a changing world. Given that many bat species are globally threatened with extinction, perhaps the time is ripe to investigate the role of Allee effects in the dynamics of bat populations. To do this will require new approaches to the problem of poor data quality, the use of meta-analytical statistics and detailed parallel investigations of underlying mechanisms, such as those pioneering efforts of Tuttle (1976) over thirty years ago.

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Bat Conservation Trust (www.bats.org.uk)

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