2 Wildebeest in the Serengeti: limits to exponential growth

At the beginning of the 19th century Thomas Malthus wrote extensively about the power of exponential growth, pointing out that no population can continue to grow forever. Eventually the numbers of individuals will get so large that they must run out of resources. While Malthus was particularly interested in human populations, the same must be true for all kinds of populations. Charles Darwin used those ideas as one of the cornerstones of his theory of natural selection.

Because of the speed at which exponentially growing populations can increase in size, very few populations in nature will show exponential growth. Once a population has reached sufficient size to use all of the available resources, there should be only minor fluctuations in numbers. Only when there is a large perturbation of the environment, such as the introduction of a species to a new area or severe reduction in population size due to hunting or disease will you find populations increasing in an exponential manner.

2.1 Wildebeest and Serengeti ecosystem

One very well studied system for looking at population dynamics is the wildebeest (*Connochaetes taurinus*) on the Serengeti plains of East Africa. There have been regular wildebeest population surveys for over 40 years.

Anthony Sinclair and Simon Mduma from the University of British Columbia have been studying them for 3 decades.

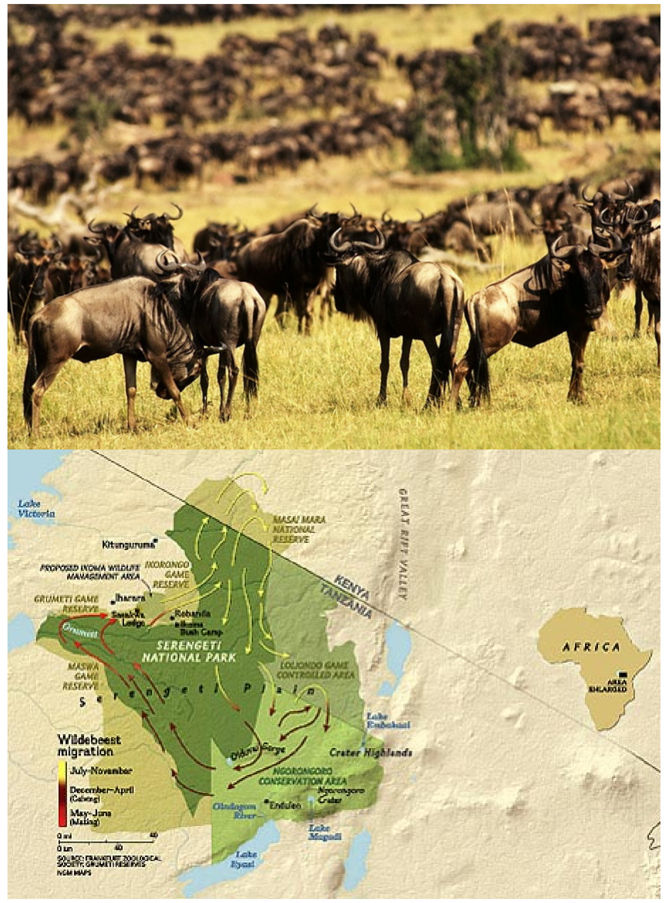


Figure 2.1. top: Herd of Wildebeest. Bottom: Map of the Serengeti-Mara ecosystem showing the annual migration route.

The Serengeti is a land dominated by rainfall patterns, with a gradient in annual rainfall from south to north. In general the southeastern shortgrass plains are the driest, receiving about 500 mm of rain per year. The northern Mara hills in Kenya are the wettest part and receive about 1200 mm of rain a year. However the rainfall is highly seasonal. During the wet season from November to May the plains are marked by abundant grass and even occasional standing water. Large herds of grazing herbivores (wildebeest, gazelles, zebras) take advantage of the flush of productivity to feed on the new growth. But after the monsoon rains stop in June, the grass withers and browns and the animals struggle to find sufficient food.

Further, the rain is highly variable among years and locations. Some years are marked by abundant rainfall, which produces more new growth, and food is plentiful for the grazers and browsers. In other years the rains end early and thousands of animals starve.

In response to the changing and unpredictable food supply, the wildebeest migrate across the landscape, producing one of the most spectacular phenomena in nature. As the fertile shortgrass plains dry up at the end of the monsoon rains, herds of a million or more wildebeest migrate west toward Lake Victoria. When that, too, starts to dry up they move north to the relatively wetter hills in the Mara region. Then, with the coming of the next rains, they move back south to the plains, completing an enormous circuit of the Serengeti each year. Early travelers were awed the “endless” plains of the Serengeti and the herds of migrating wildebeest that stretched as far as the eye could see.

2.2 **Rinderpest: a natural experiment**

In 1889 the rinderpest virus was accidentally introduced into Ethiopia in a shipment of 5 cattle. That accidental introduction started a wildlife disease pandemic. Rinderpest is an RNA virus of cattle that is closely related to the human measles virus. The virus quickly spread throughout the continent of Africa. Within a mere 8 years it killed an estimated 90% of the wild wildebeest and buffalo in east Africa. Travelers described the scene of millions of carcasses dotting the savanna. (Cattle herds, too, were decimated which caused enormous hardship for the traditional herding communities that depended on cattle). In the Serengeti, the population of wildebeest was reduced from over a million to only about 200,000 individuals by 1900. Throughout the 20th century periodic outbreaks of the rinderpest virus continued to occur and kept the population of wildebeest at a low level.

That all changed in the late 1950s when a vaccine against the virus became available. The Kenyan government began a systematic vaccination campaign of all domestic cattle and by 1963 the disease was effectively eliminated. The wild populations of ungulates that had been infected by the cattle-borne disease began to recover.

The recovery of the wildebeest population from the rinderpest virus has produced an enormous natural experiment that allows us to examine the growth and regulation of the population on a grand scale. In the decade following the introduction of the vaccine, the population of wildebeest in the Serengeti increased from 200,000 to over a million animals. Then, starting about 1975, the population growth ceased and

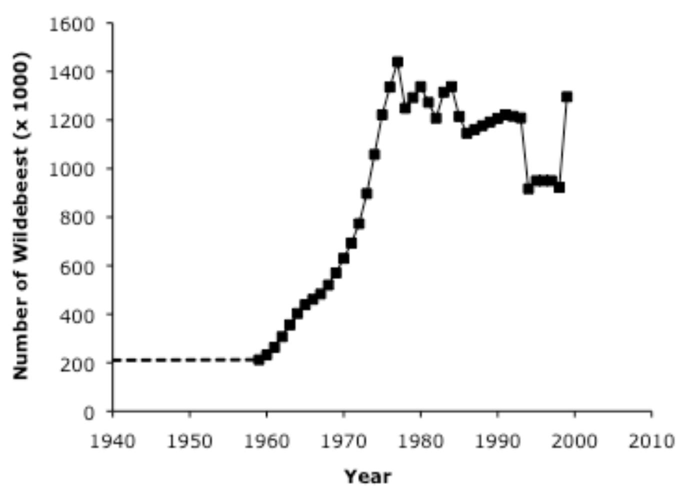


Figure 2.2. Wildebeest population size estimates, 1959 to 2001

stabilized at a population of around 1,200,000. What were the factors that caused the growth of the population to stop?

2.3 Wildebeest Population Dynamics

The population of wildebeest has been censused every year since the late 1950s when a father and son team from the Frankfurt Zoological Society started using a small plane to follow and monitor the vast herds on the Serengeti. The same basic technique is still in use today. It is not possible to count every individual wildebeest since the population size is well over a million. Instead, they must use a sampling scheme. Generally they will fly predetermined transects over the plains and take photographs at regular intervals. Later the number of wildebeest in each photograph is counted. By precisely maintaining a constant altitude above the ground, they can determine the area covered in each photograph and hence the density of wildebeest. This method is not foolproof: there will be slight biases caused by different observing conditions and different habitat types, but biologists have learned to make the necessary corrections to account for those variations.

Population estimates for the Serengeti wildebeest in December of each year are shown in Figure 2.2. Initially, the population grew rapidly from the low of 200,000 animals to about 1.2 million. Then, starting around 1975 the growth of the wildebeest population ceases.

- Looking only at the first 15 years of data (1960 to 1975) is the pattern of growth consistent with exponential increase? How could you tell?

- What factors do you think cause the population to stabilize?

The pattern of rapid initial growth that is then followed by a period of stasis is common in biological systems, whether you are describing the growth of bacteria in culture or duckweed in a pond.

2.4 Logistic population growth model

In chapter 1 we saw that under pure exponential growth only two results were possible. When r>0 then pops will grow exponentially without bounds. When r<0 then the population will decline to extinction. However we know that wildebeest are neither extinct nor infinite. These populations have existed for a long time without going extinct, so r must be positive when N is reasonably small. We also know that the population is not infinite, so r must be negative when N is very large. The simplest way to get that is to have r decrease linearly as the population size increases.

Recall that under exponential growth $\frac{dN}{dt} = rN$. We can add an additional term to that model to make the growth rate decline linearly with population size: $\frac{dN}{dt} = r(1 - cN)N$.

Let the constant "c" be r/K and you can rearrange to get the **logistic equation**:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \qquad \text{eq. 2.1}$$

The new term in parentheses is sometimes called a "braking" factor that slows the rate of population growth as N increases.

There are lots of mathematical models of density dependence that we might come up with besides this simple linear dependence on N. But this simple description is a good place to start. As you will see, it can describe some populations very well and it can give us insights into some general features of population growth.

The equation to predict population size from a given intrinsic rate of increase and carrying capacity is somewhat more complicated than the corresponding equation for exponential growth, but the principles involved are the same. The population size at time t is given by:

$$N_t = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}} \qquad \text{eq 2.2}$$

which is shown in Figure 2.3.

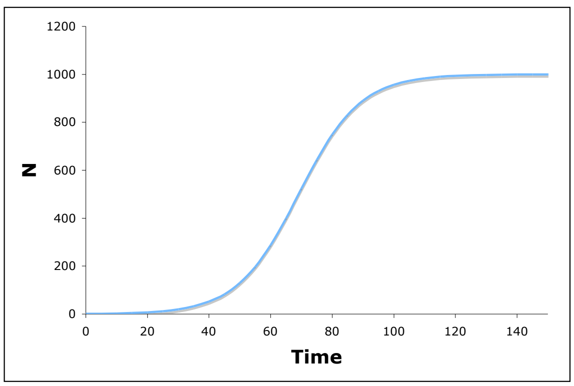


Figure 2.3 Logistic population growth model for the values r=0.1, K=1000, and N_0=1.

How would the graph in Figure 2.3 change if *r* was half as big? Sketch the trajectory for *r*=0.05 on the figure.

Initially the population increases approximately exponentially. But after several generations the rate of growth decreases and finally ceases altogether as the population stabilizes at a constant population size. In terms of equation 2.1, when N is near zero the quantity in parentheses is close to 1 so we have the familiar equation for exponential growth. When N=K the term in parentheses is zero so dN/dt=0 and the population size stays constant. K is called the "carrying capacity" of the population.

2.4.1 A non-rigorous derivation of the logistic equation, via a thought experiment.

Assume that the habitat is divided into some number ("K") locations that are each able to support exactly one individual. Starting with a single individual the population can grow at a rate "r". Because the locations are all empty, 100% of the sites are available. As N increases and the fraction of sites begins to fill, there are fewer locations left in the environment. The proportion of the original locations that are left is 1-N/K. The population can then grow only at the rate r(1-N/K). Substituting that adjusted growth rate into the basic equation for population growth and rearranging, you end up with the logistic growth model:

$$\frac{dN}{dt} = rN(1-\frac{N}{K}).$$

2.5 Assumptions of the logistic growth model:

- All individuals are identical. We can ignore differences between adults and juveniles or between males and females and simply keep track of the total population size, N.
- The population is closed, so there is no immigration or emigration.
- r and K are constant.
- Density dependence is linear: each additional individual reduces the population growth rate by a constant amount.

The logistic population growth model forms the basis of most of ecological theory. That simple model is well-understood and it captures the essential features of population dynamics for most species. That general pattern that populations increase when densities are low and resources are abundant, and then reach a relatively steady plateau of abundance when resources become limiting is a characteristic feature of most organisms.

These assumptions are rarely, if ever, completely correct. But the model captures the essential dynamics of populations and is a very useful starting point. In later chapters we will use extensions of this basic model to understand competition between species.

2.6 Exploring the logistic model

It is interesting to explore the logistic model by graphing the function in different ways. For example, how does the population growth rate, dN/dt, change with population size? For logistic growth the graph of dN/dt vs N is a humped curve as shown in Figure 2.4. (To see that it is a quadratic function of N, expand equation 2.1 and notice that there is an N^2 term).

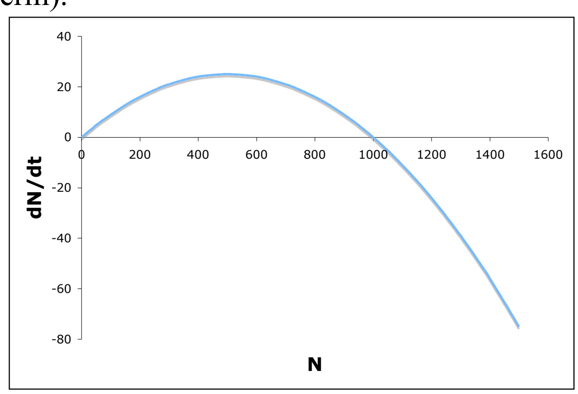


Figure 2.4 Logistic population growth model for the values r=0.1, K=1000..

When the population is small the growth rate of the population is also small. The growth rate increases to a maximum at intermediate population size and then decreases at larger population sizes. If the population is too big, the growth rate of the population will become negative.

In terms of equation 2.1, when population is small the dN/dt will be small because N is near zero. As N approaches K, the growth rate again declines because the quantity is parentheses is near zero. Then when N>K, growth rate becomes negative because the quantity in parentheses is negative.

What would the graph of dN/dt vs N look like for pure exponential growth?

The population is at equiibrium when dN/dt=0.
By definition, the population size does not change if it is at equilibrium, i.e. dN/dt=0. Figure 2.4 shows that dN/dt is zero at two population sizes, so there are two equilibria. One equilibrium is at N=0. If the population starts with zero individuals there can be no births or deaths so the population will not change.

The second equilibrium occurs when the population reaches the carrying capacity, K. Is that equilibrium *stable*? A stable equilibrium is one where the population will return to the equilibrium value following a small perturbation. For example assume a population has reached its carrying capacity (K) so it is no longer growing. Now, imagine that a severe storm comes through and kills some individuals so N is slightly less than K. Figure 2.4 shows that when N<K, the growth rate is positive so the population will grow and eventually return to the carrying capacity. Similarly, if you imagine that by some perturbation the population size became slightly larger than K, Figure 2.4 shows that when N>K the growth rate will be negative and the population will decrease in size until it is again at the carrying capacity.

Is the first equilibrium (N=0) stable? __________
(Again imagine a small perturbation away from equilibrium where you add a few individuals to a population that starts at zero. Will the population size return to zero?)

Maximum growth rate of the population
Looking at Figure 2.4, at what population size is the growth rate maximized?_____________
.
In general, how can we determine at what population size the growth rate is maximized? The same way we find the maximum of any function: find the second derivative of the function, set it equal to zero and solve for N. For the logistic equation, $\frac{d^2N}{dt} = r - 2r\frac{N}{K}$. If we set that equal to zero, then $r = 2r\frac{N}{K}$ so $N = \frac{K}{2}$.

For the logistic model, the growth rate of the population is always highest when the population is at half the carrying capacity.

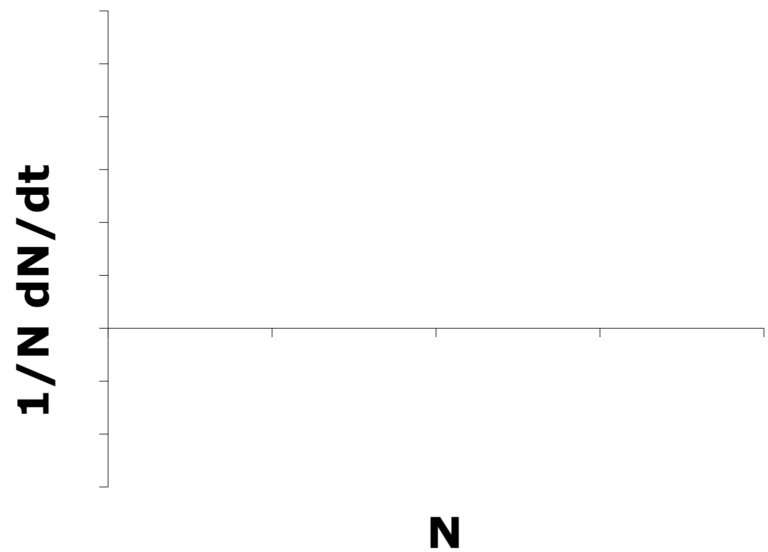
The per capita growth rate declines linearly

Remember that the logistic growth equation was derived assuming that the reproductive rate of an individual declines linearly as population size increases. Each additional individual in the population always reduces the average reproductive rate by a constant amount. If the population grows at a rate dN/dt, then the *per capita growth rate* is $\frac{1}{N}\frac{dN}{dt}$.

Starting with equation 2.1, write an expression for the per-capita growth rate.

$$\frac{1}{N}\frac{dN}{dt} = \_\_\_\_\_\_\_\_\_\_\_\_$$

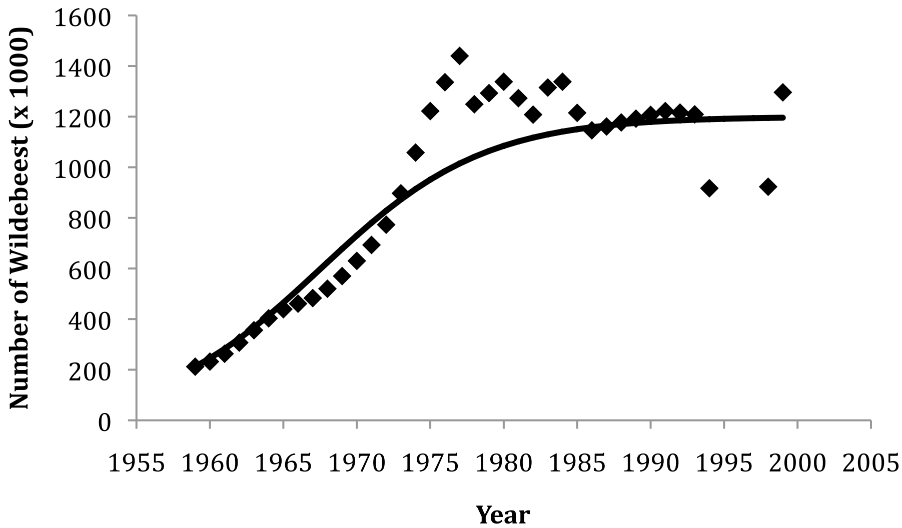
Sketch a graph of the per capita growth rate as it relates to population size. Label r and K on the graph. (hint: at what population size will the per capita growth rate be highest? At what population size will the per capita growth rate be zero?



How would that graph look different for exponential growth?

Notice that we have used the term growth rate in related, but slightly different, ways. The parameter r is the **intrinsic growth rate** of the population: the rate of growth when the population size is very small. In this model it is assumed to be constant. In contrast, the actual **growth rate of the population** is measured by dN/dt. That realized growth rate shows the actual number of new individuals that are added in a time step and will depend on the number of parents and the distance of the population size from the carrying capacity. Finally, the **per-capita growth rate** (1/N dN/dt) shows the number of new individuals per parent. It, too, depends on the distance of the population size from the carrying capacity. In the logistic model it is assumed to decline linearly as N increases.

2.7 Density dependent growth of the wildebeest population



What is the approximate carrying capacity for this population? ___________

For this real system, the logistic population growth model captures the general pattern of population growth but not all of the details. Initially, the population grows almost exponentially and the logistic equation fits fairly well. When the population stabilizes it is also fairly close to the value predicted by the logistic equation. However, between 1970 and 1977 the population grew much faster than expected. And in 1994 the population suddenly dropped to less than a million.

What kinds of factors might cause the deviations from the expected logistic growth? ____________________+______________

2.8 The biological basis of population regulation

The implicit assumption of logistic population growth model is that population growth rate declines because the animals become limited by some resource, usually food. The reduction in the amount of food available per individual increases mortality (through starvation) or decreases birth rate, so the net population growth declines. Nevertheless, food does not show up anywhere in the logistic equation. Instead, the model uses population size as a surrogate for the resources that are being used. The assumption is that in a constant environment, if population size increases there will be less food available per individual. The model works phenomenologically, but it bypasses the actual mechanism of population regulation.

In the case of wildebeest, the food available for an individual can decrease because a) rains don't come or b) too many wildebeest share too little food. The logistic model essentially assumes that only the latter is important. It should be possible to get a better model for the regulation of wildebeest populations by directly incorporating food supply into our model. For example, the wildebeest population grew faster than predicted by the logistic model during the years 1972 to 1977, a period of higher than average rainfall when the savannas remained lush and green. The drop in population in 1994 followed an extremely severe drought.

2.8.1 *** OPTIONAL PART ***

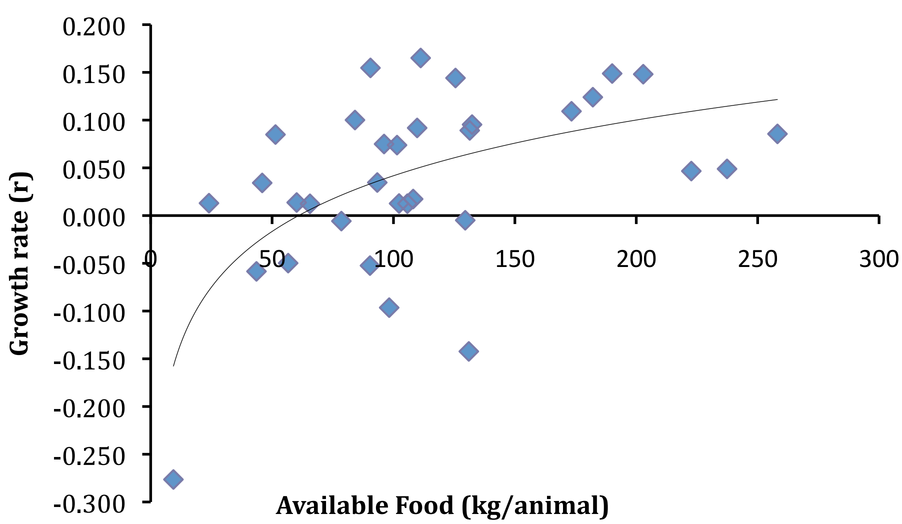
How can we calculate the available food? For that we would need to know the amount of grass available (which depends on rain) and the number of wildebeest that are sharing that resource. Long-term studies of the rate of growth of grass on the Serengeti and he has shown that the amount of grass biomass production is directly proportional to rainfall. Grass production per hectare can be predicted by a very simple equation: $G = 1.25R$. During the dry season the animals are spread over about 500,000 ha. Combining that, the total available food can be predicted with this simple formula:

Food supply = 625000 * Rainfall (mm)

Using data in appendix A, calculate the food available *per animal* in 1965 vs 1981, years with similar rainfall but very different population size.

- 1965 ________
- 1981 ________

- Calculate the food available per animal in 1992 vs 1993, years with similar population size but different amounts of rain.
  - 1992 ________
  - 1993 ________



The fit isn't perfect, but the population growth rate clearly increases with the available food supply.

What is the minimum food supply to prevent population from declining? ___________

2.9 What is the use of this model?

In general, models are use to 1) to make a prediction and/or 2) to understand the system. Understanding the population dynamics of wildebeest allows us to make some predictions about the system. For example, if the population declines due to another drought, how long will it take for the population to return to its carrying capacity? Or, given the link between population growth and rainfall patterns, what is the minimum rainfall necessary to support the wildebeest population? If global climate change alters the rainfall regime on the Serengeti, will the wildebeest population persist?

It is perhaps more useful as a tool for understanding, however. Our analysis showed us that population growth is density dependent and controlled by a combination of intrinsic factors (density) and extrinsic factors (unpredictable rainfall). All else being equal, the logistic model showed us that the population size should remain stable at or near its carrying capacity.

That understanding can come at various points in the analysis. For example, we found that the logistic growth model captured some of the most basic features of the population dynamics, the rapid initial growth followed by stabilization of the population at approximately 1.2 million animals. In particular the fact that rate of population growth slowed and finally stabilized showed that it was not a simple case of exponential growth.
But there were some systematic departures of the data from our simple prediction. That led us to notice that the population grew faster than expected during a series of years with higher than average rainfall, and pointed to rainfall as a key factor.

2.10 Density dependent vs density independent population regulation.

The standard logistic growth model is based only on the population density and shows that it is possible for density dependent processes to maintain populations at a stable carrying capacity. However the actual wildebeest counts were also related to the rainfall, an extrinsic factor that is unrelated to population size. There has been a longstanding debate among ecologists regarding the importance of density dependent factors vs density independent factors in regulating populations.

Some ecologists point to large and erratic fluctuations in population size of organisms to say that populations are rarely at equilibrium and are instead kept well below their carrying capacity by extremes of weather or other extrinsic factors. Graphs of per capita growth rate vs population size rarely show a perfect linear decline. Others argue that even if weather can affect population abundance, real populations fluctuate within fairly narrow bounds that are determined by density dependent factors. The jury is still out, but real populations are probably controlled by a combination of density dependent and extrinsic factors.

2.11 **Further reading:**

Mduma, S. A. R., A.R.E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40 year record. J. Animal Ecology 68:1101-1122.

Sinclair, A.R.E. and P. Arcese (eds). 1995. Serengeti II: Dynamics, management and conservation of an ecosystem. University of Chicago Press.

2.12 **Your turn**

The cockroach (*Blattella germanica*) is one of the most common household pests in the world. The highly-adaptable species has been associate with humans for thousands of years and is found throughout the world. Cockroaches are often associated with "uncleanliness". Populations thrive in places where there is poor sanitation (i.e. a food source), household clutter (i.e. hiding places) and unrepaired leaks (i.e. moisture source). Adult cockroaches can breed at any time, so the population fits the continuous time models of population growth.

One estimate of the population growth rate for cockroaches is r=0.056 *per day*. The maximum density of cockroaches varies widely. It will depend on the supply of food and water, but let's say that K for an average infested kitchen is about K=400 cockroaches.

Starting with an initial pair of cockroaches, how many would there be after a year?

Now imagine two scenarios: chemical control vs scrupulous sanitation. How will each of those affect r and K?
Imagine a 75% reduction in *r*, or a 75% reduction in *K*. Which strategy is likely to be more effective in controlling the cockroaches?

Table 1 Population size and rainfall data (from Mduma et al. 1999). Wildebeest counts are for the number of Wldebeests in December, after the dry season and before new alcves are boen. Rainfall is for the period July to December.

Year	Number of wildebeest (x 1000)	Dry Season Rainfall (mm)
1959	212	
1960	232	100
1961	263	40
1962	307	102
1963	356	104
1964	403	168
1965	439	168
1966	461	166
1967	483	78
1968	520	91
1969	570	78
1970	630	133
1971	693	192
1972	773	235
1973	897	159
1974	1058	211
1975	1222	258
1976	1336	205
1977	1440	303
1978	1249	188
1979	1293	85
1980	1338	100
1981	1273	162
1982	1208	97
1983	1315	230
1984	1338	207
1985	1215	84
1986	1146	45
1987	1161	114
1988	1177	191
1989	1192	201
1990	1207	126
1991	1222	255
1992	1216	152
1993	1209	19
1994	917	227

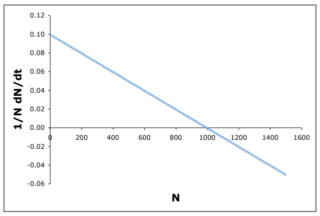
Answers:

p 3. Growth starts out close to exponential (graph lnN vs time and see if it is linear0

p4. If r is half as big, N will approach K more slowly, but it will still eventually increase to K.

p 6 dN/dt vs N is a straight line with slope=r for pure exponential growth
The equilibrium at N=0 is not stable
dN/dt is maximum at 1/2 K (500)

p 7.



for exponential growth, this would be a horizontal line (i.e. r is constant)

p. 8 K = 1,200,000
variation in the environment is a likely cause of the deviations

p 9. Food/animal is
1965: 239 kg/animal
1981: 80 kg/animal
1992: 78 kg/animal
1993: 10 kg/animal
p 10. Minimum food is about 60 kg/animal
(from that you could figure out what the carrying capacity would be for a given rainfall amount)

Cockroaches:
After a year with logistic growth (r=0.057, K=400) → N=400
Pesticides will affect the death rate (i.e. r) whereas food supply determines K.
75% reduction in r: (r'=0.014) , N=182
75% reduction in K: (K'=100) , N=100