# *Density dependence*

## *Key concepts*

- State variables *vs.* parameters
- Density dependence
- Intrinsic rate of increase and carrying capacity
- Stability
- Resilience
- Allee effect

## *Population growth of muskox on Nunivak Island*

The muskox *Ovibos moschatus* is a large mammal closely related to sheep and goats native to the North American Arctic and Greenland. It is one of the few Pleistocene megafauna to survive the Pleistocene/Holocene extinction event, but declined in the 19th century due to overhunting. In 1931, the US Fish and Wildlife Service introduced 31 animals to Nunivak Island, Alaska, where the species had previously been extirpated. Frequent censuses since that time show that the habitat of Nunivak Island was suitable and the population grew (Figure 2).

Figure 1: Muskox (*Ovibos moschatus*).

When we first considered the growth and decline of populations, we assumed that any change in the population was due to continuous reproduction and mortality that occurred at fixed rates. Thus, we arrived at a simple differential equation

$$dn/dt = (b - d)n = rn \tag{1}$$

and its solution

$$n_t = n_0 e^{rt}. \tag{2}$$

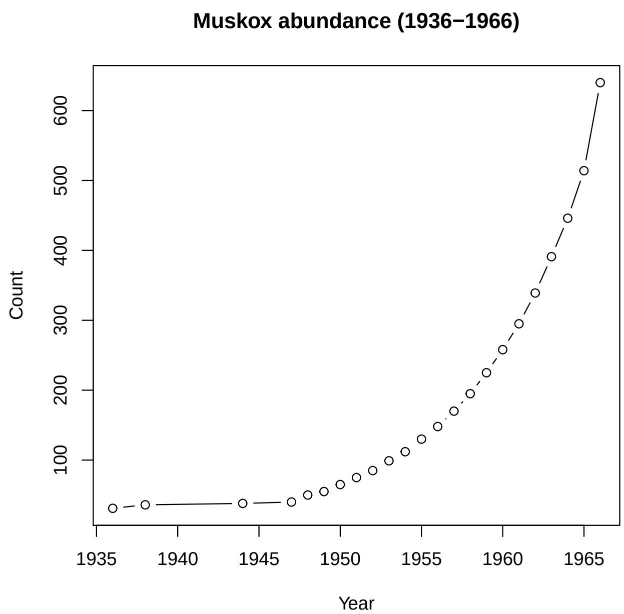


Figure 2: Increase in the muskox population of Nunivak Island.

In this expression, the variable $n$ is the is the variable undergoing change and therefore referred to as the *state variable*, whereas $b$, $d$, $r$ are constants referred to as *parameters*. In this model, $b$ is the instantaneous *birth rate*, $d$ is the instantaneous *death rate*, and $r = b - d$ is known as the *intrinsic rate of increase*.

State variables and parameters

Alternatively, if a population reproduces seasonally its fluctuations may be described by a *discrete time map*

Continuous *vs.* discrete time dynamics

$$n_{t+1} = (b - d + 1)n_t = \lambda n_t \tag{3}$$

with solution

$$n_t = \lambda^t n_0. \tag{4}$$

In this model, $\lambda$ is referred to as the *geometric growth rate*. From 1 and 4 we see that under these assumptions there are a limited number of possible trajectories:

Possible solutions of *density independent* models

- If $r > 0$ or $\lambda > 1$ the population will grow without bound
- If $r < 0$ or $\lambda < 1$ the population will decline asymptotically toward zero
- Finally, if $r = 0$ or $\lambda = 1$ the population stay at its current value (but this is an extremely delicate condition that isn't expected to obtain in nature)

Clearly, the muskox of Nunivak Island most closely match the first scenario. But what is the intrinsic rate of increase of this population? To determine this, we derive an *estimator* of $r$ as follows. First, we observe that by rearranging equation 2 we can relate the intrinsic rate of increase over any interval of time (designated $\tau$) to only observable quantities, namely population size at the start of the interval ($n_0$), population size at the end of the interval ($n_\tau$), and the duration of the interval ($\tau$):

$$\hat{r} = \ln(n_\tau / n_0)/\tau, \tag{5}$$

where ln is the natural logarithm and the "hat" symbolizes that this is an estimator, not necessarily the "true" value. If we now consider all subsequent intervals between 1936 and 1966 we obtain 22 different estimates for the intrinsic rate of increase $r$ (Table 1).

| Years | $\tau$ | $n_0$ | $n_\tau$ | $\hat{r}$ |
|---|---|---|---|---|
| 1936–1938 | 2 | 31 | 36 | 0.074765867 |
| 1938–1944 | 6 | 36 | 38 | 0.009011204 |
| 1944–1947 | 3 | 38 | 40 | 0.017097765 |
| 1947–1948 | 1 | 40 | 50 | 0.223143551 |
| 1948–1949 | 1 | 50 | 55 | 0.095310180 |
| 1949–1950 | 1 | 55 | 65 | 0.167054085 |
| 1950–1951 | 1 | 65 | 75 | 0.143100844 |
| 1951–1952 | 1 | 75 | 85 | 0.125163143 |
| 1952–1953 | 1 | 85 | 99 | 0.152468594 |
| 1953–1954 | 1 | 99 | 112 | 0.123379021 |
| 1954–1955 | 1 | 112 | 130 | 0.149035579 |
| 1955–1956 | 1 | 130 | 148 | 0.129677823 |
| 1956–1957 | 1 | 148 | 170 | 0.138586163 |
| 1957–1958 | 1 | 170 | 195 | 0.137201122 |
| 1958–1959 | 1 | 195 | 225 | 0.143100844 |
| 1959–1960 | 1 | 225 | 258 | 0.136859183 |
| 1960–1961 | 1 | 258 | 295 | 0.134015771 |
| 1961–1962 | 1 | 295 | 339 | 0.139024751 |
| 1962–1963 | 1 | 339 | 391 | 0.142707453 |
| 1963–1964 | 1 | 391 | 446 | 0.131611392 |
| 1964–1965 | 1 | 446 | 514 | 0.141904313 |
| 1965–1966 | 1 | 514 | 640 | 0.219244911 |
| Average | | | | 0.1306 (s.d. 0.0495) |

Table 1: Estimates of the intrinsic rate of increase of muskox on Nunivak Island from 1936-1966.

One thing this table shows is how remarkably constant the intrinsic rate of increase was from 1936-1966. Is it possible that the assumption of constant vital rates is perfectly acceptable for the muskox of Nunivak Island? In answer to this this question, Figure 3 shows what the population size would be up to the year 2010.

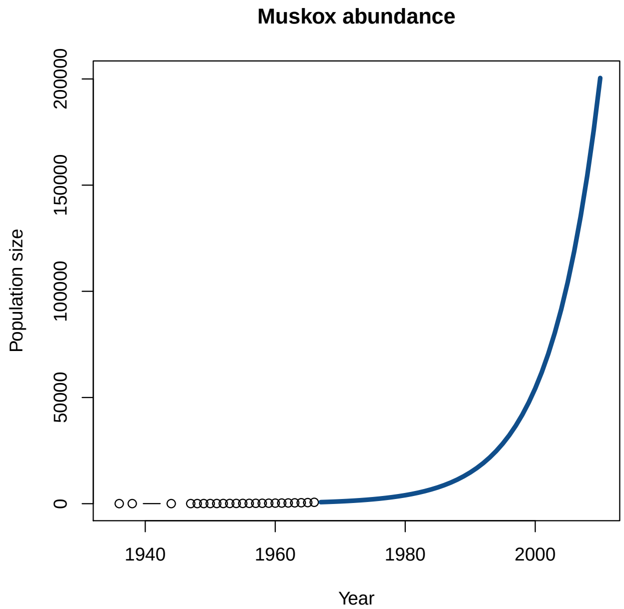


Figure 3: Projected increase in the muskox population of Nunivak Island.

As in Figure 1, observations from 1936 to 1966 are shown as points. In addition, this plot shows (as a blue line) extrapolations to 2010 based on the observed period. According to this model, if the Nunivak Island muskox population had grown at the same rate after 1966 that it had up until that time it would now number approximately 200,000 animals. Incidentally, this is roughly twice the total world population of muskox.[1] The Nunivak Island population, by contrast, numbers about 550 animals.[2]

[1] A. Gunn and M. Forchhammer. IUCN Red List of Threatened Species: Ovibos moschatus, 2008

[2] EJ Wald. Nunivak island reindeer and muskoxen survey - 2009. Technical report, US Fish & Wildlife Service, 2009

## *Density dependent vital rates*

The reason populations don't grow without bound isn't mysterious, but is rather one of the most fundamental observations of population ecology. Many resource such as food, territories, or light are such that use by one individual prevents their simultaneous use by other individuals, that is they are *rivalrous* resources. Competition for rivalrous resources ensures that at some point the available quantity of one or more resources becomes limiting and further growth is restrained.

How does this limitation occur? Our demographic theory of population dynamics (*i.e.*, dynamics of the kind envisioned by equation 1 or 3) requires that any effect of limiting resources act through the vital rates. One way to represent this *density dependence* is to allow the birth rate or the death rate to be a function of the population size. Thus, for instance, we might allow the birth rate to decline with population size,

$$b(n) = b_0 - b_1 n, \tag{6}$$

or let mortality increase with population size

$$d(n) = d_0 + d_1 n. \tag{7}$$

## *Logistic model*

If we substitute $b(n)$ for $b$ and $d(n)$ for $d$ in equation 1 we may derive a new *density-dependent* model for the population growth.

$$dn/dt = (b(n) - d(n))n = ((b_0 - b_1 n) - (d_0 + d_1 n))n. \tag{8}$$

Rearranging and substituting $r = b_0 - d_0$ and $k = (b_0 - d_0)/(b_1 + d_1)$ we obtain the canonical form of the *logistic model*:

$$dn/dt = rn(1 - n/k), \tag{9}$$

where the parameter $k$ must be greater than or equal to zero. This model is one of the most analyzed formulas in all of ecology. Although it may occasionally suffice as a realistic model for some population or other, this situation is rare. Rather, the value of this model is heuristic. For instance, if we think of the linear equations 6 and 7 as the simplist possible expressions of the idea of density-dependent vital rates, or as linear approximations to any more complicated expressions, then the logistic model is the simplest density-dependent population growth model. Despite this simplicity, many very general lessons can be learned from this model.

## *Equilibria*

One property of this model is that is posesses one or more *equilibria*. In population ecology, as in other areas of science, an equilibrium is a state of the system at which it is unchanging. We have in fact already seen an equilibrium in this chapter. One of the three possible trajectories for the linear models in equations 2 and 4 was that there was no change. This occurred only when $r = 0$ or $\lambda = 1$, respectively. We asserted that these conditions would not obtain in nature. Why? Because if $r$ is just slightly greater than or less than 0 (or if $\lambda$ is just greater than or less than 1) then the the system is no longer at an equilibrium. These equilibria are fleeting conditions that exist only under extraordinarily fortuitous and unlikely circumstances concerning the models parameters.

By contrast, there can also be conditions concerning the state variable $n$ that give rise to equilibria. That these conditions can be robust can be seen with the logistic model. However, first we must identify the equilibria. By definition, such equilibria are states of the system (values of $n$) at which the population size is unchanging. To find these, we set equation 9 equal to zero and solve for $n$. By simple inspection we determine that the logistic model exhibits two equilibria. Conventionally, we designate these as $n^*$, so the equilibria are given by $n^* = 0$ and $n^* = k$.

In addition to being equilibria, these two states of the system also have special ecological significance. The lower equilibria, $n^* = 0$, is the condition that there are zero individuals in the population. We call this condition *extinction*. The upper equilibrium, $n^* = k$, is the maximum positive value that the population can achieve without then being forced to decline. It is called *carrying capacity*.

How do populations subject logistic growth behave? This question also can be answered by inspecting equation 9. First, obviously, the answer is that it depends on what values the variables take, including both the parameters and the state variable. However, if we're willing to choose value of $r$, $k$, and $n$ we can always evaluate equation 9 to obtain the growth rate. If the growth rate is positive this means the population will increase from this condition. If the growth rate is negative then the population with decrease from this condition.

The range of possibilities can be illustrated by a graph showing the population size on the x-axis and the growth rate on the y-axis. Figure 4 plots equation 9 where $r > 0$. (Note: we will always assume $k > 0$ since the model is biological nonsense otherwise.) The dashed horizontal line is the zero line. Portions of the growth curve above this line correspond to population sizes as which growth is positive and the population increases; portions of the growth curve below this line correspond to population sizes as which growth is negative and the population decreases. The equilibria are clearly indicated by the intersections of the growth curve and the zero line. The vertical dashed line is at $n = k$, carrying capacity. What this plot shows is that populations less than carrying capacity increase (with the exception of zero itself), while populations greater than carrying capacity decrease.

What about populations where the intrinsic rate of increase is negative? We can investigate this possibility too. Although the ecological sensibility of this model is questionable (what does it mean to have a "carrying capacity" when the population cannot sustain itself even at small population sizes?), it may nevertheless suffice at small popu-

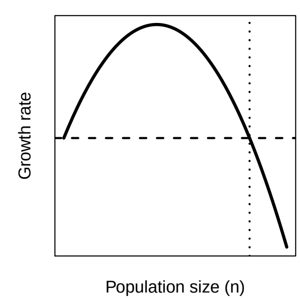


Figure 4: Growth rate in the logistic model with $r > 0$.

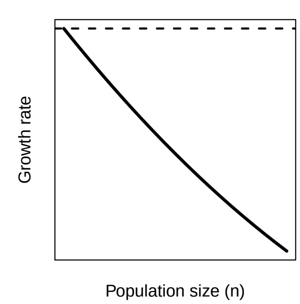


Figure 5: Growth rate in the logistic model with $r < 0$.

lation sizes. In this case, Figure 5 shows that the population growth rate is everywhere negative. As one intuitively expects, the population declines to extinction.

What do these growth curves imply concerning population trajectories? We start by considering the first (typical) case where $r > 0$ and look at populations initially both above and below carrying capacity? Solutions of the model in equation 9 are given by the equation

$$n_t = \frac{k}{1 + (k/n_0 - 1)e^{-rt}}. \tag{10}$$

Using this equation, we can plot the population size over time for a given combination of $r$ and $k$ and initial population size.

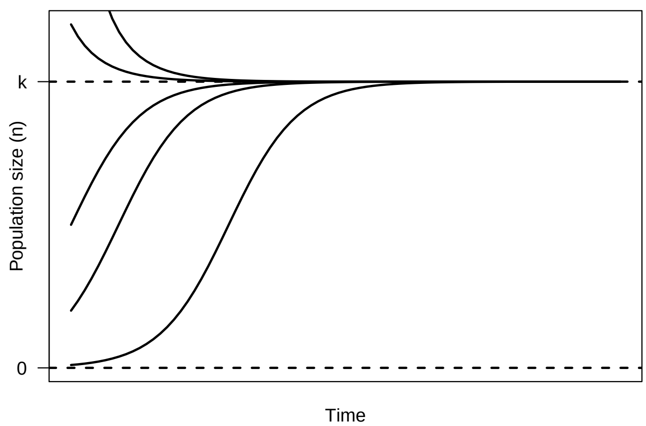


Figure 6: Solutions of the logistic model with $r > 0$. Dashed lines show carrying capacity ($n = k$) and extinction ($n = 0$).

As one expects, when $r > 0$ populations initially below carrying capacity increase to asymptotically approach the equilibrium value $n = k$ while populations initially above carrying capacity decline in the same fashion (Figure 6). In contrast, when $r < 0$ populations universally decline to extinction (Figure 7).

What these plots show is that trajectories may either converge to or diverge from equilibria. Which of these situations occurs can be determined by evaluating the growth rate (equation 9) somewhere near to (but not exactly at) the equilibrium. An equilibrium from which population trajectories diverse is called *unstable* while an equilibrium to which trajectories converge is called stable. In the logistic model with $r > 0$, carrying capacity ($n = k$) is a stable equilibrium and extinction ($n = 0$) is unstable. However, when $r < 0$ the only ecologically sensible equilibrium is extinction, which is unstable.

Stability of equilibria

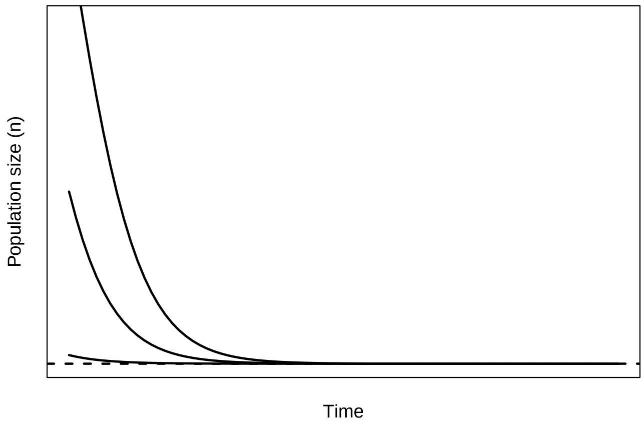


Figure 7: Solutions of the logistic model with $r < 0$. Dashed line shows extinction ($n = 0$).

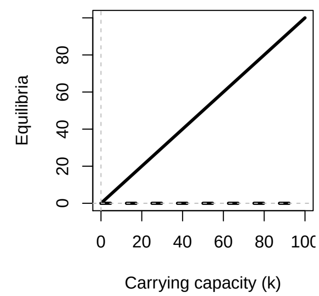


Figure 8: Bifurcation diagram of logistic model.

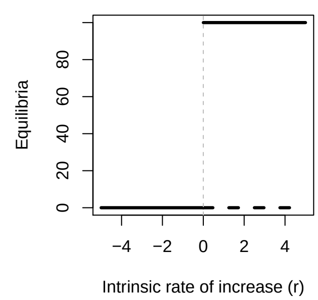


Figure 9: Bifurcation diagram of logistic model.

## *Catastrophic extinction & resilience*

All of the analysis up to this point has proceeded by assuming a single combination of values for $r$ and $k$. Can we possibly say anything more general? One approach is to ask how the equilibria change as $r$ and $k$ are varied over their possible ranges. A *bifurcation diagram* is a plot of the equilibria of a system against one or more of its parameters, which are referred to as the *bifurcation parameters*. Thus, for instance, if we choose to use $k$ as the bifurcation parameter we draw the plot in Figure 8. Conventionally, the stable equilibrium is plotted as a solid line and the unstable equilibrium is plotted as a dashed line. The plot is called a bifurcation diagram because the point at $k = 0$ is a special point at which the two branches of equilibria meet and "exchange" stability. This point is called a *transcritical bifurcation*. What this plot shows is that as the carrying capacity declines from some large value (*e.g.*, $k = 100$) toward extinction, then the equilibrium value the population tends to also declines proportionately. Given what we know about the logistic model already, this is unsurprising.

What if we consider instead $r$ as the bifurcation parameter. As before there is a transcritical bifurcation where two branches of the bifurcation diagram exchange stability. At values of $r$ greater than zero the population equilibrium is a positive stable value. Indeed, this value is the carrying capacity. However, unlike in the case with $k$ as bifurcation parameter, as $r$ declines toward the critical point at $r = 0$ there is no decline in the equilibrium population size. Instead, at the instant that $r$ declines to zero the upper branch of equilibria disappears and the unstable equilibrium at extinction becomes stable. Such discontinuities correspond to large jumps in the state of the system (in this case annhilation of the population) and are referred to as dynamical *catastrophes*. Thus, a decline in the intrinsic rate of increase may result in *catastrophic extinction* whereas as decline in carrying capacity does not.

Catastrophic extinction

Catastrophic extinction is an interesting – and practically important – phenomenon. But, is it really the case that a population can be subject to a change such as declining intrinsic rate of increase without exhibiting any evidence of this fact? In fact, no. Even though, in this model, there is no effect of decreasing $r$ on the equilibrium at carrying capacity, there is another effect. To illustrate, we consider two scenarios. Both situaations are governed by the logistic model with $k = 10$. In the first case we have a population with a robust intrinsic rate of increase of $r = 2$, but in the second case we assume the instrinsic rate of increase is very close to the critical point at $r = 0$, say $r = 0.1$. What is the difference? In fact, if both populations are at carrying capacity the model suggests that there will be no difference: a population at carrying capacity will stay at carrying capacity, barring perturbations that displace the population size from carrying capacity. Of course, real populations (rather than mathematical models) are subject to such perturbations. Does this make a difference? Yes. In Figure 10 we look at these two scenarios under a perturbation of size $\Delta n$. Such a perturbation could be an *exogenous shock* such as might be caused by a weather event (*e.g.*, a hurricane) or *intrinsic noise* due to the fact that population growth and decline will never follow deterministic differential equations directly. It doesn't matter. It also doesn't matter whether the perturbation is small or large. All we care about is that it is non-zero.

Extrinsic and intrinsic noise

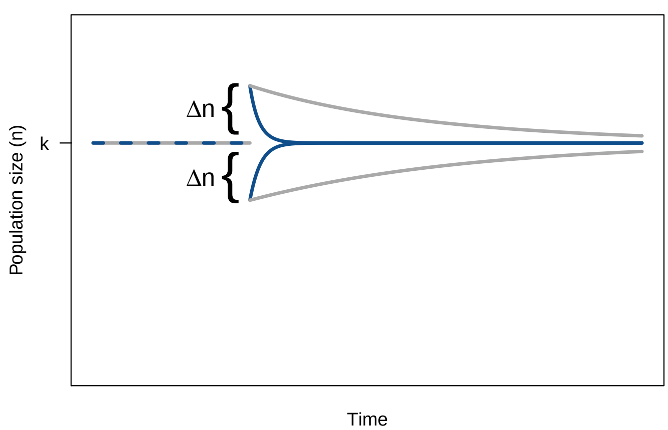


Figure 10: Solutions of the logistic model after a perturbation. The gray and blue curves correspond to two populations, each of which is at carrying capacity prior to a perturbation of size $\Delta n$ (which may be either in the positive or negative directionb). Blue line shows subsequent return to equilibrium by population with $r = 2$. Gray line shows return to equilibrium by population with $r = 0.1$.

What we see in Figure 10 is that for the same perturbation the population with $r = 2$ returned to the original equilibrium value (carrying capacity) much faster than the population with $r = 0.1$.

Accordingly, we say that the population with $r = 2$ is more *resilient* than the other population. Further, the return to equilibrium is essentially the same whether the perturbation is in the positive direction (increasing the population above carrying capacity) or in the negative direction (decreasing the population below equilibrium).

Resilience

## *Allee effects*

To conclude our discussion of density dependence we return to our study of Muskox on Nunivak Island. The density dependence studied so far is sometimes called *negative density dependence* because the effect of density is to reduce the effective population growth rate. However, if we look at our estimates of $r$ we see that the first four estimates of the growth rate, occurring in the first 15 years, were also the four lowest, hovering just above the replacement rate of $r = 0$ (Figure 11). Plotting instead against population size, we see that these were also the times when the population size was lowest (Figure 12). In this case, contrary to the assumptions of the logistic model, there appears to be some set of small population sizes over which the per capita population growth rate increases with increasing population size. Such a phenomenon often arises when individuals engage in some kind of cooperative activity such as foraging or defense. Alternatively, in species that reproduce sexually or are obligately outcrossing hermaphrodites, mate encounter may be rare in sparse populations resulting in increasing reproductive frequency as population density increases. Populations in which the per capita population growth rate increases with population size or density over some interval are said to exhibit *Allee effects*, named for the ecologist Warder Clyde Allee who spent much of his career studying cooperation and its population level effects.

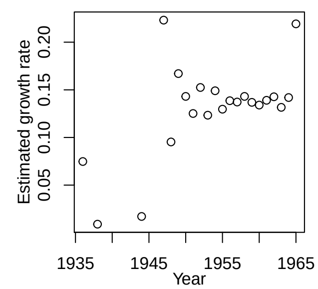


Figure 11: Lowest growth rates of muskox occurred in the first fifteen years after introduction.

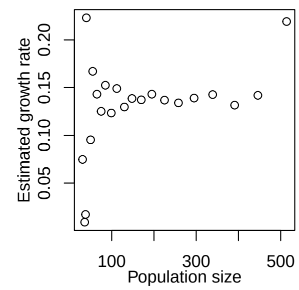


Figure 12: Lowest growth rates of muskox all corresponded to populations sizes of 40 individuals or fewer.

Allee effects are classified into two kinds.

- *Weak Allee effects* are those where the per capita growth rate increases over some interval (in keeping with our general definition above), but is everywhere positive.

- *Strong Allee effects* occur when the effect of cooperation is so severe that at some population sizes the per capita population growth rate is negative. If we also assume that per capita growth rate is a continuous function of population size, this fact implies that there is some non-zero population size at which the per capita growth rate is zero. Such a population size is an equilibrium (by definition). As inspection of the growth curve in Figure 13 shows, this is an *unstable* equilibrium.

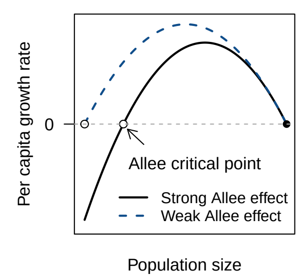


Figure 13: Allee effects occur when the per capita population growth rate increases over some interval of population sizes. A weak Allee effect (dashed blue line) occurs when the per capita population growth rate is everywhere positive. Like the logistic model, the model for a weak Allee effect has an unstable equilibrium at extinction (open circle) and a stable equilibrium (filled circle) at carrying capacity. A strong Allee effect (black line) occurs when the positive effects of deteriorating cooperation are so severe that below some critical point the per capita population growth rate is negative. This critical point (open circle) corresponds to an unstable equilibrium.

One model exhibiting a strong Allee effect is the cubic equation

$$dn/dt = rn\left(\frac{n}{a} - 1\right)\left(1 - \frac{n}{k}\right). \tag{11}$$

In this model, the parameters $r$ and $k$ serve roughly the same functions that they do in the logistic model: $k$ induces a negative density dependence and is the value of the upper equilibrium (carrying capacity) while $r$ regulates the potential for population growth. Here, the parameter $a$ ($0 < a < k$) is the critical density. Populations of size $n > a$ increase in size to carrying capacity, while populations of size $n < a$ decline to extinction. This model exhibits a cubic form characteristic of models of the Allee effect (Figure 14).

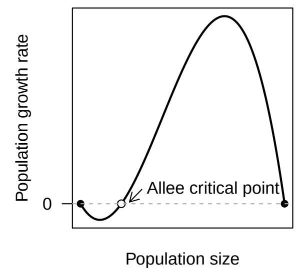


Figure 14: The Allee effect model in equation 11 exhibits a strong Allee effect.

Do muskox, then, exhibit an Allee effect? Quite possibly the answer is yes. Muskox engage in cooperative defense. When exposed to a predator, bull muskoxen will form a line protecting cows and calves. When presented with multiple predators, for instance a pack of wolves, muskoxen will engage in *circle defense*, where the adults form a tight circle facing outward protecting the young in the center of the circle (Figure 15).

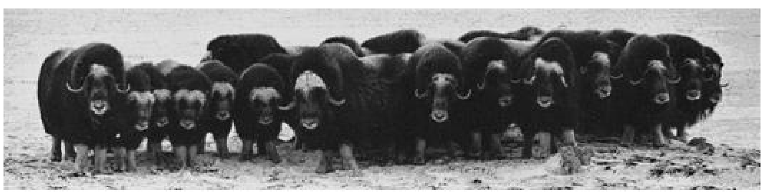

Figure 15: Muskox exhibiting distinctive circle defense formation.

Although most ecologists believe that many animal species will exhibit Allee effects if reduced to small size, documented Allee effects in natural populations are rather rare, probably because populations that are reduced in size to where Allee effects would be detectable are both small (and therefore unlikely to be observed) and at high risk for extinction (and therefore unlikely to persist long enough to measure the strength of the cooperative effect). However, muskox were among a small minority of species recently documented to exhibit Allee effects in a comparative analysis.[3]

[3] Stephen D. Gregory, Corey J. A. Bradshaw, Barry W. Brook, and Franck Courchamp. Limited evidence for the demographic Allee effect from numerous species across taxa. *Ecology*, 91(7):2151–2161, jul 2010. DOI: 10.1890/09-1128.1

## *Test yourself*

- What is density-dependence?
- Under what conditions is the carrying capacity of the logistic model stable? Under what conditions is it unstable?
- What is a bifurcation? When is the bifurcation of the logistic model catastrophic and when is it non-catastrophic?
- What is the difference between a weak and a strong Allee effect?

## *Further reading*

Kramer, A.M., B. Dennis, A. Liebhold, J.M. Drake. 2009. The evidence for Allee effects. *Population Ecology* 51:341-354.

## *Homework*

1. Derive the estimator in equation 5 from equation 2.

2. The standard deviation of our estimate for the intrinsic rate of increase of the Nunivak Island muskox population is shown in parentheses in the last line of Table 1. Using this and other information in the table estimate the 95% confidence interval of $r$. Use this information to put lower and upper bounds on the population size extrapolated to 2010.

3. Our record of the population of muskox on Nunivak Island is remarkably good. Suppose instead of annual censuses the only follow up censuses had been conducted at year 10 (1946) and year 20 (1956). What would you predict the population size to be in 2010. What are the lower and upper bounds of your estimate?

4. Derive an estimator for $\lambda$ from equation 4.

5. Derive the canonical form of the logistic model in equation 9 from the form in equation 8.

6. Solve equation 9 to obtain the solution in equation 10

7. In the equation for exponential growth, the per capita population growth rate at all population sizes is given by the parameter $r$ and was called the intrinsic rate of increase. In the logistic equation the percapita population growth rate declines with population size, but is at its maximum, which also is equal to $r$, in the limiting case where $n = 0$ (*i.e.*, as population size becomes small the behavior of the exponential growth model is recovered). Thus, in this case, also, $r$ may be called the intrinsic rate of increase because it is the maximum per capita growth rate. However, this interpretation of $r$ no longer holds in the model for the Allee effect given in equation 11. Here the maximum per capita population growth rate occurs at an intermediate population size $\hat{n}$, $0 < \hat{n} < k$. Find an expression for $\hat{n}$ and the intrinsic rate of increase (maximum per capita population growth rate) for a population with an Allee effect as in equation 11.

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