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BOOK REVIEWS

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Allee Effects in Ecology and Conservation

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At the dawn of the founding of conservation biology as an organized science, Gilpin and Soulé (1986) warned of four 'extinction vortexes', namely biological phenomena that amplify extinction risk as a population becomes rarer, that could hasten the demise of a rare species: demographic variability, fragmentation, loss of fitness from reduced genetic heterozygosity and loss of evolutionary responsiveness due to reduced genetic diversity.

It is characteristic of those times that most of the various biological forces now collectively termed 'Allee effects' did not make the cut for being enshrined as extinction vortexes. An Allee effect, defined succinctly in the book under review here as a 'causal positive relationship between the number of individuals in a population and their fitness', arises through a variety of possible mechanisms, one example being an increasing lack of mating encounters as a population becomes scarce. In the 1930s, ecologists were starting their discussions about the various mechanisms of population regulation leading to negative 'density dependence', that is, fitness decreasing with density or numbers, and those discussions continue to this day (Sibley *et al*. 2006). Lost in the din were some complementary points made in a pair of volumes by Warder Clyde Allee (1931, 1938), namely that various biological mechanisms would likely lead to increasing fitness with density, at least in sparse populations. The study of the subject languished and, by the 1980s, it is fair to say that Allee effects were simply not on ecologists' radar as a potentially important drag on rare species' recovery chances. The extant investigations of Allee effects were rare and scattered, and were suffering an Allee effect of sorts of their own in the scientific literature. 'Send it to a genetics journal,' harrumphed one editor of a respected ecological journal at a manuscript of mine, apparently misreading 'Allee' as 'allele' in the title; the paper, part of my 1982 Ph.D. dissertation, was eventually published after almost a decade of rejections (Dennis 1989).

What a difference two decades have made. In their important new book, Courchamp *et al*. have impressively surveyed the veritable explosion of empirical and theoretical investigations of Allee effects that have appeared since the emergence of conservation biology. Courchamp *et al*. discuss mounting evidence that Allee effects are widespread, if not common, and explain the now-numerous modelling studies that attempt to quantify the consequences of Allee effects.

One of the possible consequences of Allee effects is horrifyingly sickening to those concerned about biological diversity: a rare species might have a lower critical threshold density (well above one male and one female), representing an unstable equilibrium above which the species might recover, but below which the species is essentially doomed to extinction in relatively short order. Extinction vortex becomes extinction black hole.

In Chapter 1, Courchamp *et al*. briefly review some of the early history of Allee effects studies, as well as carefully establish some definitions and terminology for the rest of the book. Chapter 2 tackles a variety of mechanisms potentially causing Allee effects, including mate finding limitation, broadcast spawning and pollen limitation in sessile organisms, and reproductive facilitation in colonial breeders, environmental conditioning (such as bigger groups leading to more favourable temperatures), protection from predation through dilution or enhanced defence in larger prey groups, increased survival of young in colonial nesting species and increased vigilance in larger prey groups.

Those interested in mathematical population modelling and density dependence will find Chapter 3 an essential read; the authors dive into a comprehensive review of the many theoretical studies involving Allee effects as a key ingredient in population models, with special emphasis on the recent investigations of multiple variable models: predation, competition, stage structured and spatially explicit. Chapter 4 discusses a variety of genetic mechanisms that can cause Allee effects. Chapter 5 is devoted to Allee effects in conservation and management, with the overwhelming conclusion emerging that propagule size dramatically affects the probability of establishment of a population, and that often a threshold propagule size must be exceeded for the population to have worthwhile chances of establishment or recovery. Chapter 6 is a forward-looking series of sections collectively titled 'Conclusions and perspectives.'

Allee's footnote to the 'density dependence' ideas of the 1930s is looming ever larger in our contemporary struggles to preserve the Earth's biological diversity. Allee effects now deserve more than passing mention in undergraduate ecology textbooks, and rare species management should now err on the side of caution (the 'precautionary principle') by accounting for the possibility of Allee effects, even if undetected. With the collection in *Allee Effects in Ecology and Conservation* of the many empirical studies of Allee effects, both those that detected Allee effects and those that did not, and of the growing number of theoretical population modelling studies exploring Allee effects, Courchamp *et al*. have rendered a great service to future researchers. I thoroughly recommend the book for graduate reading seminars, and as an essential acquisition for libraries and ecologists' bookshelves.

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