

# The Allee Effect

by Jo Gascoigne



Courtesy of Jo Gascoigne

Dr Jo with Queenie; Queenie is on the left

The top five most famous Belgians apparently include a cyclist, a punk singer, the inventor of the saxophone, the creator of Tintin, and Audrey Hepburn. Pierre François Verhulst is not on the list, although he should be. He had a fairly short life, dying at the age of 45, but did manage to include some excitement—he was deported from Rome for trying to persuade the Pope that the Papal States needed a written constitution. Perhaps the Pope knew better even then than to take lectures in good governance from a Belgian. . . .

Aside from this episode, **Pierre Verhulst** (1804–1849) was a mathematician who concerned himself, among other things, with the dynamics of natural populations—fish, rabbits, buttercups, bacteria, or whatever. (I am prejudiced in favour of fish, so we will be thinking fish from now on.) Theorizing on the growth of natural populations had up to this point been relatively limited, although scientists had reached the obvious conclusion that the growth rate of a population ( $dN/dt$ , where  $N(t)$  is the population size at time  $t$ ) depended on (i) the birth rate  $b$  and (ii) the mortality rate  $m$ , both of which would vary in direct proportion to the size of the population  $N$ :

$$\frac{dN}{dt} = bN - mN. \quad (1)$$

After combining  $b$  and  $m$  into one parameter  $r$ , called the **intrinsic rate of natural increase**—or more usually by biologists without the time to get their tongues around that, just  $r$ —equation (1) becomes

$$\frac{dN}{dt} = rN. \quad (2)$$

This model of population growth has a problem, which should be clear to you—if not, plot  $dN/dt$  for increasing values of  $N$ . It is a straightforward exponential growth curve, suggesting that we will all eventually be drowning in fish. Clearly, something eventually has to step in and slow down  $dN/dt$ . Pierre Verhulst’s insight was that this *something* was the capacity of the environment, in other words,

*How many fish can an ecosystem actually support?*

He formulated a differential equation for the population  $N(t)$  that included both  $r$  and the **carrying capacity**  $K$ :

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right), \quad r > 0. \quad (3)$$

Equation (3) is called the **logistic equation**, and it forms to this day the basis of much of the modern science of population dynamics. Hopefully, it is clear that the term  $(1 - N/K)$ , which is Verhulst’s contribution to equation (2), is  $(1 - N/K) \approx 1$  when  $N \approx 0$ , leading to exponential growth, and  $(1 - N/K) \rightarrow 0$  as  $N \rightarrow K$ , hence it causes the growth curve of  $N(t)$  to approach the horizontal asymptote  $N(t) = K$ . Thus the size of the population cannot exceed the carrying capacity of the environment.

The logistic equation (3) gives the overall growth rate of the population, but the ecology is easier to conceptualize if we consider *per capita* growth rate—that is, the growth rate of the population per the number of individuals in the population—some measure of how “well” each individual in the population is doing. To get *per capita* growth rate, we just divide each side of equation (3) by  $N$ :

$$\frac{1}{N} \frac{dN}{dt} = r \left( 1 - \frac{N}{K} \right) = r - \frac{r}{K} N.$$

This second version of (3) immediately shows (or plot it) that this relationship is a straight line with a maximum value of  $\frac{1}{N} \frac{dN}{dt}$  at  $N = 0$  (assuming that negative population sizes are not relevant) and  $dN/dt = 0$  at  $N = K$ .

Er, hang on a minute . . . “a maximum value of  $\frac{1}{N} \frac{dN}{dt}$  at  $N = 0$ !” Each shark in the population does best when there are . . . zero sharks? Here is clearly a flaw in the logistic model. (Note that it is now a *model*—when it just presents a relationship between two variables  $dN/dt$  and  $N$ , it is just an equation. When we use this equation to try and analyze how populations might work, it becomes a model.)

The assumption behind the logistic model is that as population size decreases, individuals do better (as measured by the *per capita* population growth rate). This assumption to some extent underlies all our ideas about sustainable management of natural resources—a fish population cannot be fished indefinitely unless we assume that when a population is reduced in size, it has the ability to grow back to where it was before.

This assumption is more or less reasonable for populations, like many fish populations subject to commercial fisheries, which are maintained at 50% or even 20% of  $K$ . But for very depleted or endangered populations, the idea that individuals keep doing better as the population gets smaller is a risky one. The Grand Banks population of cod, which was fished down to 1% or perhaps even 0.1% of  $K$ , has been protected since the early 1990s, and has yet to show convincing signs of recovery.

**Warder Clyde Allee** (1885–1955) was an American ecologist at the University of Chicago in the early 20th century, who experimented on goldfish, brittlestars, flour beetles, and, in fact, almost anything unlucky enough to cross his path. Allee showed that, in fact, individuals in a population can do worse when the population becomes very small or very sparse.\* There are numerous ecological reasons why this might be—for example, they may not find a suitable mate or may need large groups to find food or express social behavior, or in the case of goldfish they may alter the water chemistry in their favour. As a result of Allee’s work, a population where the *per capita* growth rate declines at low population size is said to show an **Allee effect**. The jury is still out on whether Grand Banks cod are suffering from an Allee effect, but there are some possible mechanisms—females may not be able to find a mate, or a mate of the right size, or maybe the adult cod used to eat the fish that eat the juvenile cod. On the other hand, there is nothing that an adult cod likes more than a snack of baby cod—they are not fish with very picky eating habits—so these arguments may not stack up. For the moment we know very little except that there are still no cod.

Allee effects can be modelled in many ways. One of the simplest mathematical models, a variation of the logistic equation, is:

$$\frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) \left( \frac{N}{A} - 1 \right). \quad (4)$$

where  $A$  is called the **Allee threshold**. The value  $N(t) = A$  is the population size below which the population growth rate becomes negative due to an Allee effect—situated at

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\*Population size and population density are mathematically interchangeable, assuming a fixed area in which the population lives (although they may not necessarily be interchangeable for the individuals in question).

a value of  $N$  somewhere between  $N = 0$  and  $N = K$ , that is,  $0 < A < K$ , depending on the species (but for most species a good bit closer to 0 than  $K$ , luckily).

Equation (4) is not as straightforward to solve for  $N(t)$  as (3), but we don't need to solve it to gain some insights into its dynamics. If you work through Problems 2 and 3, you will see that the consequences of equation (4) can be disastrous for endangered populations.

## Related Problems

- (a) The logistic equation (3) can be solved explicitly for  $N(t)$  using the technique of partial fractions. Do this, and plot  $N(t)$  as a function of  $t$  for  $0 \leq t \leq 10$ . Appropriate values for  $r$ ,  $K$ , and  $N(0)$  are  $r = 1$ ,  $K = 1$ ,  $N(0) = 0.01$  (fish per cubic metre of seawater, say). The graph of  $N(t)$  is called a **sigmoid growth curve**.

(b) The value of  $r$  can tell us a lot about the ecology of a species—sardines, where females mature in less than one year and have millions of eggs, have a high  $r$ , while sharks, where females bear a few live young each year, have a low  $r$ . Play with  $r$  and see how it affects the shape of the curve. *Question:* If a marine protected area is put in place to stop overfishing, which species will recover quickest—sardines or sharks?
- Find the population equilibria for the model in (4). [*Hint:* The population is at equilibrium when  $dN/dt = 0$ , that is, the population is neither growing nor shrinking. You should find three values of  $N$  for which the population is at equilibrium.]
- Population equilibria can be stable or unstable. If, when a population deviates a bit from the equilibrium value (as populations inevitably do), it tends to return to it, this is a stable equilibrium; if, however, when the population deviates from the equilibrium it tends to diverge from it ever further, this is an unstable equilibrium. Think of a ball in the pocket of a snooker table versus a ball balanced on a snooker cue. Unstable equilibria are a feature of Allee effect models such as (4). Use a phase portrait of the autonomous equation (4) to determine whether the nonzero equilibria that you found in Problem 2 are stable or unstable. [*Hint:* See Section 2.1 of the text.]
- Discuss the consequences of the result above for a population  $N(t)$  fluctuating close to the Allee threshold  $A$ .



Copper sharks and bronze whaler sharks feeding on a bait ball of sardines off the east coast of South Africa

Deag Perrine/Catly Images

## References

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## ABOUT THE AUTHOR



Courtesy of Jo Gascoigne

After a degree in Zoology, **Jo Gascoigne** thought her first job, on conservation in East Africa, would be about lions and elephants—but it turned out to be about fish. Despite the initial crushing disappointment, she ended up loving them—so much, in fact, that she went on to complete a PhD in marine conservation biology at the College of William and Mary, in Williamsburg, Virginia, where she studied lobster and Caribbean conch, and also spent 10 days living underwater in the Aquarius habitat in Florida. After graduating, she returned to her native Britain and studied the mathematics of mussel beds at Bangor University in Wales, before becoming an independent consultant on fisheries management. She now works to promote environmentally sustainable fisheries. When you buy seafood, make good choices and help the sea!