PART I

Introduction and the physical environment

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Fred D. Singer
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Chapter 1

What is ecology in action?

INTRODUCTION

The Serengeti-Mara ecosystem in northern Tanzania and southern Kenya is a showcase of vertebrate life, home to over 650 species of birds and 79 species of large mammals. Equally impressive, many of the species are present in enormous quantities. In the early 1960s, there were approximately 250 000 wildebeest (*Connochaetes taurinus*), 200 000 zebras (*Equus burchelli*), 30 000 buffalo (*Syncerus caffer*), and 750 000 Thomson's gazelles (*Gazella thomsoni*) roaming through the ecosystem. Every year, the zebras, wildebeest, and gazelles spend the wet season in the southeast portion of the Serengeti, eating the grasses and herbaceous plants that grew during the wet season, which extends from November through May. These grasses have very high levels of nutrients, which are particularly important to pregnant females who give birth in the middle of the rainy season and begin the nutrient-demanding process of lactation. As rainfall diminishes in June, many of the zebras, wildebeest, and gazelles migrate to the northwest portion of the ecosystem, munching on taller but less nutritious grasses that grow in the much wetter northern and western plains. When the wet season returns in November, so do the large mammals that have survived the dry season, to begin the cycle anew.

Many researchers have converged on the Serengeti to answer important ecological questions. We will follow in their footsteps, using the Serengeti ecosystem to gain an understanding of what types of questions ecologists ask. We will then see how ecologists use the entire scientific toolbox to answer these questions, but that ecological questions, because they tend to be so broad, may require a researcher willing to tackle numerous levels of the biological hierarchy. Let's go back to the beginnings of ecosystem studies in the Serengeti.

KEY QUESTIONS

1.1. What are ecological questions?

1.2. How do ecologists test hypotheses about ecological processes?

1.3. How do ecologists use observation, modeling, and experimentation?

1.4. How do ecologists ask questions that link different levels of the biological hierarchy?

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CASE STUDY: Birth of a research program

The western world was introduced to the Serengeti by a German father-and-son team, Bernhard and Michael Grzimek, who together created a movie, *Serengeti Shall not Die*, which was wildly popular around Europe. Tragically, in 1959, as Michael filmed from a low-flying airplane (Figure 1.1a), a griffon vulture flew into the plane, causing it to crash and killing him. Michael was buried atop Ngorongoro Crater, east of the Serengeti; his epitaph reads "He gave all he possessed including his life for the wild animals of Africa." His father joined him at the same site almost 30 years later (Figure 1.1b).

Though Michael gave his life for the Serengeti, he and his father gave birth to a growing global awareness of the beauty, drama, and potential plight of this vast ecosystem, and in particular they uncovered many features of the large mammal migrations. Bernhard, as director of the Frankfurt Zoological Garden, used proceeds from the movie to help fund Serengeti research. In addition, John Owen, then director of Tanzania National Park, used his position to establish the Serengeti Research Institute in 1961, which funded three scientists to continue working on the wildebeest migrations. Within a few years, several other researchers joined the Institute and began investigating other parts of the ecosystem.

Meanwhile, in England, Tony Sinclair was having some issues about what he was going to do for the rest of his life. His father, a New Zealander employed as a judge for the British government, was stationed primarily in Tanzania during the first 10 years of Sinclair's life. There, Tony spent much of his time outdoors hanging out with his friends, learning about the culture, becoming fluent in Swahili, and discovering the large diversity of non-human animals that lived in this ecoregion. At age 10, Tony was shipped off to England to continue his education. To him a career in biology meant medicine, and given his disdain for illnesses of all kinds, he entered a program in engineering, math, and physics. But these fields did not captivate him, and one day, at age 16, he just said, "What am I doing? I can do biology that's not medicine – I can do zoology."

Having switched his career path, he knew he needed to get back to Africa, so when he entered the University of Oxford he immediately sought out Professor Arthur Cain, asking him, "How do I get to Africa?" Cain informed him of his plans to go there the following summer to study bird

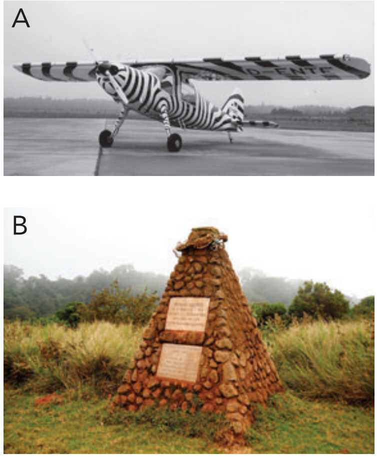
A
B


Figure 1.1 A. Michael Grzimek's airplane. B. Gravesite of Michael and Bernhard Grzimek atop Ngorongoro Crater.

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migration (which Sinclair already knew something about), and Sinclair made enough of a nuisance of himself that he was invited to come along as a research assistant for the Serengeti Research Institute. That did it for Sinclair – he was hooked.

Recall that Sinclair was more experienced in surviving the Serengeti experience than most Oxford expatriates. He was fluent in Swahili, so if he needed help, he could explain his needs to the local people. He was also familiar with the wildlife and the environment, so that he knew where to find animals for observation, and also how to avoid getting eaten or gored by his subjects. After observing Sinclair's abilities to survive in the bush while collecting data under challenging circumstances, the researchers at the Institute presented him with a problem that was to be the focus of his PhD dissertation. They thought that the number of buffalo and wildebeest in the Serengeti-Mara ecosystem had been increasing in the past few years, but they did not know why. Could he come back and figure that out? He responded, "I can do anything you want – just get me there." And so was born a research program that has continued for over 40 years. We will use Sinclair's research in the Serengeti to help us understand what ecologists do, and how they do it.

1.1 WHAT ARE ECOLOGICAL QUESTIONS?

To get started on his project, Sinclair needed to answer two of the most basic questions addressed by population ecologists. The first question is: What is the abundance of a population? Or, how many individuals are there in the population? The second question is: What is the **distribution** of the population? Or, where are the individuals actually located in space and time? Later in this chapter, we will explore how Sinclair addressed a third important ecological question: How do interactions with the environment influence the distribution and abundance of organisms?

The buffalo challenge

The question of why the buffalo and wildebeest populations were increasing proved very challenging for several reasons. First, the buffalo were petrified of humans, because they had recently been targets of very heavy poaching. So anytime Sinclair got remotely close to a herd, they took off in terror – and motivated buffalo can run very quickly. Second, before discovering why buffalo abundance was increasing, Sinclair first needed to show that abundance was indeed higher than in previous years. Even if he could ultimately figure out how to count the current buffalo population, it would be challenging to go back in time to measure their abundance in previous years. Last, if he could show that buffalo were increasing, there were several potential causes of the increase. Each cause would be difficult to explore with any degree of rigor. We'll look at how Sinclair solved these problems sequentially, keeping in mind that he was actually working on all three problems at the same time.

Though his PhD research was on buffalo, Sinclair was also keeping track of the migrating wildebeest, in cooperation with other researchers at the Institute. Upon completing his dissertation research in 1970, Sinclair began working as a postdoctoral associate for the Institute, focusing on the wildebeest populations. Thus in the remainder of the chapter we will discuss research on buffalo, wildebeest, and other large Serengeti mammals.

Estimating buffalo and wildebeest abundance

Because buffalo were so afraid of humans, Sinclair's only option was to survey them from the air. Trained pilots and observers photographed the buffalo while flying about 200 m above the surface. Buffalo range almost exclusively in open woodlands, so there was no need for Sinclair to census areas that were exclusively grassland. As a result, all suitable habitats were screened in just a few days. Fortunately, buffalo are huge, but even from 200 m it was challenging, yet possible, to distinguish individual animals.

Wildebeest congregate in much larger herds than buffalo, and are much more tolerant of humans and their flying machines. Because wildebeest congregate so close together and are smaller than buffalo, the researchers needed a higher magnification on their telephoto lenses to see them, and thus only a small fraction of the herd could be photographed in one picture frame. One complete survey required 2770 frames and took 9 months to count.

> **Thinking ecologically 1.1**
>
> What types of problems might a researcher encounter when conducting aerial surveys? How might a researcher deal with these problems?

Estimating historical buffalo and wildebeest abundance

To estimate sizes of past populations, Sinclair did historical research on populations of both buffalo and wildebeest. Some of his information came from interviews with people who had lived in the Serengeti, but most came from books, articles, travelogues, and especially photographs taken in previous decades. As one example, Sinclair knew that Martin and Osa Johnson had written a travelogue called *Safari* back in the 1920s, which described their experiences in Africa. He knew

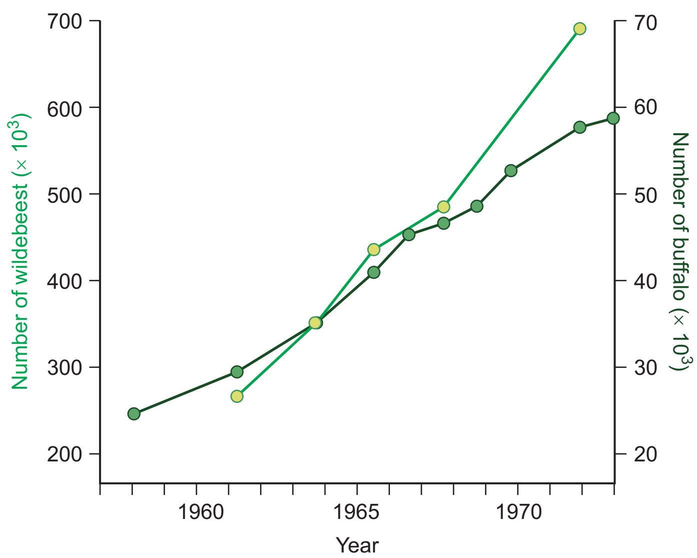

Figure 1.2 Increases in populations of buffalo (dark green) and wildebeest (light green) in 1958–1972.

that for every book there are thousands of journal writings, pictures, and stories that don't make it into the book, and in 1981 Sinclair discovered the Martin and Osa Johnson Museum in Chanute, Kansas, Osa's hometown. It was a repository for much of the Johnsons' travel documents and pictures, and Sinclair was able to convince the curator to grant him access to all of their materials. In return, he organized the collection, so the curator and future patrons would know which materials were from the Serengeti.

Because he knew the Serengeti so well, Sinclair could identify exactly where many of the photographs were from. So he now had historical records of the vegetation from 1926, 1928, and 1933. One set of aerial photographs included a series of contiguous pictures that encompassed the entire wildebeest migration, which allowed Sinclair to estimate an abundance of approximately 90 000 animals. He was not so fortunate with historical research on buffalo, so we have no good early estimates of buffalo abundance.

More recent estimates of buffalo and wildebeest populations, beginning in the late 1950s, are more accurate, though they have a margin of error as well. Based on estimates by previous researchers, and Sinclair's more refined techniques in the late 1960s, the buffalo and wildebeest populations more than doubled in the 1960s, and continued to increase through the mid-1970s (Figure 1.2).

Having established that his colleagues at the Serengeti Research Institute were correct about a sudden increase in the buffalo and wildebeest herds, Sinclair's next task was to figure out why this was happening. He considered several hypotheses to explain why population sizes were increasing. We will use this question to explore how ecologists use hypotheses and predictions to answer questions.

1.2 HOW DO ECOLOGISTS TEST HYPOTHESES ABOUT ECOLOGICAL PROCESSES?

To answer questions about biological processes, ecologists test hypotheses that are provisional explanations for their observations. To be worthy of study, hypotheses must be plausible and generate testable predictions. Predictions are logical outcomes that are likely to be true if the hypothesis is true. Philosophers of science have extensive and sometimes passionate discussions about the relationship between hypotheses and predictions, which we will not delve into. Rather, we will simply point out that if a prediction is shown to be true, we feel somewhat more inclined to accept the hypothesis, but if we are good scientists, we will continue testing the hypothesis by exploring other predictions it generates. If the prediction is shown to be false, the hypothesis, as stated, is very unlikely to be true, unless there is something wrong in the methods we used to test the prediction.

This relationship between hypotheses and predictions will become clearer as we consider three hypotheses for why buffalo and wildebeest populations increased so sharply in the 1960s and 1970s. Sinclair's research also brings home the point that, ideally, researchers will consider all hypotheses when attempting to understand a biological process.

The food availability hypothesis

Perhaps herbivore populations were increasing because their food was becoming better in quality, or more abundant. If this hypothesis was correct, Sinclair predicted that food quality and abundance would have increased sharply in the early 1960s and remained high during that entire decade.

Sinclair and his colleagues suspected that the amount of rainfall would profoundly influence grass production – the amount of grass that was available to the grazers. To test this hypothesis, the researchers established a series of fenced areas, or exclosures, that prevented grazers from accessing the vegetation within the fences. They periodically harvested the vegetation, and measured the amount of grass that had grown in relation to the amount of rainfall that had recently fallen in the area. They predicted that there would be a positive **correlation** between rainfall and grass production (see Dealing with data 1.1 for a discussion of correlation). The results were striking – as rainfall increased, grass production also increased (Figure 1.3). The researchers concluded that rainfall has a significant positive effect on grass availability (Sinclair 1975).

This strong correlation between rainfall and food availability allowed Sinclair to use rainfall as an index of food availability. Sinclair did not begin his buffalo research until 1966, so he relied on measures of rainfall as his indication of grass availability during the early and middle 1960s. If increased food availability was causing the increase in buffalo and wildebeest abundance, he

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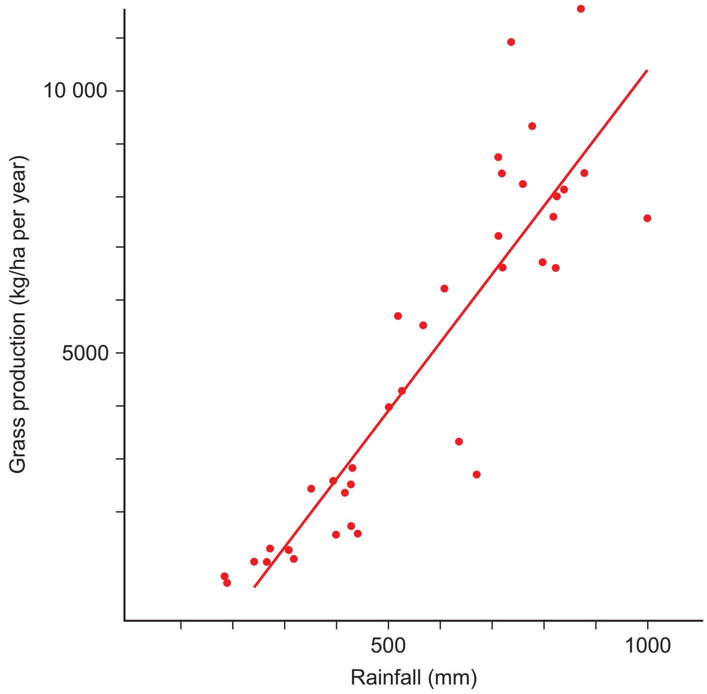


Figure 1.3 Relationship between rainfall and grass production.

Thinking ecologically 1.2

Draw a scatterplot showing how rainfall in the Serengeti varied over time. Year should be the *x*-axis label, and mean monthly rainfall (mm) should be the *y*-axis label. Is this a strong or weak correlation? Is this a positive or negative correlation?

Dealing with data 1.1 Correlation analysis

When both variables are numeric or continuous (have values that can be counted or measured), we can use a correlation analysis to evaluate the relationship between the two variables. In the exclosure example described previously, Sinclair and his colleagues predicted a positive correlation between the amount of rainfall and grass production. The researchers found

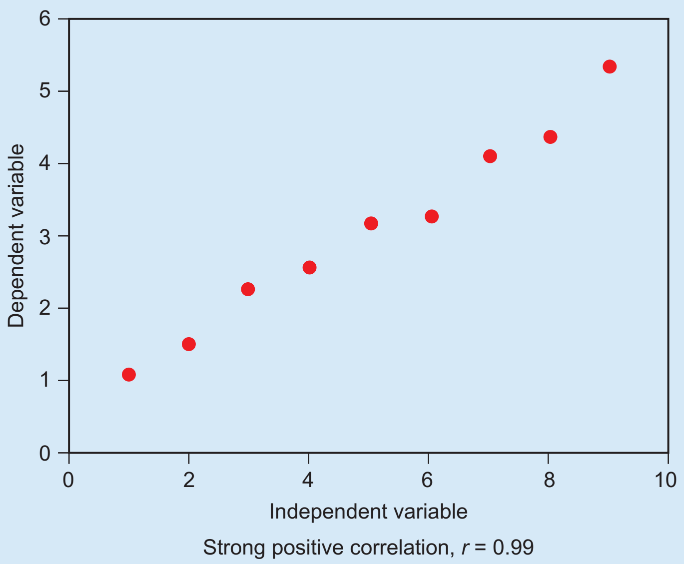
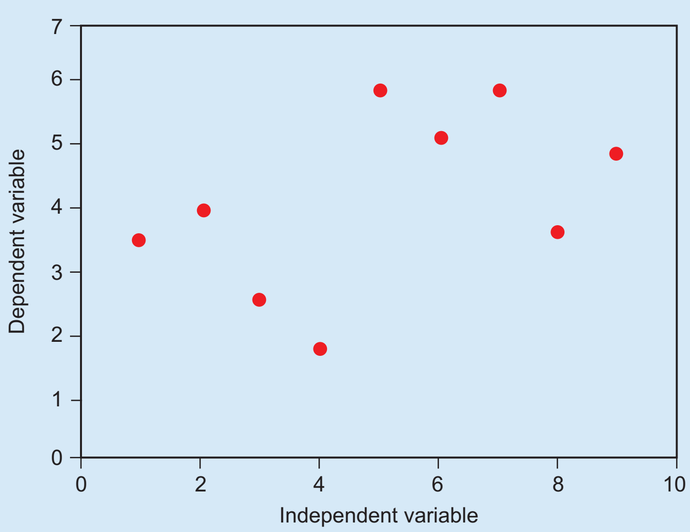


Figure D1.1.1

a strong positive correlation, which means that as rainfall increased, so did grass production. Figures D1.1.1 and D1.1.2 are examples of strong and weaker positive correlations.

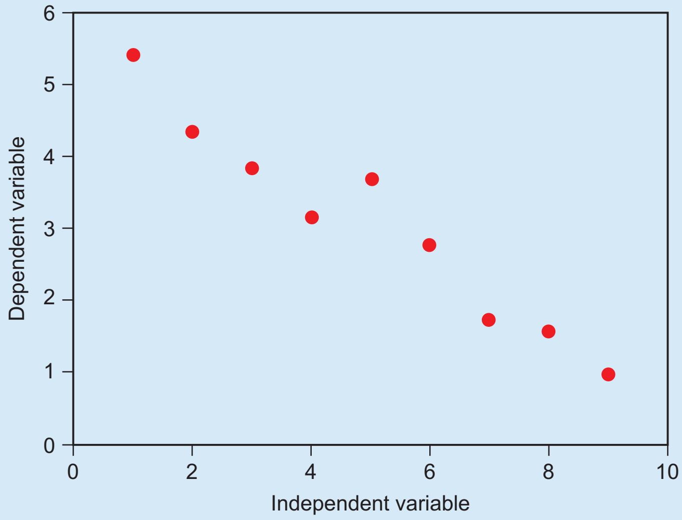
Statisticians use the **correlation coefficient (*r*)** to describe the strength of the correlation. If *r* is equal to 1.0, then all the data points will line up perfectly together to make a straight line. If *r* is less than 1.0, there will be a general upward trend. The closer *r* is to 1.0, the less scatter there is in the data (the closer the data points are to forming a line). The closer *r* is to 0, the more scatter there is in the data. If $r = 0$, there is no correlation between the two variables. A graph showing this type of relationship is often called a scatterplot or scattergram. For Figure 1.3, $r = 0.96$, which indicates a strong positive relationship between rainfall and grass production.

Many relationships between numeric variables have negative correlations. These are sometimes called inverse correlations. In this case, as one variable increases, the other variable decreases. As one example, Figure 1.10 illustrates a negative correlation between wildebeest abundance and the percentage of burned area. The exact same rules apply as for a positive correlation: As *r* approaches −1.0, the negative correlation grows stronger, and there is less scatter among the points. Figures D1.1.3 and D1.1.4 show strong and weak negative correlations. We will not discuss the mathematical formulas that calculate *r*, but you can refer to Gotelli and Ellison (2004) to learn how this is done. You will be expected to use simple statistical software packages for all statistical analyses in this text. These packages will do the work for you – in this case they will generate an *r*-value.



Weak positive correlation, $r = 0.46$

Figure D1.1.2



Strong negative correlation, $r = -0.97$

Figure D1.1.3

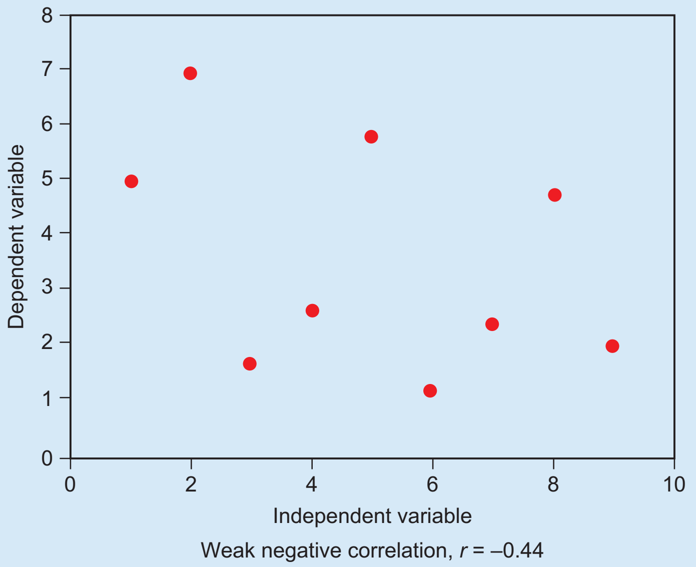


Figure D1.1.4

Cautionary note: A strong correlation does not necessarily mean that one variable caused a change in the other variable. Correlation analyses simply measure the strength of association between two variables.

predicted that there would have been higher than average rainfall during that decade.

Historically, dry-season rainfall in the central and northern Serengeti woodlands has averaged 37.5 mm per month. Table 1.1 gives rainfall data for 1962–1969. Restricting ourselves to the 1960s, you can see that average monthly dry-season rainfall during the 1960s – 36.96 mm – was very close to the historical average. Sinclair concluded that the abundance of buffalo and wildebeest was increasing for reasons other than increased food availability.

Given the lack of support for the food availability hypothesis, Sinclair considered an alternative hypothesis.

The predator release hypothesis

Perhaps herbivore populations increased during the 1960s because there was a reduction or release from high levels of predation. If this hypothesis was correct, Sinclair predicted that the abundance of predators capable of killing buffalo and wildebeest would have declined during the 1960s.

Unfortunately, the data on the abundance of predators in the Serengeti is a bit spotty, but all indications are that predator numbers actually increased during the 1960s and into the late 1970s. Lions and hyenas are the two most important predators in the Serengeti. Jeannette Hanby and David Bygott (1979) surveyed all of the lions in the Serengeti in 1974–7, and compared their numbers to George Schaller's surveys conducted in 1966–8 (Schaller 1972). Hanby and Bygott showed that the number of lion groups or prides increased from 18 to 24 between the mid-1960s and the mid-1970s. In addition, the mean number of lions per pride increased from about 15 to 19. Hanby and Bygott also surveyed the number of hyenas in the mid-1970s, and estimated 3391 hyenas in 1977 in comparison to Hans Kruuk's estimate of 2117 for the same area in 1964–8 (Kruuk 1972). In contrast to the prediction of the reduction in predation pressure hypothesis, the number of lions and hyenas was actually increasing during the same time period that wildebeest and buffalo populations were increasing rapidly.

A final hypothesis focused on the complicated effects of a disease – rinderpest – on buffalo and wildebeest populations.

Table 1.1 Estimated abundance of wildebeest and mean monthly dry-season rainfall for the central and northern Serengeti woodland in 1962–1969.

	1962	1963	1964	1965	1966	1967	1968	1969
Wildebeest abundance	309 743	*	397 624	439 124	461 208	483 292	535 663	588 034
Mean monthly rainfall (mm)	38.75	*	54.25	32.50	38.00	29.25	33.50	32.50

*There were no measurements in 1963.

The rinderpest release hypothesis

Having rejected two important hypotheses as explanations for the increase in buffalo and wildebeest populations during the 1960s and early 1970s, Sinclair was left with one other option to consider. Rinderpest is a measles-like virus that attacks and kills cattle and other *ruminants*. Ruminants are mammals, such as buffalo and wildebeest, that digest plant-based food by initially softening it within their rumen, where it ferments with the help of microorganisms that live there. They then regurgitate the semi-digested mass, chew it, and swallow it again. Sinclair knew that the Great Rinderpest Plague of 1890 originated in Europe and killed about 95% of the cattle in southern and eastern Africa. He also knew that several other waves of rinderpest had caused serious damage to the African ruminant populations in the early and mid-twentieth century. He reasoned that perhaps the increase in wildebeest and buffalo populations in the 1960s resulted from a reduction or release from high levels of rinderpest infection. Perhaps rinderpest infection had been keeping the populations of buffalo and wildebeest unnaturally low during the 1950s, and that somehow, the animals were no longer being infected by rinderpest in the early 1960s. Sinclair's task was to test the predictions of the rinderpest release hypothesis.

Prediction 1: A negative correlation between rinderpest infection and ruminant abundance

One prediction of the rinderpest release hypothesis is that rinderpest infection should have declined substantially in association with an increase in the abundance of buffalo and wildebeest. If this was true, then blood from animals born in the early and mid-1960s, when the populations began increasing, should have fewer antibodies to the rinderpest virus than blood from animals born in the 1950s, when the populations were more stable.

Veterinarians were very interested in rinderpest because it killed cattle owned by local tribesmen and devastated the local economy. Walter Plowright, a veterinarian working for the East African Veterinary Research Organization, helped develop a vaccine against rinderpest, and began inoculating cattle in East Africa in 1956. He knew that wildebeest also contracted the disease, so he carried out a wildebeest-monitoring program in the early 1960s. He discovered that juvenile wildebeest received passive immunity from their mother's milk, but by 7 months of age were highly susceptible to infection. He discovered that wildebeest from Tanzania showed no evidence of rinderpest antibodies in 1962, in contrast to an infection rate of about 70% in 1959–61 (Plowright and McCulloch 1967).

Though Plowright moved back to England in 1964, his paper indicates that there was no evidence of major rinderpest infection in wildebeest from 1963 to 1967. But Plowright was a veterinarian interested in eradicating rinderpest, and he was not working on the question of why the wildebeest and buffalo populations were increasing. He was delighted that rinderpest was no longer

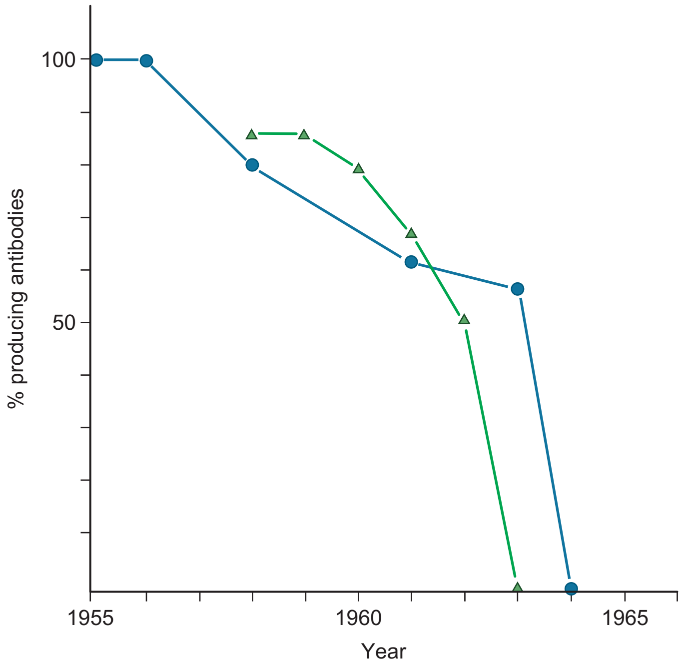


Figure 1.4 Percentage of buffalo (circles) and wildebeest (triangles) producing antibodies to rinderpest from 1955–1964.

present in the population but warned that it was likely to return, as it had several times in the past.

In contrast, Tony Sinclair was profoundly interested in the correlation between rinderpest release in wildebeest and population growth. But he also knew that a simple correlation between rinderpest release and population growth did not mean that wildebeests were increasing because they were no longer being infected by rinderpest. He needed more confirmation of the rinderpest release hypothesis.

One of Sinclair's first actions was to work with other veterinarians to measure rinderpest levels in the buffalo. The rinderpest release hypothesis predicts that rinderpest should also have disappeared in buffalo in the early 1960s. Fortunately, veterinarians had supplies of buffalo blood in the freezer, and they also knew (much to Sinclair's delight) the age of each animal that had provided the sample. The results of their analysis showed that rinderpest had completely disappeared from the buffalo population by 1964 (Figure 1.4).

Prediction 2: No correlation between rinderpest infection and non-ruminant abundance

Encouraged, Sinclair proceeded to test other predictions of the rinderpest hypothesis. He argued that Serengeti mammals that were not susceptible to rinderpest (animals that were not ruminants) would not show a trend of population growth over the 1960s, because rinderpest release would, of course, not affect them in any significant way. Zebra were the only large non-ruminant for which there were good survey data and, as predicted, there was no trend for zebra populations to increase over the 1960s (Figure 1.5).

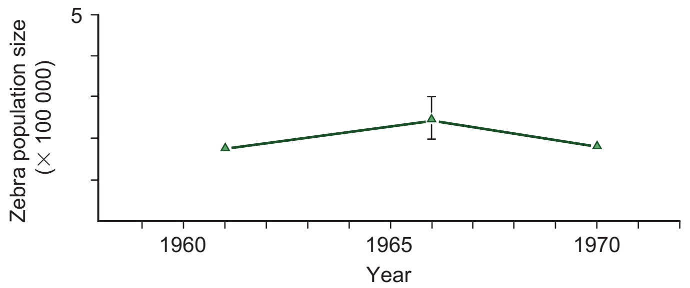


Figure 1.5 Estimates of zebra abundance in the 1960s.

Prediction 3: Increased survival rate in juvenile ruminants

Sinclair also knew that rinderpest had historically killed juveniles after the passive immunity from their mother's milk wore off. If rinderpest release was responsible for the population increase, he predicted an increase in the survival rate of juveniles. One way of measuring juvenile survival is using aerial surveys to measure what percentage of the population is made up of 1-year-old juveniles. An early survey of wildebeest indicated that juveniles made up 8% of the population (Talbot and Talbot 1963). After 1963, that percentage was much higher, usually between 14 and 17% (Sinclair 1977b).

Recall that Sinclair considered two other hypotheses – the food availability and the predator release hypotheses – to explain the increase in buffalo and wildebeest abundance, but the data did not support the predictions of these two alternative hypotheses. When Sinclair came up with the rinderpest release hypothesis, he systematically tested each prediction generated by the hypothesis and was able to support each prediction with data based on observations, models, and experimentation. As each prediction was confirmed, Sinclair's confidence in the rinderpest release hypothesis increased. As Sinclair's experiences reflect, ecology is no different than any other science, in that observation, modeling, and experimentation lie at its heart.

1.3 HOW DO ECOLOGISTS USE OBSERVATION, MODELING, AND EXPERIMENTATION?

In some ways, ecology is a very complex science because it happens in the real world, where controlling variables is difficult, and where replication may be impossible. Sinclair's question of why the buffalo and wildebeest were increasing was especially challenging, because it was an event that happened only once and sample sizes of one are very difficult to test with any degree of certainty. Working under this handicap, a successful ecologist must be a keen observer, able to pick up on small nuances of patterns, and able to extract small amounts of information from a large amount of background noise.

Observations

Scientists use three types of observations. First, they observe actual processes with their senses, or with devices that are extensions of their senses. To estimate abundance and proportions of juveniles, Sinclair used airplanes and cameras. Second, scientists observe and learn from the published literature, which was essential for Sinclair's knowledge of abundance levels prior to his study, in the 1950s and early 1960s. Last, they observe from what other people are doing or saying. Sinclair's ability to speak Swahili helped with his historical research into wildebeest abundance, and his social skills enabled him to establish a rapport with the veterinarians and collaborate with them on the buffalo antibody analyses. Perhaps most importantly, Sinclair got to hang out with a dozen or so senior researchers at the Serengeti Research Institute, bounce ideas off of them, and benefit from their many years of accumulated knowledge. Sinclair states that one of his golden rules is: "If you want to conserve and manage an ecosystem, you need to know all there is to know about it." Much of this knowledge comes from these three types of observations described above. These observations can also be used to construct scientific models.

Scientific models

There are many types of models with very different goals, and you will learn – and hopefully master – some of them as you work through this text. Models seek to describe a system, or to predict what the system will do in the future. All models are simplifications of reality, but ideally each model contains the essential attributes of what it seeks to describe or predict. For example, a map has some of the essential attributes of a landscape, while a global climate model has some of the essential attributes of the world's climatic conditions. But both are simplifications of reality. And both aspire to have enough of the essential attributes to accomplish their goal. In the case of the map, the goal is primarily descriptive, so that the user will be able to make good decisions when on an unfamiliar route. In the case of a global climate model, the goal is primarily predictive, so that citizens can understand the repercussions of their actions and make informed decisions.

Sinclair's research used many models of population growth and of ecosystem function. Sinclair hypothesized that with rinderpest release, buffalo and wildebeest abundance would continue to increase until the populations were limited by grass availability during the dry season. At that point, the populations would begin to level off. One of the problems of making this prediction is that rainfall is highly variable; for example, dry-season rainfall increased sharply in the early and mid-1970s from a mean of about 150 mm to about 250 mm. Based on the correlation between rainfall and food availability (Figure 1.3), and making certain assumptions about predation rates, Ray Hillborn and Sinclair (1979) created a simple mathematical model that predicted wildebeest abundance in relation to dry-season rainfall (Figure 1.6A).

Based on this model, wildebeest abundance could exceed 4 million if dry-season rainfall remained above 250 mm. However, Hillborn and Sinclair issue three warnings in association with this model. First, it would take several decades for the population to reach equilibrium. Second, rainfall levels were